

VERN BURROWS

3rd *International
Oat Conference*



Lund, Sweden, July 4 - 8 1988

PROCEEDINGS

3rd International Oat Conference



Lund, Sweden, July 4 - 8 1988

Editors

Bengt Mattsson
Roland Lyhagen

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DEMONSTRATION OF EQUIPMENTS

An exhibition was arranged at Svalöf AB with equipments from:

Wintersteiger, Austria

Hege, West Germany

Kamas Westrup, Sweden

Svalöf AB, Sweden

EXCURSIONS

Participants including partners visited the experimental fields and laboratories at Svalöf AB and Weibulls AB. The last day there was an excursion to two different farms and a stud farm. There Swedish Farmers Supply and Crop Marketing Association invited to the last lunch.

ACKNOWLEDGEMENTS

The local organizing committee will thank Svalöf AB for arrangements at the exhibition and the field trip, for the banquet at Örenäs and for financing the printing of these proceedings. We also thank Weibulls AB for excellent arrangement including supper and the farmers Nils Bertil Offesson, Odarslöv and Otto Ramel, Övedskloster and Ingvar Fredriksson, Flyinge Stud Farm for great hospitality. For an excellent lunch we thank The Swedish Farmers Supply and Crop Marketing Association. Finally we thank the International organizing committee and particularly the chairman Kenneth Frey for great help with the planning work

THE DOMESTICATION AND HISTORY OF OATS

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Oats are of secondary importance among the cereals of the Old World, and have been domesticated several millennia after wheat and barley. Nevertheless, three different species of oats, diploid, tetraploid and hexaploid have been utilized by man (Table 1). Harlan (1975) defines domestication as an alteration of morphologic and genetic characteristics of plants and animals that makes them better adapted to the ecological environment created by man. Identification of the first steps of domestication is an essential element in reconstructing the evolution and history of cultivated crops. Information of relevance in this regard concerns 1) the identity of the wild progenitor, 2) the time and place of domestication, and 3) the mode of domestication. Given adequate knowledge on these three points it is possible to follow the trend of evolution under domestication, the diffusion of the crop and the time scale for these processes.

The genus *Avena* contains diploid, tetraploid and hexaploid species. Although the cultivated oats are mostly hexaploids, man has domesticated and still grows diploid and to some extent tetraploid oats as well. The origin of these oats, the place and time of their domestication are described here, and an attempt is made to determine their mode of evolution.

Table 1: Cultivated oats and their wild progenitors

<u>Plody</u>	<u>Cultivated</u>	<u>Wild</u>
2x	<i>A.strigosa</i> <i>A.brevis</i> <i>A.nudibrevis</i>	<i>A.hirtula</i>
4x	<i>A.abyssinica</i>	<i>A.barbata</i>
6x	<i>A.sativa</i> <i>A.byzantina</i>	<i>A.fatua</i> <i>A.sterilis</i>

Hexaploid oats

The cultivated hexaploid oats evolved from the hexaploid wild forms. Among the latter two major morphological types can be distinguished which in the taxonomic literature are even treated as two separate species: the *A.sterilis* type, in which the florets of the same spikelet shed as one unit at maturity, and the *A.fatua* type, in which florets are shed individually. The difference in seed dispersal between the two types is governed by a single gene. In addition they differ with respect to ecological preferences and geographic distribution. *A.sterilis* is a major component of the herbaceous vegetation in the Mediterranean vegetation zone of the Middle East, particularly in the warmer parts. It is also an aggressive weed in man-made habitats throughout the Mediterranean agricultural belt. It invaded the New World where it has become

naturalized in regions having a Mediterranean-like climate. In contrast, A.fatua is found almost exclusively in man-made habitats, particularly as a weed in cultivation, and in higher altitudes and cooler climates.

The two wild hexaploid oats are fully interfertile with one another and with the cultivated hexaploid oats.

The place of domestication is determined according to the earliest remains of the plant found in archeological digs. These remains are usually charred seeds with or without husks, whole or broken, and their diagnostic characteristics are usually found to be damaged or considerably destroyed. Hence the frequent difficulty of identifying the species to which the seed belongs and determining whether it is of a cultivated or of a wild plant. In addition, although there is a rapidly increasing volume of paleobotanical evidence which make it possible to identify with some confidence the places of origin of certain crops, one should bear in mind that future findings may indicate different localities.

Elimination of the seed dispersal mechanism is perhaps the first and most critical step in domestication of Old World cereals. In cultivated oats the spikelets remain intact long after maturity and during threshing the seeds are separated by fracturing of the spikelet axis. Thus, in charred material from archeological digs wild hexaploid oats may be identified by the large deep oval scar at the base of the diaspore, while in cultivated forms the base of the seed is rather blunt and exhibits visible fracturing.

In the natural habitats of wild wheat and barley in the Middle East, A.sterilis is even more abundant than the other two wild cereals. Nevertheless, only wheat and barley were domesticated in that region. In most of the Neolithic settlements studied in the Middle-East, cultivated wheat and barley have been identified, but not even a single instance of cultivated oat was recorded. There are a few reports of wild oats from that period (Hansen and Rensfrew 1978, Hole and Flannery 1967, Helbaek 1960, Van Zeist and Bakker-Heeres 1982), but in most cases species identification was not possible. In Beidha, however, a form of A.sterilis was identified from PPNB, about 7000 BC (Helbaek, 1966). The archeological records point to a more consistent and frequent appearance of oats in Europe several millennia later. In the Neolithic period in Europe, about 2000 b.c., wheat and barley have already been established as crops. Although there are some reports of oats from the Neolithic Age, it is from the middle Bronze Age that both A.fatua and A.saliva were identified on repeated occasions in Denmark, southern Sweden, Germany, Switzerland and the British Isles (Jensen 1985, Hopf 1982, Godwin 1975). Large quantities of A.fatua seeds from the Bronze Age uncovered in Germany (Hopf 1982) indicate that the wild oats, growing as weeds in the fields were utilized by man, probably for fodder, and were eventually domesticated.

The available paleobotanical evidence thus corroborates Vavilov's view of oats as a secondary crop (Vavilov 1951), which

originated from a weed that was common in cultivated fields. Coffman (1977) argues that A.sterilis is the progenitor of all the hexaploid oats, and that the original cultivated form was A.byzantina. The first part of Coffman's theory sounds feasible as A.sterilis is adapted to primary habitats, exhibits also weedy tendencies, and is a major component of plant communities in the Mediterranean vegetation, whereas A.fatua is confined to man-made habitats and is therefore secondary. But if, as the paleobotanical evidence suggests, cultivated oats were derived from A.fatua, it is more reasonable to conclude that A.sativa was the first domesticated hexaploid oat. In both A.sativa and A.byzantina the florets are separated by fracturing of the rachilla (spikelet axis) and not by abscission as in the wild hexaploids. In A.fatua the rachilla segment is attached to the lower seed, whereas if the seeds of A.sterilis diaspore are forcibly separated the rachilla segment remains attached to the upper seed. The fracturing pattern of the rachilla in A.sativa is generally more like that of A.fatua, whereas the pattern in A.byzantina resembles that of A.sterilis. Although there are many exceptions to this rule and intermediate forms have been reported, it is unlikely that domestication of the A.fatua wild type gave rise to a cultivated oat of the A.byzantina type. This latter type could have evolved by introgression from A.sterilis when the crop was introduced into the Mediterranean region.

While there is sound evidence for the domestication of the hexaploid oats as secondary crop in central-north Europe during the late Bronze Age, their mode and rate of diffusion are not yet clear. It is reasonable to assume that the diffusion of the oat crop to southern Europe or to the Middle East occurred rather slowly, simply because it could not compete with wheat and barley as food. There is no mention of oats by ancient Egyptians nor in the Bible, and although mentioned in the Mishnah by Rabbinical writers, they were probably referring to a kind of barley (Feliks 1967). Greek and Roman sources usually refer to oats as weeds or forage plants. Pliny (1st century a.d.) described oats as a noxious weed and the main obstruction to crops. His astonishment at learning that inhabitants of Germany sowed oats for food is an indication that oats were not used as food by the Romans. Even the word *avena* in Latin probably refers to a forage crop (see Coffman 1977).

How oats reached as far as China is not clear either. It seems that naked oats were grown in China already in the fifth century a.d. (see Stanton 1955). It is pertinent to note that barley received a mention in the Chinese literature at about 1300 b.c. (Harlan 1970), and wheat at about 2500 b.c. (Liu 1927), roughly in the period that oats were domesticated in Europe. One possibility is that cultivated oats migrated to China along the caravan routes from Tibet or the Himalayas, and evolved there into a naked form which is endemic to the Far East. It is equally possible, however, that A.fatua traveled as a contaminant in wheat and barley as they moved eastward all the way to China and was domesticated there and later a form of naked oat evolved from it.

Both A.fatua and A.sterilis have been reported from the Nepalese Himalayas, the latter as a cultivated form at altitudes below 1800 m and the former as a weed in wheat and barley fields at altitudes of 2000-3000 m (Nakao and Mori 1956). A.fatua is known as a weed in cultivation also in Pamir, Mongolia and western China. It is less likely that the naked oat evolved directly from A.fatua. This evolution would have required a sequence of two major mutations, as floret disjunction and seed nakedness are controlled by two independent loci (Jensen 1961). China thus has become the source of large naked oat, and this is probably why Vavilov considered China as a secondary center of oats.

Oats were introduced into the western hemisphere after its discovery, by the Spaniards to the southern USA and California, and to the eastern USA by English settlers as early as 1586 (see Coffman 1977).

Evolution under domestication of the hexaploid oats involved mainly spikelet and seed characteristics such as: reduction or even complete elimination of awns and lemma's hairs, seed size and shape, dormancy and nakedness.

Diploid oats

The cultivated diploid oats are known as the A.strigosa group which includes the interfertile taxonomic species A.strigosa, A.brevis and A.nudibrevis. A.strigosa has been identified in archeological remains, and is distinguished from A.sativa, by its thinner seeds and narrower fracture at the seed base. Its most reliable diagnostic character is the presence of bristles at the tip of the lemma, but unfortunately these are found only rarely in charred material. Nevertheless, the available evidence indicates that the time and place of A.strigosa domestication overlap those of A.sativa, and that it made its first appearance during the late Bronze and early Iron Ages in central and western Europe (Godwin 1975, Jensen 1985).

The wild forms A.wiestii and A.hirtula are fully interfertile with the cultivated diploid oats and are therefore thought to be their progenitors. A.wiestii is an ecotype with adaptation to relatively dry conditions that are prevalent in steppes that bordering the Mediterranean vegetation zone, while A.hirtula is an ecotype with affinity to more humid conditions and grows throughout the Mediterranean basin. Both ecotypes are confined to primary habitats and show little weedy tendency. It may therefore be assumed that the diploid oats were domesticated within the natural distribution range of A.hirtula, probably in the Iberian peninsula where relatively large populations of this ecotype are common even today. Since A.hirtula is a rare weed in cereal fields it seems unlikely that the domestication of the diploid and the hexaploid oats followed the same pattern. The chances are slim that among the few A.hirtula plants that grew at the edges of his field, the one selected by man was a plant with non-shattering panicles. However, if he grew the wild form A.hirtula for forage, types with non-shattering panicles could have been established as a result of the continuous cycles of

sowing and harvesting. The fact that A.strigosa is used today mainly as a forage crop may be taken as a further clue to the mode of origin of this diploid oats. On the other hand the existence of naked types of this oat, known as A.nudibrevis, suggests that this oat was used also as food.

Tetraploid oats

At the tetraploid level oats have not yet established themselves as a pure crop, and have the status of semi-domesticated form or a tolerated weed. This type is known as A.abysinnica and is restricted mainly to the Ethiopian highlands. A.abysinnica has non-shattering panicles, is dispersed by man but never deliberately cultivated. In the Ethiopian highlands it is found exclusively in cereal (mainly barley) fields where the oat plants can be distinguished from other cereals only after the panicle has emerged from the flag leaf. If the barley crop is successful farmers may weed out the oat plants, but if for any reason a poor crop is anticipated they allow the oats to mature and harvest them together with barley. The winnowing technique used by the Ethiopian farmers does not permit the separation of oat from barley seeds. Thus, the presence of oats as a contaminant in barley is very common in rural markets in Ethiopia, they are consumed and sown with barley seeds.

A.abysinnica is closely related to A.barbata, a wild oat which is common in primary and man-made habitat in the Mediterranean basin. It tolerates lower temperatures and grows in higher altitudes than A.sterilis. A.abysinnica and A.barbata are interfertile with one another, and the difference in their modes of seed dispersal is controlled by two complementary recessive genes (Ladizinsky 1975). A.barbata is a common weed in cereal fields in Ethiopia at altitudes of 2000-3000 m, but it never grows outside the field. This distribution pattern suggests that A.barbata is not an indigenous plant there, and was probably introduced to Ethiopia as a weed among wheat and barley seeds.

To conclude: although a relatively young crop and of secondary importance as food, oats have been domesticated from three different wild species. Two forms, the cultivated hexaploid oats and A.abysinnica, evolved from weeds that infested cereal fields outside the main distributional range of their progenitors. In contrast, the diploid oat A.strigosa was apparently domesticated within the distributional range of its wild progenitor, A.hirtula. As this latter form shows hardly any weedy tendencies, it seems reasonable to assume that the wild A.hirtula was grown for fodder before the cultivated form was selected. Evolution under domestication of oats involved mainly spikelet and seed characteristics and selection of types which represent the domesticate syndrome also in wheat and barley.

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OAT GERMPLASM COLLECTIONS AND THE 1986 TURKEY-UNITED STATES EXPEDITION

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There are three main types of oat germplasm collections: (1) working collections within breeding/research programs of individual oat workers, (2) national collections held by a governmental agency within individual countries, and (3) new collections resulting from plant exploration but not yet integrated into individual or national collections. This paper will focus attention on oat germplasm collected during the 1986 Turkey-United States Expedition (category 3), including the rationale for germplasm exploration and the potential usefulness of materials collected.

Well established, national oat germplasm collections such as the USDA Oat Collection in the Germplasm Resources Laboratory, Agricultural Research Service, Aberdeen, Idaho; the Canadian Oat Collection maintained by Plant Gene Resources of Canada, Ottawa, Ontario; and those in many other countries contain a great diversity of materials ranging from wild species to breeding stocks to released cultivars (Forsberg and Shands, 1989). National collections are enhanced by the addition of entries with unique traits, unique trait levels, or unique or superior combinations of genes. The usefulness of these collections depends upon the continual and conscientious submission of useful stocks by oat workers.

Entries representing noncultivated diploid, tetraploid, and hexaploid oat species also comprise an important and valuable component of oat collections. Expansion of evaluation/classification efforts and of data collection, storage, and dissemination capabilities (Perry and Bohning, 1987) will increase the value and utility of collection entries. Sources, maintenance, and utilization of germplasm collections in general have been discussed by Forsberg and Smith (1980).

The search for new species, genetic variants within existing species, and useful genes, along with germplasm preservation, are worthy goals of germplasm exploration. These goals, in concert with geographical access, determine geographical priorities and exploration feasibility.

THE 1986 TURKEY-UNITED STATES OATS EXPEDITION

The 1986 Turkey-United States Oat Expedition was conducted during 22 July to 14 August. The goals were: (1) to gain new knowledge about the distribution of wild oat species in Turkey, (2) to collect samples of wild oat species for increase and entry into the National Plant Genetic Resources Collection in Turkey, and (3) to collect samples of wild oat species for entry into the USDA Oat Collection, Aberdeen, Idaho. Participants in the Expedition were (Fig. 2): Dr. Cetin Tuten, Aegean Regional Agricultural Research Institute (ARARI), Menemen, Izmir, Turkey; Dr. Marr D. Simons, ARS/USDA and Department of Plant Pathology, Iowa State University, Ames, Iowa (USA); and Dr. Robert A. Forsberg, Department of Agronomy, University of Wisconsin-Madison, Madison, Wisconsin (USA). The team was ably assisted by Ozcan Gench of the ARARI.

The areas searched (Fig. 1) and routes traveled (Table 1) comprise three main regions in Turkey from which samples were collected: (1) the northern or Black Sea region from Zonguldak to Trabzon; (2) the interior region, with the Ankara-Sivas-Erzincan highway as the southern edge of that region; and (3) the northeastern region, generally north of the Erzurum-Kars highway. The collection team traveled nearly 7000 kilometers.

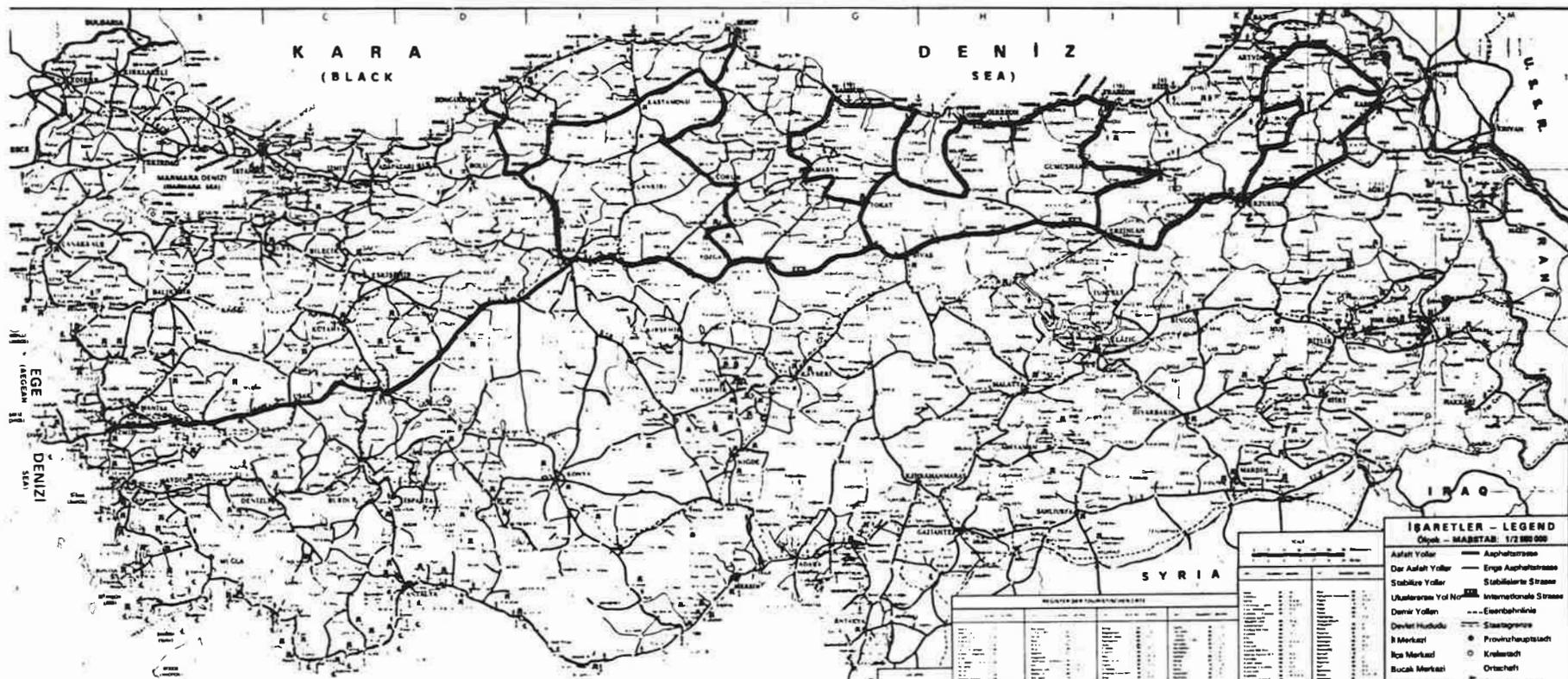


Fig. 1. Map of Turkey showing areas searched and routes traveled during the 1986 Turkey-United States Oat Collection Expedition.

Table 1. Daily routes, distances traveled, elevation ranges, and number of collections made by each of the three collectors during the 1986 Turkey-United States Oat Collection Expedition.

Date July/Aug.	Route	Distance travelled km	Elevation range (collection sites) m	Coll. site numbers
22	Izmir-Afyon-Ankara	650	940-1250	1-2
23	Ankara-Kizilcahamam-Gerede-Devrek-Zonguldak	280	-----	3-9
24	Zonguldak-Gerede-Karabük-Safranbolu-Araç-Kastamonu	280	-----	10-16
25	Kastamonu-Tasköprü-Sinop	300	-----	17-25
26	Sinop-Erfelek-Boyabat	100	350 ¹ -1050	26-32
27	Boyabat-Kargi-Tosya-Iskilip-Çorum	330	200-1650	33-43
28	Çorum-Alaca-Yozgat-Sorgun-Akdagmadeni-Yildizeli-Tokat	400	750-1400	44-55
29	Tokat-Turhal-Amasya-Suluova-Havza-Samsun	360	450 ¹ -680 ¹	56-67
30	Samsun	0	-----	
31	Samsun-Ünye-Akkus-Niksar-Tokat	260	0-1300	68-80
1	Tokat-Niksar-Resadiye-Koyulhisar-Mesudiye-Golkoy-Ordu	300	300-1600	81-91
2	Ordu-Giresun-Dereli-Giresun-Görece-Trabzon	300	010-0020	92-94
3	Trabzon-Gümüşhane-Bayburt	370	220-1950	95-106
4	Bayburt-Köse-Kelkit-Erzincan-Tercan-Askale-Erzurum	360	1200-1900	107-117
5	Erzurum	0	-----	
6	Erzurum-Pasinler-Horasan-Karakurt-Selim-Kars	400	1350-1950	118-132
7	Kars-Susuz-Göle-Susuz-Hanak-Ardahan	350	1700-2100	133-146
8	Ardahan-Savsat-Artvin	300	1550-1750	147-150
9	Artvin-Yusufeli-Olur-Oltur-Narman-Tortum-Erzurum	340	400-2000	151-162
10	Erzurum-Erzincan-Sivas	450	1350-1750	163-170
11	Sivas-Yozgat-Ankara	450	1300-1350	171-176
12	Ankara (Simons and Forsberg collections shipped to U.S.)	150		
	Total	6,730		
13	Ankara-Afyon-Izmir	650		
14	Izmir-Aegeon Regional Agricultural Research Institute	0		

¹Elevation of all sites this date not recorded by the authors.

Collections were made from Avena plants that were sighted from the car while driving along roadways in both well-traveled and remote areas. Fields, valleys, and hills not accessible by car were searched on foot. Collections were made at 176 sites, and at least three separate collections were usually made at each site, one each by Tuten, Simons, and Forsberg. Collections were made as bulk populations on a species basis, with seeds from two to over 60 plants of the same species comprising a single (bulk) collection. In some cases, seeds from an individual plant were maintained as a distinct sample. If wild oats were abundant, we stopped approximately once every 10 kilometers. If they were rare, we stopped upon sight. The team made over 900 total collections, i.e. about 300 each by Tuten, Simons, and Forsberg. Preliminary classification revealed that approximately 4.5% of the samples collected were tetraploid Avena barbata, 42.5% hexaploid A. fatua, 39.3% A. sterilis, and 13.7% A. sativa.

The two wild hexaploid species, A. fatua and A. sterilis, were widespread and plentiful, mainly occurring as weeds in spring barley (Hordeum vulgare L.), spring wheat (Triticum vulgare L.), sugarbeets (Beta vulgare L.), lentils (Lens culinaris Medikus), and chickpeas (Cicer arietinum L.). They were generally not present in winter wheat. Avena barbata, which was relatively rare, was found in fence rows, thickets, and road sides, i.e. areas inaccessible by cattle or sheep. Although the hectareage of cultivated oats was small, we observed cultivated-oat fields from lower to higher elevations. At lower elevations where temperatures were higher, most of the cultivated oats were phenotypically of the red-oat or A. byzantina type. In the Akkus area at elevations of 1100 to 1400 m, the oats were grown for hay or green fodder. Oats were judged superior to barley or wheat for this purpose due to pseudo stiffness caused by shorter plant height. Resistance to lodging caused by high rainfall was a critical need in this area. We also observed green, immature oats to be harvested for hay east of Göle (north of Kars near site 136), elevation 2200 m.

Stem rust (Puccinia graminis Pers. f. sp. avenae Erickss. and E. Henn.) was relatively severe on A. sterilis and A. fatua at many sites. The selection pressure from such infection may mean that potentially useful sources of either oligogenic or polygenic resistance, or of tolerance, to stem rust might be found in this material. Leaf (crown) rust (Puccinia coronata Cda. f. avenae Erickss. and E. Henn.) was found at only a few locations, suggesting that there has been relatively little selection pressure for resistance to this disease (Forsberg and Simons, 1987). The most severe barley yellow dwarf virus (BYDV) was observed at site 72 (1100 m elev.) between Ünye and Akkus where crown rust also was observed. Crown rust, stem rust, and BYDV were all observed at site 71 (750 m elev.), south of Ünye and 9 km north of site 72. These were the only sightings of BYDV, in part because the trip was planned to coincide with seed maturity at which stage only healthy, mature plants were observed. The plants at site 72 (higher elevation) were still green (early dough stage).

Following appropriate quarantine measures, entries in these collections will be entered into the U.S. and Turkey Collections where they will be available for agronomic, disease, and biochemical-trait evaluation.

Nearly all A. sterilis and A. fatua plants occurred as weeds in other crops or in noncultivated fence rows, ditch banks, or roadsides. We found no clusters of species growing in isolation in cultivated or remote areas due to open and intense grazing by large and small herds of cattle and sheep, and there is no evidence that grazing pressure will diminish in the foreseeable future in many areas of Turkey. At the same time, modern farming methods, including weed control, are making rapid progress in many areas of Turkey (Forsberg and Simons, 1987). Both continued grazing and increased weed control will reduce populations of A. sterilis and A. fatua in Turkey. Germplasm

preservation thus becomes equally as important as the search for genetic variants and for useful genes in Turkey and in many other countries of the world.

Acknowledgement. The authors are grateful to the Turkish government for allowing this search and collection of oat germplasm; to the Director of the Aegean Regional Agricultural Research Institute for allowing Dr. Cetin Tuten and Ozcan Gench to participate and for providing a trustworthy vehicle; and to Dr. Cetin Tuten for his planning, leadership, and participation.

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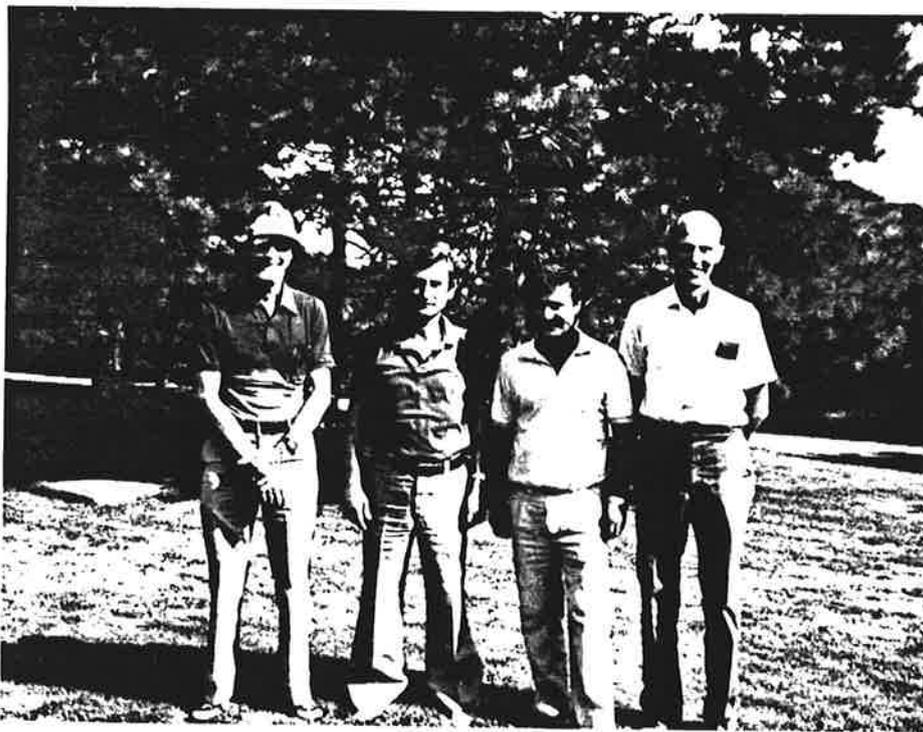


Fig.2. Participants in the 1986 Turkey-United States Oat Collection Expedition (from Left to right): Dr. Marr Simons, Dr. Cetin Tuten, Ozcan Gench, and Dr. Robert Forsberg.

NEW SPECIES OF AVENA

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As a result of collecting expeditions undertaken in the late 1950s and early 1960s it became clear that there is a range of variation amongst weed species of Avena that would be desirable to introduce into the cultivated oat. In the first place most of the interest was centred around the search for resistance to pests and diseases. The potential of the weed species as a source of such resistance had been realised a number of years before that period, e.g. E.T. Jones, working at Aberystwyth attempted to use mildew resistant accession of A.hirtula, collected in Spain in 1934 in his oat breeding programme in the 30s. The earlier attempts to utilise variation from weed species in breeding programmes other than the hexaploids A.sterilis and A.fatua were frustrated by the sterility of the hybrids and a lack of understanding of the factors responsible for the expression of the sterility. The collecting expeditions of the late 50s and early 60s also coincided with greater interest in the cytogenetic relationships between the cultivated forms and wild species, which led to a better understanding of the cytogenetic mechanisms responsible for the isolation of the weed and cultivated species (Rajhathy and Thomas, 1974). Using the knowledge gained from these studies it has been possible to develop procedures for manipulating these mechanisms to effect the transfer of useful genes into the cultivated oat. In this presentation I will attempt to survey the impact that the availability of the species collected has had on evolutionary studies and in breeding programmes.

From an evolutionary point of view the main reason for the increased interest in collecting related weed species was to identify the diploid progenitors of the cultivated oat as part of an overall effort to understand the cytogenetic structure of the cultivated oat. The cultivated oat was designated the genomic formula AACDD by Rajhathy and Morrison (1959) and the earlier work of Nishiyama (1929) had indicated that the progenitor of the A genome was a member of the strigosa group of diploid species. Karyotypic investigations undertaken by Rajhathy (1963) confirmed this conclusion but the work of a number of workers reviewed by Rajhathy and Thomas (1974) showed that the relationship between the chromosomes of the diploid A genome and the cultivated oat was only partial homology. A newly described species A.canariensis (Baum et al., 1973) was recognised as having most of the morphological characteristics expected to occur in a diploid progenitor but cytogenetic studies indicated that the chromosomes were not homologous with one of the A.sativa genomes (Thomas and Leggett, 1974) but showed only partial homology.

In 1964 an accession of A.ventricosa became available for study as a result of the Canada/Wales collecting expedition in the Mediterranean countries. A.ventricosa is completely isolated from the A genome diploids and numerous inter-pollinations failed to produce any viable hybrids (Rajhathy and Thomas, 1967). Only one report of the successful establishment of the hybrid has been made by Nishiyama and Yabuno (1975) and the low chromosome pairing in the A.strigosa x A.eriantha hybrid confirmed the differentiation of the two genomes. There was little evidence of any residual homology between the chromosome complements of the two species since the majority of the chromosomes remained unpaired in the F₁ hybrid. These observations supported the hypothesis proposed by Rajhathy (1966) that A.ventricosa was the likely diploid progenitor of the C genome of the hexaploid species. In the tetraploid hybrids involving the A and C genome diploids and A.sativa the amount of chromosome pairing observed indicated only partial homology between the diploid genomes and their corresponding genomes in A.sativa. If these diploid species are the original progenitors of the A and C genomes of the hexaploids the chromosomes have become structurally differentiated since their involvement in the evolution of the polyploid form. The possible progenitor of the third genome (D) of the hexaploid is not known.

A significant landmark in plant introduction and genetic resources within the Avena was the discovery of the tetraploid species initially named A.magna (Murphy et al., 1968), but more recently renamed A.maroccana (Baum, 1977). Prior to that collection (Rajhathy et al., 1964) in Morocco the only known tetraploid species of Avena were those of the A.barbata group with the genomic formula AABB. The cytogenetic studies of the F₁ hybrid A.barbata x A.maroccana revealed that the two species were not closely related (Rajhathy and Sadasivaiah, 1968). F₁ hybrids between A.sativa and A.maroccana were also self-sterile. Morphological similarities between A.maroccana and the wild hexaploid forms, together with the meiotic behaviour of the pentaploid hybrids with A.sativa, led Ladizinsky and Zohary (1971) to propose that A.maroccana was the tetraploid base in the evolution of the hexaploid species and it has been designated the genomic formula AACC (Rajhathy and Sadasivaiah, 1968). Chromosome pairing in the F₁ hybrid A.maroccana x A.sativa indicated that the species share two common genomes, however there were deviations from the expected $14_{II} + 7_I$ if the two genomes were completely homologous. The presence of multivalents in the pentaploid hybrids has been shown to be due to translocation differences between the AC genomes in A.sativa compared with those of A.maroccana (Thomas and Bhatti, 1975).

The diploids A.canariensis, A.damascena, A.atlantica and A.prostrata are chromosomal variants of the A genome and their discovery has not thrown any further light on the actual progenitor of the A genome of the hexaploid species. The recently described tetraploid A.agidiriana is a variant of A.barbata (Leggett, 1987). The other interesting tetraploid species which

was collected recently is A. macrostachya, which is unique in being both perennial and an autotetraploid species. This species can be crossed with A. sativa but the meiotic behaviour of the hybrid showed no evidence of homology between the chromosome complements of the two species.

Newly described species and new accessions of previously described species have substantially increased the variation available for breeding. The desirable variation present in these accessions is summarised in Table 1, but it must be stressed that the accessibility of the germplasm to the oat breeder can vary depending on the strength of the isolation mechanisms that exist between the weed species and the cultivated oat. The wild hexaploid species have been widely used in breeding programmes because they form fertile hybrids with the cultivated oat and the transfer of genes can be accomplished through a conventional backcrossing programme (Frey, 1986). The main concern being the amount of the unadapted genome of the weed species that can be tolerated by the cultivated species without affecting its overall agronomic performance. All the hexaploid species so far collected and described are genomically similar to A. sativa and produce fertile hybrids when crossed with cultivated oat, and with the exception of the constraints imposed by some translocation differences (McMullen *et al.*, 1982) the introgression of genes from A. sterilis can be readily accomplished.

Table 1. Desirable variation in newly described species of Avena

Species	Character	Accessibility
<u>A. ventriosa</u>	Mildew resistance	+
<u>A. prostrata</u>	Mildew resistance	+
<u>A. maroccana</u>	Protein level of groat	++
	Large groat	++
<u>A. murphyi</u>	Mildew resistance	++
	Protein level of groat	++
<u>A. macrosatchya</u>	Winter hardiness	-
	BYDV resistance	-

Key: + gene transfer possible using chromosome manipulation techniques
 ++ gene transfer possible by backcrossing
 - gene transfer not possible

A. maroccana has a high percentage of protein in the groat and a characteristic large grain. Although the husk is extremely thick and fibrous and constitutes 47% of the weight of the seed, the groat is also larger than the average size found in the cultivated oat. These two features, the large groat size and protein content are two characters that are desirable to transfer into the cultivated oat germplasm. The F₁ pentaploid hybrid between

A.maroccana and A.sativa is self-sterile but its meiotic behaviour clearly shows that the chromosomes of the two species form chiasmate associations confirming a homologous relationship between the common genomes of the two species. Backcrossing the F₁ hybrid to the cultivated oat leads to a restoration of fertility and euploid chromosome number of 42 (Ladizinsky and Fainstein, 1977a; Thomas et al., 1980). The most effective method of obtaining BC₁ seeds is to grow the pentaploid hybrids in the oat nursery, saturating the plants with pollen, and the resulting natural cross pollination results in a seed set of 1-2%. Backcrossing is an effective procedure to introgress characters from A.maroccana into the cultivated oat genome (Thomas et al., 1979). In general up to two backcrosses are required in order to recover genotypes in which most of the undesirable characters of A.maroccana have been lost. However, it is possible to select cultivated oat types after only a single backcross. Only two of the genomes A and C are given the opportunity of recombining in the A.maroccana x A.sativa hybrid compared with all three genomes in the A.sativa x A.sterilis hybrid, the D genome should be recovered without change after one backcross to A.sativa. This could lead to the requirement of less backcrosses to eliminate the undesirable genes of A.maroccana.

A limitation in the use of a backcrossing programme to eliminate the undesirable genes of the wild species is a corresponding diminution of the desirable genes, if stringent selection procedures are not adopted. Naturally this poses a greater problem in a polygenically controlled character since it would be extremely difficult to reconstitute a genotype comparable to the cultivated form but incorporating the whole complex of genes controlling the targeted character, e.g. protein content and size of the groat. However, we have been able to isolate lines which have a 25% superior protein content than the A.sativa parental material without any adverse negative effects on yield. Lines with improved 1000 grain weight have also been isolated and one particular line is now in advanced trials. Both these have been achieved by selecting from the derivatives of the BC₁ and BC₂ generations. Intercrossing the BC₁ hybrids and selecting adapted cultivated types and high protein content for use in the second backcross should increase the chances of retaining the high protein genes of A.maroccana. A.maroccana is undoubtedly an important accessible source of variation to be used in breeding programmes.

It has been reported by Ladizinsky and Feintstein (1977a) that it is also possible to backcross the F₁ hybrid to A.maroccana and fertile 4x progeny have been isolated. On the evidence that some of the derivatives from the backcross retained the seeds at maturity, having inherited this character from A.sativa, Ladizinsky and Feinstein (1977b) proposed that it might be worthwhile breeding tetraploid oats with high levels of protein in the seeds. In order to achieve the development of cultivated tetraploid forms it would be advantageous to introduce some of the adapted hexaploid genotype into the derivatives. Wahab (1985) (a post-graduate student at Aberystwyth), did show that it was

possible to introgress characters from the cultivated oat into A.maroccana but many cycles of crossing would be required to develop the basic material for selecting a cultivated tetraploid cultivar.

The other species described and the new accessions of those already available did provide a further source of genes for resistance to diseases, the most commonly researched were mildew and rust. To transfer this extremely valuable source of variation into the A.sativa germplasm requires overcoming strong isolation barriers which result in sterility in inter-polyploid hybrids. The advances that have been made in understanding the cytogenetic relationships between species has contributed to the adoption of procedures for such gene transfers e.g. irradiation and genetic induced transfers (Thomas, 1980).

In conclusion it can be said that the interest in collecting germplasm of Avena outside the cultivated oat gene pool has made a significant contribution to studies of evolution and breeding. However, the exact progenitors of the hexaploid species remain to be described and have not been found within the areas accepted as being the centres of diversity. This could be due to the fact that the genomes of the actual progenitors have become so structurally changed since their incorporation in polyploid species that conventional cytogenetic methods have not been able to detect them. The partial homology between the diploid As and C genomes and their corresponding genomes in A.sativa could be a reflection of such structural changes. From the breeding point of view this differentiation makes it virtually impossible to obtain natural recombinants involving characters of the weed species and techniques of chromosome manipulation have to be applied.

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Breeding oats for Mediterranean-type environments
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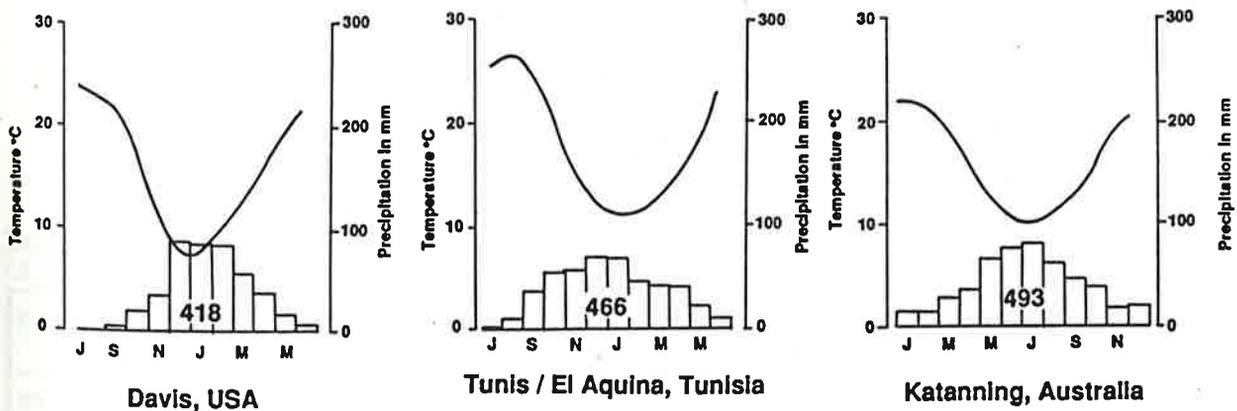
The centre of diversity of the Avena genus lies in the Mediterranean region. From there, several species have spread to become serious weeds over a wide range of climatic and geographic zones. The major cultivated species, A. sativa is thought to have evolved in central Europe and at present is most important as a crop in the higher latitudes. Australia is an exception as the majority of its oat crop is grown between latitudes 23° and 40° - a range similar to that of the Avena genus in its original habitat. The establishment of cultivated and wild Avena species in the agricultural systems of southern Australia is examined in this paper as an example of plant adaptation to Mediterranean climates. It is suggested that wild species from the Mediterranean region and the naturalised Avena of Australia may provide valuable germplasm for the improvement of the crop in Mediterranean-type environments.

1. THE MEDITERRANEAN-TYPE CLIMATE AND ITS IMPACT ON PLANT GROWTH

The definition used in this paper for a "Mediterranean-type environment" is extracted from Cooper and Gregory (1981), viz., "Crop production takes place against a background of limited, variable and often chronically deficient rainfall. Rain occurs mainly during the cool or cold winter, and to a lesser extent during the warmer spring; the rainy seasons are followed by a hot and dry summer." Implicit in the term "Mediterranean-type environments" is the assumption that such areas will be bounded by latitudes 20° and 40°. This type of climate may be found in North Africa, southern Europe, Western Asia, the Cape Province of South Africa, parts of Argentina and Chile, California and northern Mexico and also southern Australia (Kassam, 1981). Specifically, the Australian regions that meet these criteria are the south-west of Western Australia, South Australia and the western and central parts of Victoria.

Rainfall and temperature profiles for three locations with Mediterranean-type climates (Figure 1) show that both exhibit marked seasonal differences and that the peak of rainfall coincides with the trough of temperature and vice versa. The relationship between rainfall distribution and temperature regime common to these environments results in a crop water availability pattern (Nix, 1975; Figure 2) which limits the cropping options to winter grown annuals such as wheat, barley and grain legumes such as chickpea and lentil. Small areas are sown to oats, triticale and rye.

Figure 1 : Temperature and rainfall profiles for three locations with "Mediterranean-type" climates

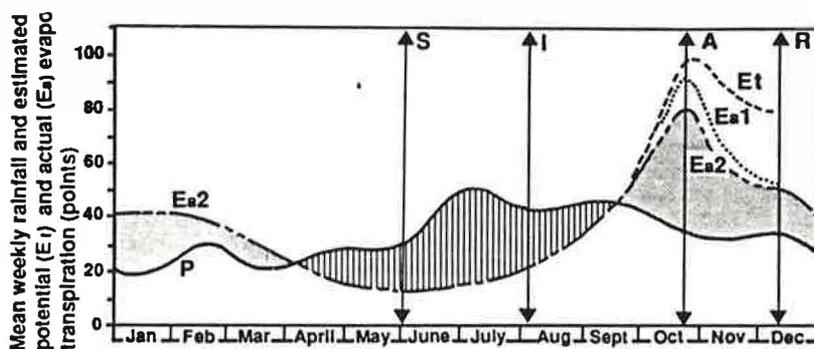


The cycles of wetting and drying (Figures 1 and 2) of soils characteristic of Mediterranean-type environments exert a strong influence on soil pedogenesis, often resulting in sharp textural contrasts between horizons (Chittleborough, 1981). The A horizon is often shallow and is underlain by a B horizon of less permeable soil which may present a physical and hydraulic barrier to root growth.

A cereal crop in a Mediterranean-type environment is often sown into a

seedbed prepared quickly at the end of the hot, dry summer. Soil temperatures are high while the moisture supply is often variable until the winter pattern of low temperatures and more reliable rainfall is established. In mid-winter, tillering is proceeding at low, but not freezing, temperatures, low irradiance and high soil moisture. The combination of low evaporation, high winter rainfall incidence and poorly structured soils often leads to waterlogging. This can seriously impair plant growth and in some cases cause tiller death. By early spring, daylength and temperature are increasing quickly and the probability of worthwhile rains decreases rapidly. During stem elongation, there is often a very rapid transition from over-supply of water to a shortage. From anthesis onward, crops may be subject to radiation frost, high temperatures (which may reduce yields even when soil water is not limiting) and drought stress. Drought stress results from the combined effects of low rainfall, high evapotranspiration and poor moisture holding properties of the soil. Crop physiologists have proposed 12 characters for improved plant performance in Mediterranean-type environments (Table 1).

Figure 2 : Seasonal patterns of rainfall, evaporation from bare fallow and crop evapotranspiration at Horsham, Victoria (after Nix, 1975).



(Et-estimated potential evapotranspiration; Ea₁-estimated actual evapotranspiration, long fallow; Ea₂ estimated actual evapotranspiration, short fallow; P-precipitation; S-seeding; I-initiation; A-anthesis; R-ripe).

Table 1 Desirable plant characteristics in a Mediterranean-type environment

1. Rapid germination and early establishment of deep roots
2. Rapid phenological development
3. Developmental plasticity
4. Diaheliotropic and paraheliotropic leaf movements
5. Leaf expansion highly sensitive to water deficits
6. Stomata sensitive only to large vapour pressure deficits and insensitive to low leaf water potentials
7. Ability to adjust osmotically
8. Large transfer of assimilates from stem to grain
9. Dehydration tolerance particularly at seedling and grain filling
10. Tolerance to radiation frosts during anthesis and grain filling
11. Tolerance of high temperatures during anthesis and grain filling
12. Tolerance of periods of waterlogging during tiller formation

1-9 Turner and Begg (1981); 10-11 Smith and Harris (1981); 12 Fisher (1981)

Yields in Mediterranean environments are low (Table 2) and variable. Furthermore, the rate of yield increases is much slower than for cropping environments at the higher latitudes (Turner and Begg, 1981). Turner and Begg compare the rate of increase of wheat yields in the United Kingdom, Syria and Australia for the period 1941 to 1977. The latter two countries have made only slow progress while U.K. yields have nearly doubled in that period. This reflects both the potential for improvement and the degree of difficulty of such improvements in the two types of environments.

Climatic profiles for two environments (Figure 3) where higher oat yields are achieved are strikingly different from those Mediterranean-type environments shown in Figure 1. The phenology of a winter oat grown in England and a short season, spring oat grown in the mid-west of the U.S.A. (Figure 4) are compared to that of an oat grown in South Australia. The figure shows how an adapted variety must fit the available growing season.

Figure 3 : Temperature and rainfall profiles for Rothamstead, U.K. and Des Moines, U.S.A.

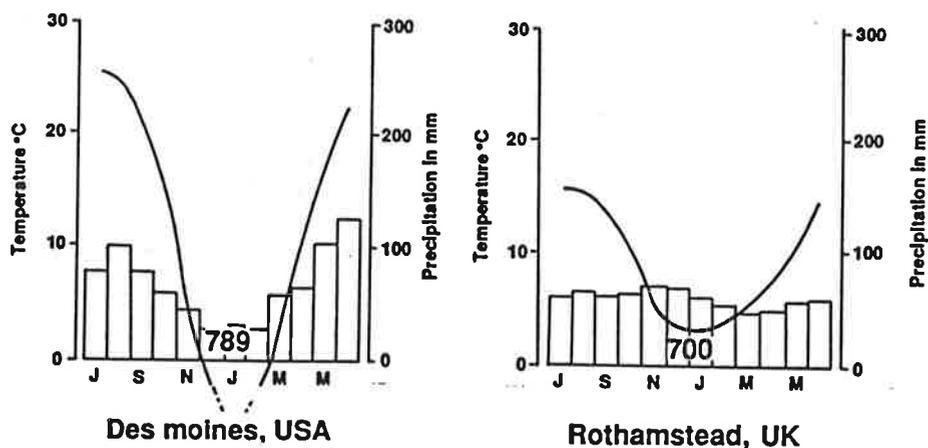


Figure 4 : Developmental patterns for oats grown in locations with contrasting climates

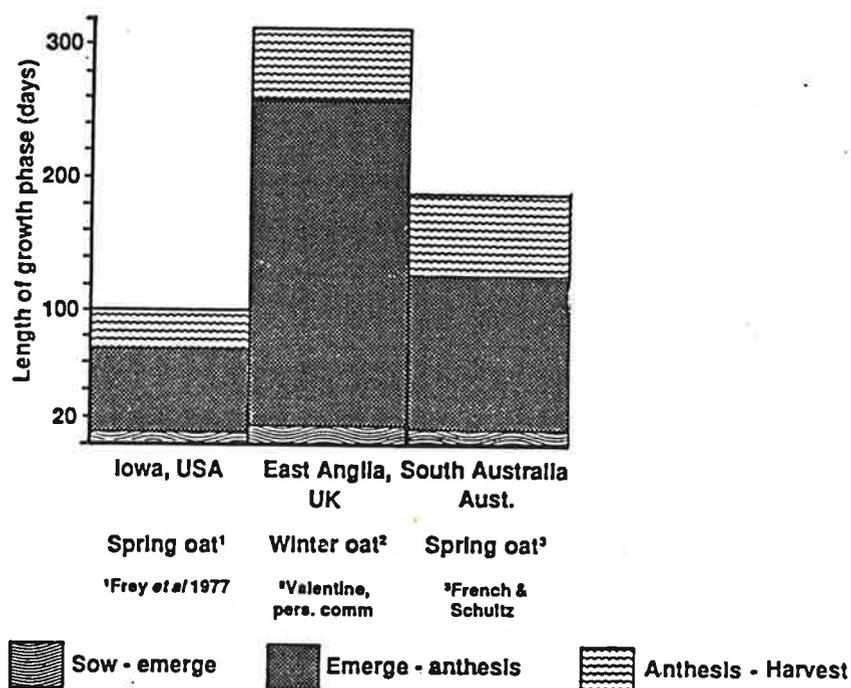


Table 2 : Comparison of the area sown and grain yield of oats in 1983 in relation to the latitude (after Forsberg, 1986)

Country	Climatic Zone ¹	Latitude of oat areas	Yield (kg/ha)	Area (ha x1000)
UK	Temperate	51-58	4306	108
Sweden	Temperate	55-60	3139	404
Canada	Temperate	49-53	1980	1,400
USA	Temperate/Subtr. sum.	40-49	1882	3,682
USSR	Temperate	50-60	1278	12,516
Australia	Subtropics winter	23-38	1183	1,995
Spain	Subtropics winter	36-43	1009	466

¹ see Kassam, 1981 in Figure 1

2. THE AUSTRALIAN EXAMPLE

Both cultivated and wild Avena species have been introduced into Australia and their history gives an insight into the problems and possibilities for oat improvement in a Mediterranean-type environment.

2.1 INTRODUCTION AND ADAPTATION OF WILD AVENA

The wild species A.fatua, A.sterilis and, to a lesser extent, A.barbata are very serious weeds in many countries. A.sterilis developed in the fertile crescent of Asia Minor and is usually a weed in its native habitat or in other Mediterranean climates (Jones, 1976). A.fatua probably originated in temperate Europe and is the dominant wild oat of the U.K., north-west Europe, North America and areas of similar climate (Holden, 1976). A.barbata is also Mediterranean in origin but it is usually a weed of roadsides and waste places (Baum *et al.*, 1972). Their naturalization in Australia is interesting because the climatic and edaphic conditions over vast areas mimic those of the Mediterranean basin.

These three weedy species were repeatedly introduced into Australia as contaminants in seed, feed grain, fodder and ballast or adhering to clothing and footwear (Whalley and Burfitt, 1972; Kloot, 1985; Kloot, 1986). Grain and fodder were imported from many countries including the United Kingdom, Italy, Turkey, S. Africa, U.S.A., New Zealand, Japan, Chile, India and France over a period of 150 years (Anon., 1845-1910; Anon., 1901-1940) until strict quarantine laws were enforced. The imports have varied from small consignments for seed to over two million bushels of feed oats in 1915 following the calamitous drought of 1914. Much of this grain would have been fed to horses, and since wild oat seed can pass through the gut without loss of viability (Jones, 1976), there would have been many opportunities for new, weedy introductions to establish. Seed and fodder from ports en route to Australia such as Lisbon and Capetown, have almost certainly contributed to the Australian Avena flora. Jones, 1976 points out that South African wild oat types have "...many affinities with Australian types and some with Kenya, Algeria, Portugal, France, Malta, Greece, Sicily, Israel ...". Italian, Egyptian and Indian ports may also have been fodder stops for ships bound for Australia after the opening of the Suez canal in 1869. Free trade between Australian states would have ensured redistribution of different ecotypes.

There are a number of less frequent, but possibly important, routes for introduction of wild Avena. For instance, A.sterilis was introduced as an ornamental into South Australia in 1859 (Kloot, 1983). Immigrants from Afghanistan, Pakistan and north-western India came to Australia in the mid-nineteenth century (Rajkowski, 1987) bringing with them their camels, fodder and saddlery (packed with straw). Several weeds have been traced to this influx (Jessop, 1978) and it is plausible that they may have brought wild Avena to the northern parts of the cropping belt.

The only countries in the centre of diversity of the Avena genus that did not export grain, hay or any other vehicle for the introduction of seed to Australia are Iran and Iraq. Given the diverse sources from which wild Avena came to Australia, one would expect the naturalised flora to be very variable. Four major studies confirm this. Whalley and Burfitt (1972) showed a wide range of morphological and physiological variability in all three Avena species. A range of responses to vernalization were found in both hexaploid species while A.barbata "... required vernalization to flower...". They concluded that "...multiple introductions with some environmental sorting..." were responsible for the situation they found among 31 A.sterilis, 17 A.fatua and 5 A.barbata samples collected in New South Wales and Queensland. Cartledge (1973) recognised about 20 strains of A.fatua and A.sterilis collected in Queensland. Variability for maturity, plant size, number of seeds, growth habit, dormancy and tolerance to herbicides was found. The greatest variability in ecotypes present at a single location was encountered on research centres. Wild oats in grain samples for experimental work may be another important method of introduction and dispersal of new variants.

Paterson (1976) examined 910 accessions of the three wild species collected in Western Australia. Variation for all morphological traits examined including husk hairiness, husk hair colour, basal hair colour and awn texture were found. More importantly, differences in response to photoperiod and vernalization were identified. These studies indicate that the wild species have had sufficient time since introduction to become closely adapted to the niches they now occupy.

Burdon *et al.* (1983) found considerable variation in seedling resistance to

stem and crown rust of 21 populations of wild oats collected in New South Wales. Interesting parallels can be drawn from this work and that of Wahl (1970) which was conducted in Israel. Wahl found that both seedling and adult plant resistance to Puccinia coronata f.sp. avenae race group 264-276 was prevalent and widespread in ecotypes growing in Israel.

It is likely the naturalised Avena of Australia are a representative subset of the variability present in the genus in its centre of origin and may, therefore, represent a valuable germplasm resource for oat improvement.

2.2 CULTIVATED SPECIES-A HISTORICAL PERSPECTIVE

The first area was sown to oats in 1791, just three years after European settlement of Australia (Walkden-Brown, 1975). The first varieties grown were late-maturing types such as Potato, Dun, Scotch Grey, Ligowo and Tartarian which were introduced from the United Kingdom. Small grains were originally grown in the temperate, coastal environments of N.S.W. and Tasmania and these varieties from England would have some merit in such situations. However such areas were small and crop varieties adapted to the semi-arid environments of southern Australia were required before expansion was possible. Wheat made this transition in the mid-to-late-19th century as improved varieties became available from vigorous introduction programmes and very successful selection programmes undertaken mostly by farmers (Wrigley and Rathjen, 1981). Meanwhile the oat industry languished as it relied on European varieties. No evidence can be found that new introductions nor farmer selections contributed to oat improvement in the same way as it had for wheat in this period.

In the 1880's, Algerian oats, probably a land race from Algeria appears in the literature of the colony (Anon., 1888-96). Algerian rapidly became the most popular variety in the semi-arid, cereal belt where it was used for grain, forage and hay (Anon., 1888-96; Anon., 1897-1918; Callaghan, 1932). Algerian provided a substantial improvement in productivity and reliability over the European introductions. It proved so good that its introduction may have led to complacency about seeking further improvements. Introductions from the Cape of Good Hope area and sold just as cv. Cape oats and cv. Champion, of unknown origin, were other oats of significance in the late 1800's in S.A. (Anon., 1888-1896; Anon., 1922).

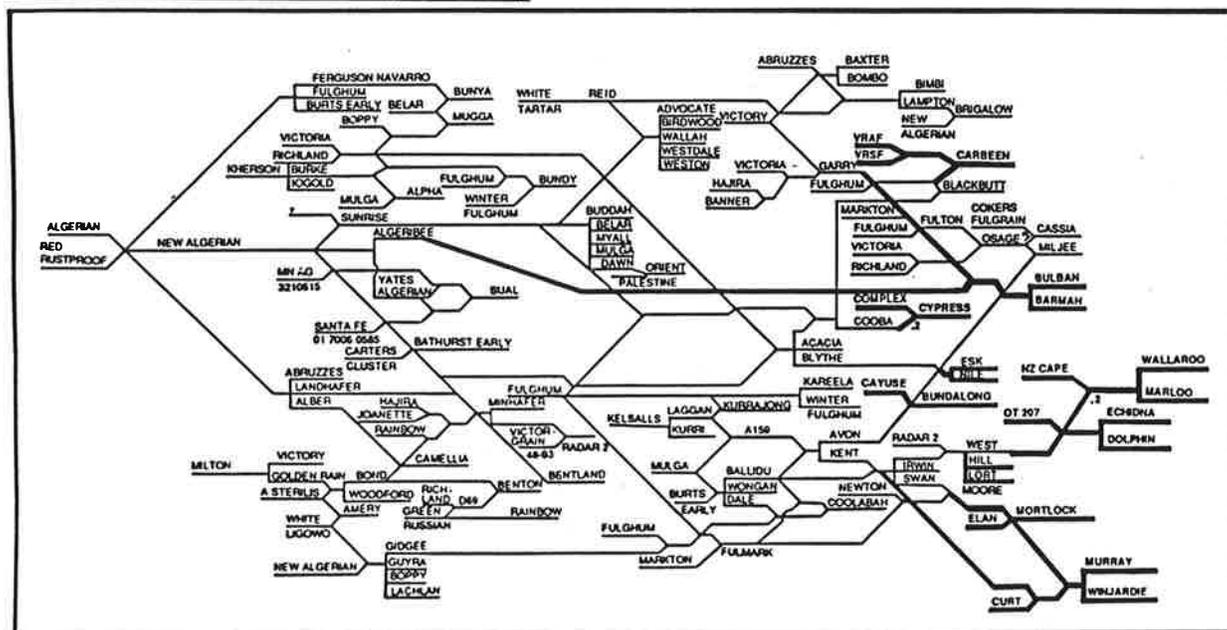
William Farrer was a pioneer of plant improvement in Australia. He worked in New South Wales and although his principal interest was in wheat he also was involved with oat selection. His philosophies on cross-breeding and selection were to have a great impact on subsequent oat improvement. J.T. Pridham, after a period assisting Farrer, began his oat breeding work in N.S.W. in 1904 (Walkden-Brown, 1975). His early oat improvement concentrated on improving Algerian types for grain, dual purpose (grazing/grain), and for hay production. Pridham's most successful cross was Algerian and Red Rustproof. Further crosses from that base produced Sunrise and Belar, which at times were even more popular than Algerian had been (Walkden-Brown, 1975). By 1910, Western Australia and Victoria had established oat breeding programmes. The programmes conducted by these three Departments of Agriculture continue to the present day. Oat research in South Australia began with Roseworthy Agricultural College in the late 19th century and cv. Champion was described in early reports from the college. It is unclear whether this variety resulted from a programme of breeding, selection or introduction (Anon., 1922).

While Algerian and Red Rustproof contributed heavily to the genetic improvement of Australia's oats prior to 1950, eleven other parents were also important (Petersen, 1980; see Figure 5). The varieties were White Ligowo (France), Markton (Greece), Palestine (Syria), Hajira (Algeria), Milton (Sweden), Kherson and White Tartar (Russia), Richland, Fulghum and Burt (USA) and Victoria (Argentina). The original introductions from the United Kingdom contributed little to genetic improvement. The importance of the "Mediterranean infusion" is reflected in the pedigree (Figure 5) of Orient released in 1947 by A.R. Raw from Victoria. It was very successful in the more marginal farming areas. During this period the range of maturity was extended, large kernel types were developed and improved dual-purpose types were released. Hay types received less emphasis as horses were replaced by tractors on Australian farms.

The varieties Avon, Cooba and Swan dominated the oat growing areas in the 1960's and 1970's. Avon (1954) and Swan (1967) were bred in Western Australia by D.R. Bateman and A.J. Reaney, respectively, and were very successful grain types in Western Australia, South Australia and Victoria. Avon resulted from a three-way cross between Ballidu, Mulga and Laggan (Figure 5). Ballidu and Mulga trace directly to Algerian. Two of the key reasons for the success Avon

was that it had good resistance to shattering and to Barley Yellow Dwarf Virus (BYDV). Swan was selected from a cross between Kent, an early maturing sister line of Avon, and Ballidu. Thus Swan also has links with Algerian. Swan produces arguably the best physical quality grain of any oat ever bred in Australia, and except when attacked by stem rust, lifted the quality and marketability of oats. Swan also has moderate levels of resistance to BYDV. The BYDV tolerance of Avon and Swan almost certainly resulted from passive selection. Cooba, bred by F. Mengersen at Temora in New South Wales, dominated sowings for dual-purpose types in N.S.W. from soon after its release in 1960 to the present time. It is very tolerant of grazing and produces small grain with a very high kernel percentage. Cooba and other dual purpose types from New South Wales are unlike varieties from the southern states as they have a vernalization response and are sensitive to daylength. These varieties have never been popular in the three southern states which have Mediterranean-type climates.

Figure 5 : Pedigree chart of Australian oat varieties (after Petersen, 1980 with additions in bold by author)



All varieties produced since 1950 have resulted either from intercrossing older Australian varieties or from crosses involving Australian and North American types. The seven introductions from North America used as parents in this period were Cayuse, Garry, Newton, Elan, Radar 2, OT207 and Curt. Only Curt comes from a region of similar climate, namely California. The varieties released from W.A. in the 1970's and 1980's feature specific genes for stem rust resistance, high grain protein, shorter straw with a concomitant increase in standing ability, shattering resistance and higher grain yields. West and Mortlock are the most notable. The Victorian programme has released types with tolerance to wet soils and BYDV, shattering avoidance due to straw "arching", specific genes for stem rust and crown rust resistance and higher grain yields. These include Bulban, Barmah and Bundalong. Oat improvement was begun by the South Australian Department of Agriculture in 1977 with the object of improving grain yields, resistance to stem rust, BYDV and cereal cyst nematode, and improving quality. Four varieties, Echidna, Dolphin, Wallaroo and Marloo, have been released (Barr, 1984; Barr, in press). Echidna and Dolphin are semi-dwarf selections from a cross between West and OT207. Echidna is the highest yielding variety grown in southern Australia as its performance in the Interstate Oat Variety Trials demonstrates. It has been entered on four times and has ranked first of the 24 entries for grain yield on three occasions and fourth on the other. (Barr and Girke, pers. comm. ; McLean, pers. comm. ; Oates, pers. comm.) Echidna, in particular, has been adopted rapidly in southern Australia, especially in Victoria.

West, Bulban, Barmah, Bundalong, Mortlock, Echidna and Dolphin have all come from crosses between local and exotic types. Selection and yield testing has generally favoured segregants with developmental patterns similar to cv. Swan

(French and Schultz, 1982; Figure 4). The only exception is Echidna which matures at the same time as Swan but has a longer period prior to anthesis. Most of these recent varieties have large grain by world standards. Again, Echidna (and Dolphin) are exceptions. This may be an artefact of the exotic parent OT207 or it may be a valuable adaptive trait.

Table 3 Comparison of height, harvest index, biological yield and grain yield of Australian oat varieties from different eras.

Variety	Year	Height (cm.)	Harvest Index	Biological Yield (kg/ha)	Grain Yield (kg/ha)
NZ Cape	1900	138	17.8	9688	2140
Avon	1954	135*	-	-	5150
Swan	1967	144	27.8	12980	4770
West	1974	121	28.4	15530	4410
Mortlock	1983	110	-	-	5180
Echidna	1984	82	41.6	14380	6290
LSD 5%			6.0	3229	760

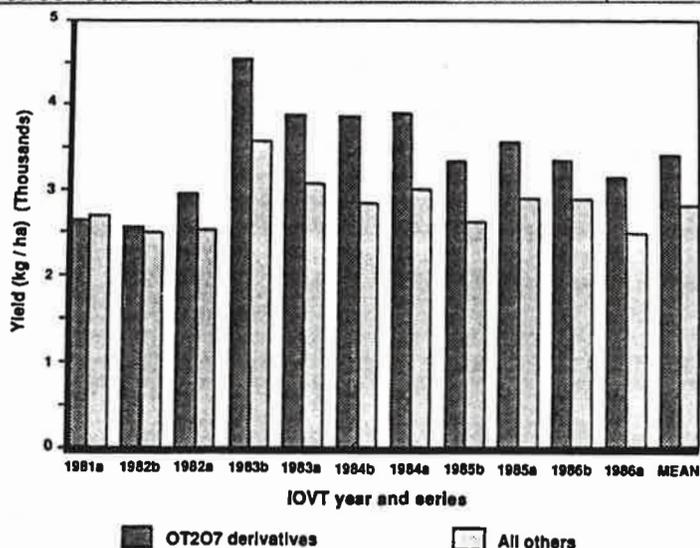
All data from Turretfield (1986) except plant height Greenpatch (1986)

* estimated from previous trials.

2.3 CURRENT OAT IMPROVEMENT

The discovery of the Dw6 gene (Simons *et al.*, 1978) for semi-dwarfism in the line OT207 (Brown *et al.*, 1980) caused a major change in direction for all mainland Australian programmes. Even though much of the Australian oat belt is classed as semi-arid, the growing season is relatively long. Most varieties have tended to be tall, produce excessive amounts of straw and have low harvest indices (Table 3). The incorporation of Dw6 into Australian material simultaneously decreases plant height by approximately one-third, increases lodging and shattering resistance past all previous standards, increases harvest index and increases grain yield. This is demonstrated by examining the results of the Interstate Oat Variety Trial (IOVT) which is conducted each year at up to 11 sites in five Australian states. Lines with Dw6 and selected in all four mainland programmes using different breeding methodologies and different adapted parents, were included in these trials. Their mean yield was 20% higher than the mean yield of all other entries (Figure 6).

Figure 6 : Comparison of grain yields of all lines carrying Dw6 with all other lines in Interstate Oat Variety Trials in Australia (1981-1986)



It is interesting to speculate why the Dw6 gene should be successful in Australia and not in other environments. Possible reasons include

1. the dwarfism is too extreme for short-season spring sown oats.
2. low straw yields are unpopular in areas where there has traditionally been a demand for oaten straw for animal bedding (Meyers *et al*, 1985).
3. difficulties in transferring Dw6 from spring to winter types.
4. incomplete emergence of the panicle from the boot which may lead to poor grain filling in basal florets (Marshall, 1986).

Further increases in yield, quality and disease resistance are being sought by intercrossing within the A.sativa pool as Dw6 is placed in superior backgrounds. Genes conditioning modified developmental patterns have been combined with Dw6 and are currently under test. The main impact of Echidna and Dolphin has been in the better oat growing areas and Australian breeders are generally optimistic that further rapid progress can be made in favorable environments. However, Echidna is too short for mechanical harvesting in some seasons in regions of low rainfall and fertility, even though a yield advantage over conventional height cultivars is maintained. It has been necessary to select for modifying genes capable of extending plant height in the presence of Dw6. This approach has been successful as lines up to 20cm. taller than Echidna have been entered in the Interstate Oat Variety Trial by several Australian breeders. This extension of plant height may provide the unexpected bonus of high hay yield and quality. Registration papers for two breeders lines, designated 75Q202 and 75Q142, which are taller than Echidna are in preparation by the Western Australian Department of Agriculture (McLean, pers. comm.).

Generally, progress in more marginal environments appears more difficult. However, four varieties, tested from 1984-1987, have demonstrated improved adaptation to low yielding environments. The varieties are Murray, from Western Australia, Bundalong, from Victoria and Wallaroo and Echidna, from South Australia. These varieties are not closely related (Figure 5) and differ in growth habit, phenology and plant height. Genotype x environment studies show that all are superior to other commercial varieties (Barr, unpublished data). The physiological basis for their superiority is worthy of attention and may provide guidelines for future screening programmes.

Crosses involving wild species have not yet produced new varieties in Australia (Petersen, 1980). However, several programmes are currently using wild relatives for resistance to the cereal cyst nematode (Heterodera avenae), resistance to stem and crown rust (Puccinia graminis and P. coronata) and for plant type in low rainfall environments. In all cases, introduced, rather than naturalised, accessions have been used.

The breeding programmes in Western Australia and South Australia are highly mechanised and with the aid of sophisticated computer software are capable of efficient and large scale yield testing systems across many environments. The aim is to maximise the selection pressure for yield and adaptation. Rapid progression through generations is achieved in South Australia with out-of-season (summer) nurseries. This is possible *in situ* with irrigation and bird-proofing and it allowed the ten generations between crossing and release of Echidna and Dolphin to be achieved in seven years.

3. OAT IMPROVEMENT PROGRAMMES IN OTHER MEDITERRANEAN-TYPE ENVIRONMENTS

There are currently very few large oat improvement programmes based in Mediterranean areas. One of note is California. The Spanish missionaries probably introduced oats into California from Spain via Mexico before the early 1800's (Coffman, 1961). In contrast, introductions to eastern America were originally from the United Kingdom and temperate Europe. Suneson *et al* bred oats from the early 1940's and Australian oats were important in their early work. The cultivar Palestine was introduced from Victoria in 1940 and it featured in the pedigree of both Indio and Curt which were released in 1956 and 1959 respectively. (Coffman, 1977). The next group of releases were derivatives of cultivated types crossed to selected A.fatua ecotypes which were naturalised in California. They were Rapida (Suneson, 1967a), Sierra Suneson, 1967b), Montezuma (Suneson, 1969) and Mesa (Thompson, 1967). It is somewhat surprising that Suneson was able to produce cultivars from single crosses to wild ecotypes given the number of deleterious weedy genes to be deleted from the progeny. However, one can draw some encouragement from his success, for if repeated backcrossing is not required, the breeder can explore many more ecotypes and cross combinations.

Little published information on oat breeding programmes from other

countries with Mediterranean-type environments is available. Reference is made in the "Oat Newsletter" and reports from "Breeding oats for developing countries" (sponsored by the Quaker Oats Company) to programmes in Portugal, Tunisia, Morocco, Algeria, Chile and Argentina.

4. PROSPECTS FOR FUTURE OAT IMPROVEMENT IN MEDITERRANEAN-TYPE ENVIRONMENTS.

The oat plant is more susceptible to drought stress than any of the other winter cereals grown in Australia (Walkden-Brown, 1975) despite nearly 90 years of oat improvement. The lack of adaptation of oats to semi-arid environments is probably not associated with the phenology of the varieties in cultivation as the oats grown in South Australia have a similar developmental pattern to well-adapted wheat and barley cultivars (French and Schultz, 1982). This inadequacy is difficult to explain when Avena species of all ploidy levels successfully colonise areas prone to severe drought stress in many countries of the Mediterranean basin (Baum, 1977). The weakness of cultivated species is probably a reflection of their origin in temperate Europe rather than in the Mediterranean (Holden, 1976). This shortcoming must be rectified if oats are to extend their range of cultivation in areas with Mediterranean-type environments.

As discussed in section 1, tolerance to drought stress is required at two discrete growth stages, namely from germination until early tillering and from anthesis through grainfilling. Larsson (1982) described screening techniques for seedling drought tolerance and found that black seeded oat cultivars were the best adapted to the particular drought stress of northern Sweden. However little published data are available on the tolerance of a range of oats to drought stress during grainfilling (see Brouwer, 1986). Most of the characteristics listed in Table 1, which may improve the performance of crops in Mediterranean-type environments, have been proposed for wheat plants but have not been investigated in oats.

Oats are not widely grown around the Mediterranean and it has been argued that germplasm developed at higher latitudes will not be a suitable source of genes conferring adaptation to Mediterranean-type environments. Three options for future improvement are ;

1. Intercrossing sativa types from programmes based in Mediterranean-type environments.

2. Introducing new germplasm from dissimilar climatic zones via crosses to lines with suitable developmental patterns (ie., local varieties)

3. Introgressing genes from wild Avena spp. either from the Mediterranean or perhaps more appropriately, naturalised ecotypes from the regions where the crop is to be grown.

All three approaches are worthy of effort but the latter requires some elaboration. Skeptics will argue that successful colonization of Mediterranean-type environments by weedy Avena will not provide a reliable indication of performance of a "future" domesticated plant under the constraints of monoculture and end use requirements. However Suneson (eg., Suneson, 1967) demonstrated that the use of naturalised A.fatua types led to improved performance of cultivated types. Lawrence and Frey (1975) reported grain yield increases in backcross progenies derived from A.sterilis, although in a vastly different environment.

A.sterilis may be the most plausible source of drought tolerance as it is widely distributed in the Mediterranean basin and it is thought to be the progenitor of the cultivated, hexaploid species. Nevertheless, Paterson (1976) and Paterson et al (1976) showed that A.fatua was better adapted to Western Australia than A.sterilis and when combined with the proven success of Suneson's approach, this suggests that A.fatua should not be discounted.

There are at least two examples of surveys of naturalised Avena populations with the goal of exploiting them for the genetic improvement of the cultivated crop. Atkins et al (1966) and Rines et al (1980) made large collections of naturalised Avena from Texas/Mexico and "western North Central U.S.", respectively and then examined the variability encompassed in that material. Most attention was placed on disease and insect resistance but Atkins et al examined the reaction to low temperatures and Rines et al considered the prospects for A.fatua to increase yield potential and provide environmental stability.

Few research groups have attempted to transfer traits with low heritability such as yield, adaptation or drought tolerance, which will be conditioned by many genes, from wild species into cultivated types. Lines containing Dw6 may be an ideal vehicle for introgressing "yield" and "adaptation" gene/gene complexes as the Dw6 gene usually reduces problems with plant height, lodging

and shattering . Frey (1975) calculated, on theoretical grounds, that the best strategy for introducing "yield genes" from A.sterilis was by backcrossing one-three times to an adapted, recurrent parent. This procedure may require modification from the strategy advocated by Frey as suitable recurrent parents carrying Dw6 may not be available . Hence a three way cross eg., (Dw6 derivative "A" x wild ecotype) x Dw6 derivative "B", followed by several generations of pedigree selection to remove weedy traits and select homozygous stocks, may be more appropriate. Modified single seed descent methods with selection against dormancy, shattering and undesirable morphological types may be useful during this phase. Selection could then progress to the field.

A.barbata is better adapted than any of the hexaploids to extreme edaphic conditions encountered in South Australia, for example, manganese deficient soils; saline, coastal dunes; deep, siliceous sands and soils prone to waterlogging. This is also true of A.barbata in its native habitat (Baum,1977). Problems associated with the crossing of tetraploid and hexaploid species would necessitate a long term strategy if introgression of genes/gene complexes from this species is sought (Rajhathy and Thomas,1974).

Novel approaches to oat improvement such as discussed above must be tried in more regions with Mediterranean-type environments. There appears to be a lack of basic research into the physiology, agronomy and genetics of the hexaploid oats in these semi-arid environments. If cultivated oats are to mimic the success of other members of the genus in colonising Mediterranean environments this shortcoming must be redressed.

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THE DEVELOPMENT OF OAT GERMPLASM AT SVALÖF.

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Oats is cultivated in most parts of Sweden. It means along a distance of more than 1.000 miles in south - north direction. The demand for different types, particularly regarding earliness, is great. Thus plant breeding is necessary to supply all Swedish farmers with a crop adapted to their specific localities.

Oat breeding at Svalöf has its main origin in the cultivation and breeding of oats in Western Europe. Zade (1918) presents the story of many wellknown cultivars. In a diagram he is showing the different steps of selections in the early breeding work (fig. 1). One of the main centers is the Probsteier oats, from which many cultivars have been selected.

The Probsteier oat lines were also used at Svalöf. One example is the improvement Hjalmar Nilsson made when he in 1897 by mass-selection released the "Svalöfs borstlösa Probsteier". (Svalöfs awnless Probsteier). This selection was a great improvement compared to the old Lant-varieties cultivated at that time.

Although mass-selection gave some results, much greater progress was obtained when the breeders started to select single plants. Doing that they were able to distinguish different characters and to maintain stable types. A fascinating story is the selection Hjalmar Nilsson made from the North American Milton oats. He selected about 30 lines from that cultivar and two of them became new cultivars, Guldregn (Goldrain) in 1903 and Seger (Victory) in 1908 (Åkerman, 1928). Both of them became widely cultivated not only in Sweden but also in many other countries. This is particularly true for Seger, which reached not only West Europe but also Russia and the U.S.A. and Canada. Since many years Seger is used as an *Avena*-standard all over the world and we still have to multiply it every year.

Herman Nilsson-Ehle succeeded Hjalmar Nilsson as oat breeder and already in 1906 he started to cross different cultivars. Besides selection for useful characters he also studied the inheritance of some other characters and proved that some of them were controlled by multigenic systems. Among other combinations he crossed Guldregn x Seger and from this cross he selected Guldregn II, which was released in 1928 and remained on the Official Swedish List of Cultivars until 1974.

It became, however, difficult to obtain further progress by crosses within the Probesteier-types and new introductions was made. One of these was the German von Lochows Gelbhafer. As a result of crosses with this cultivar the Örn (Eagle) oat was released, which later became one of the parents to Sol II (Sun II) (Fig. 2). Sol II is one of the greatest progresses in the Svalöf oat breeding and was selected by Erik Waller at the Svalöf branch station Skara. Except for out-yielding other cultivars, Sol II had a better straw stiffness and a good quality. It was released in 1943 and was cultivated for about 40 years.

A lot of other foreign cultivars have been introduced in the crossing programme. The crosses have often been planned to improve some special character and the selection applied has forced the breeding material towards the desired character. Thus the Dutch cultivar Condor proved to be a good parent for improving the stiffness of straw. Mac Key started this crosses which Gösta Olsson put forward in selection work and further crosses. The Sang cultivar is a nice example of this work. Besides very good straw characters Sang has an excellent quality (Olsson and Mattsson, 1978). The husk content is low and it is easy to dehull the kernels. Therefore, Sang is now given a higher price by the millers.

At the Weibulls plant breeding station in Sweden a corresponding work has been done. Other cross-combinations than those used at Svalöf have been performed and given some good cultivars. One of these, Selma, was popular during some years, particularly due to high yielding capacity. At Svalöf Selma and Sang were crossed together and they gave a population with a great variation. One of the selected lines was accepted as a new cultivar in 1983 (Fig. 3) and named Vital. Compared to the old Lant-varieties Vital is yielding about 30 % more.

Although the cross breeding method is still the most used one, some progress have been made with mutation breeding. Different mutagenic agents have been used like X-ray, EMS and NaN_3 . Except for chlorophyll-deficiency and other useless mutations some valuable mutants have been induced. Thus mutants with short straw, early maturity, mildew resistance and high protein content are now included in the breeding material.

During the whole period of oat breeding some attention has been paid to resistance against different diseases. However, it was not until the 1950-ies, after the heavy stem-rust attack on wheat, that the introduction of specific genes for resistance was performed. Stem-rust may occur at some localities in some years but is not a serious disease. That is also true for crown-rust and mildew but now and then they can cause serious damage. The race spectra of stem- and crown-rust proved to be surprisingly complicated (Mac Key et.al., 1963 and Mac Key and Mattsson,

1972). Sources carrying genes with stem- or crown-rust resistance were however introduced and in addition nematode resistant lines were obtained. The lines with rust resistance were kindly supplied to us by breeders from the U.S.A. and Canada while Sigurd Andersen in Denmark presented nematode resistant lines. By back-crossing he transferred resistance from A. sterilis to the Sol II oat. These lines with rust or nematode resistance was further crossed and back-crossed to advanced lines at Svalöf and that has resulted in cultivars with resistance to one or more diseases.

A lot of interest is paid to the quality of oat. For a long time the hectolitre weight has been measured and farmers have been paid for the crop according to that. Also kernel size and husk content have been noticed. Selections have been made to improve these three characters within the whole breeding material. However, during the last years special efforts have been done to improve the content of protein and fat. Cultivars with high protein content like Hinoat and Proat or with high fat content like Chihuahua and Tarahumara have been introduced in crosses (Mattsson, 1986). This work has been possible thanks to great help from breeders and institutes in North America. By back-crossing programme it seems to be possible to obtain well adapted lines with improved content of protein and fat.

In order to further widen the variation in the breeding material we now investigate wild species. In Avena sterilis and A. maroccana particularly there seems to be useful genes for improving characters like resistance, earliness, kernel size and quality. There is no sterility problems in the cross A. sativa x A. sterilis. In crosses with A. maroccana, however, there is a lot of sterility due to unbalanced chromosome-number and the breeding work must include cytological studies. Anyhow, looking at the results obtained so far, further progress seems to be possible.

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Figure 2. The pedigree of Sun II.

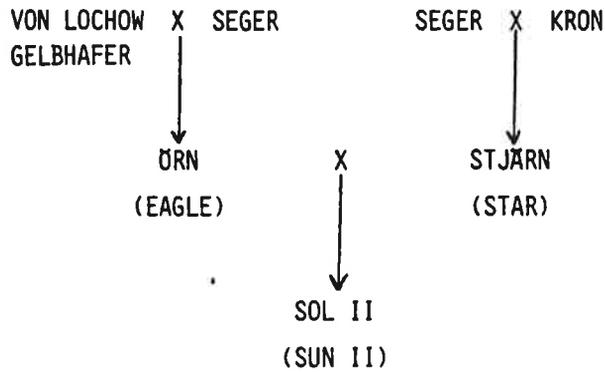
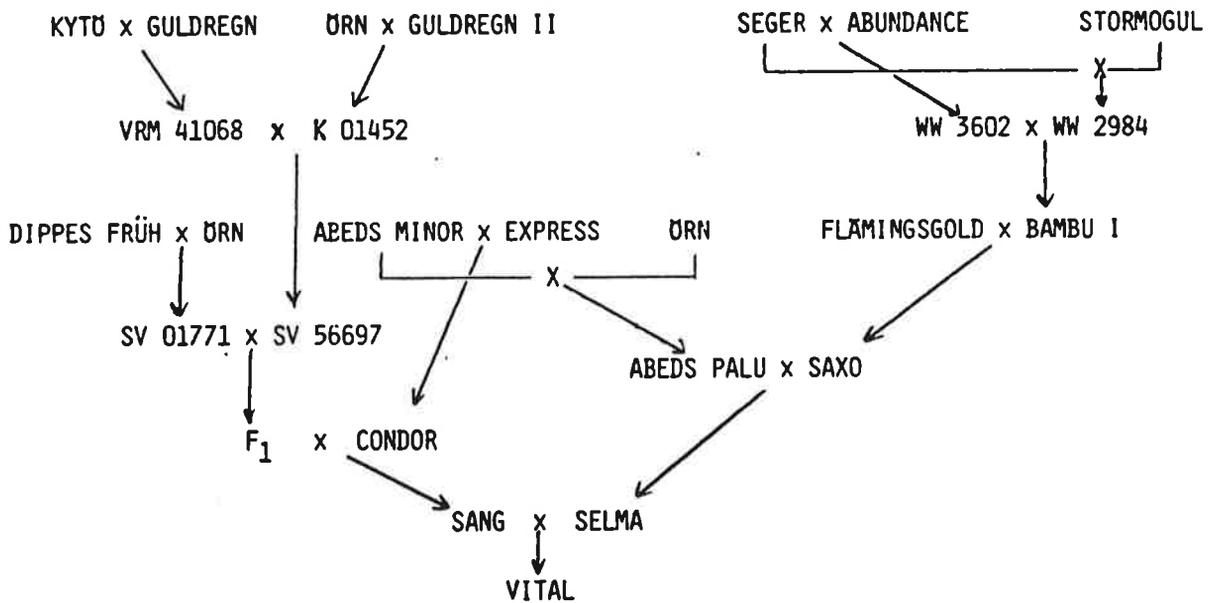


Figure 3. The pedigree of Vital



NEW GENES FOR DWARFNESS TRANSFERRED FROM WILD OATS
AVENA FATUA INTO CULTIVATED OAT

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Introduction

Dwarf plant height has allowed plant breeders to increase yield of many crops. Breeders are utilizing semidwarf and dwarf germplasm to reduce lodging and increase yield in oats. Currently, gene sources of dwarfness is quite restricted. We are looking for the new gene resources for utilizing practical plant breeding, for instance, crown rust resistance, dwarfism and grain quality. We have selected 15 dwarf wild oats (Avena fatua) in the fields of barley and wheat from East Asia. This area has involved a lot of useful gene resources, where is thought to be one of the secondary gene centers of the genus Avena.

The nature of inheritance of dwarfness is not fully understood in many of the dwarf or semidwarf lines used in breeding programs. Especially, in the materials from wild species, we have no knowledge of the number of genes involved and their inter- and intra-allelic interactions at all. Knowledge of their effects on other characters or the interaction with different dwarfing genes may allow a more rational choice among different dwarfing sources.

The aims of this study were firstly to determine if these sources for dwarfness possess similar or dissimilar genetic mechanisms and the number of genes, and secondly to transfer the genes for dwarfness from wild oats to the cultivated oat.

Materials and Methods

The fifteen dwarf accessions of Avena fatua were collected by Yamaguchi (1978). All the accessions were inhabited in the barley or wheat field as a weed, and which seem to adapt to the artificial habitats of East Asia. Their morphologies are quite different from the tall plants. The collection sites for the accessions are shown in Fig. 1. Four accessions (286, 288, 292 and 342) were derived from Korean peninsula and Chejudo Island. Six accessions (50, 151, 153, 206, 463 and 812) were from Kyūshū district of Japan. Three accessions (70, 77 and 811) were from Shikoku district. Two accessions (92 and 169) were from Honshū district.

All the materials used in this study were mostly located in the southern part of Japan and Korea. Many of accessions were localized to small fields or roadsides and were often isolated in the small islands. Inheritance of plant height was examined in the 14 accessions except for the accession 292.

Mature plant height of each generation plant was measured to the nearest centimeter from the base of the tallest culm to the tip of the spikelet, excluding awns. Height classes were established at 10 cm intervals. F3 progeny distributions and G-value analyses were used to verify F2 classification.

In order to examine genes controlling dwarfness, *A. byzantina* cv. Kanota was used as the tall female parent in all crosses. First of all the F1 hybrids were made and then the segregation of dwarfness was examined in the F2 populations of all cross combinations. According to the frequency distribution of plant height in the F2 populations, the genetic behavior of dwarfness was determined. After that, the dominant genes for dwarfness were transferred from the accessions into the cultivated oat 'Kanota' by means of successive backcrosses.

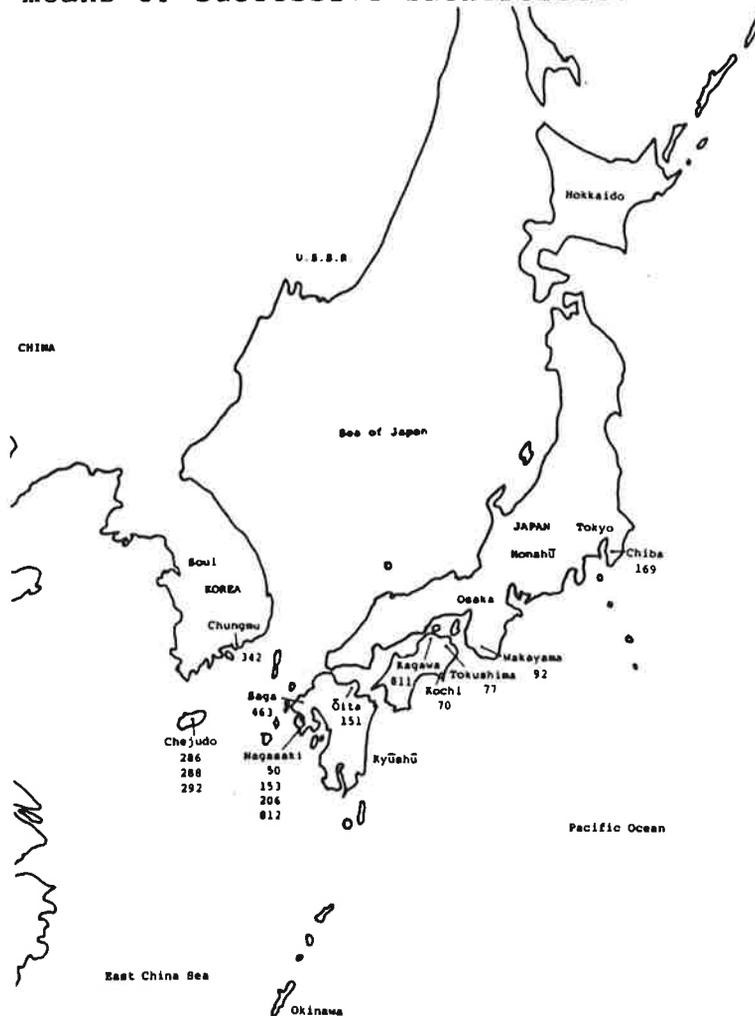


Fig.1. Collection sites for 15 dwarf oat (*A. fatua*) accessions.

Results and Discussion

Mean plant height, panicle length and internode length of the 15 dwarf accessions were examined. The results are shown in Table 1. The plant heights are ranged from 58.9cm to 99.8cm. Generally speaking, dwarf plant of oat is defined under 90cm long in plant height, which has extremely short second internode, ranging from 3.2 cm to 26.9 cm. Brown et al.(1980) reported that the reduced height of semidwarf oat OT207(*A. sativa*) was also due to the height reduction of the stem below the panicle. The panicle length was relatively uniform and was equivalent to that of tall plant in all the accessions except for 342. This panicles of the dwarf were very compact, the culms were heavier than normal, the spikelets were lacking one glume. This dwarf is quite similar to that of "Denton Dwarf" reported by Peier et al.(1964). The 288 is the tallest type of the 15 accessions, in which the plant height was 99.8 cm and is classified into semidwarf plant. The second internode length is longer than that of tall plant. The panicles of the semidwarf type usually did not emerge completely from the leaf sheath.

Table 1. Mean plant height, panicle length and internode length in the 15 dwarf accessions of *Avena fatua*

Accession	No. of plants examin.	Plant height (cm)		Panicle length (cm)		Internode length(cm)			
		height (cm)	SD	length (cm)	SD	1st	SD	2nd	SD
50	5	63.2	4.7	29.8	1.2	23.6	4.3	4.2	0.4
70	6	75.8	5.8	20.3	2.4	40.8	3.3	8.0	3.1
77	6	69.8	4.2	21.3	1.2	35.7	3.7	6.3	2.1
92	6	80.3	2.1	29.7	1.6	35.7	4.9	8.8	1.6
151	6	81.3	4.4	24.5	3.1	42.3	4.6	7.5	2.1
153	6	89.0	1.9	26.2	1.9	36.7	1.7	14.1	1.8
169	6	97.0	2.1	25.8	0.7	42.3	2.4	15.5	1.6
206	6	70.5	2.6	22.0	5.0	35.0	4.1	7.8	1.3
286	6	70.2	3.4	32.8	4.3	27.2	6.7	5.2	1.3
288	10	99.8	2.1	20.4	1.4	22.4	1.1	26.9	2.4
292	6	72.5	5.2	22.2	3.9	37.5	5.2	7.7	2.1
342	10	70.0	4.6	7.6	0.5	42.5	4.7	18.0	0.3
463	10	58.9	3.1	22.3	2.1	27.8	3.2	3.2	0.9
811	6	85.8	3.0	30.2	3.4	32.0	3.4	11.2	2.4
812	6	74.0	2.9	27.0	1.8	35.0	2.6	4.8	0.9
Kanota	10	135.0	5.9	31.0	2.2	49.1	2.3	22.9	1.6

Five types of F₂ distributions for the crosses between 'Kanota' and the dwarf accessions were shown in Fig. 2. Segregation for dwarfness in the F₂ from crosses 'Kanota' x *A. fatua* accessions was shown in Table 2. F₁ and F₂ frequency distributions for the crosses involving the accession 70,77,92,151,206,463 and 811 indicate that the major genes for

plant height are acting in a dominant manner. F1 and F2 frequency distributions for the crosses involving the accession 153,169 and 812 indicate that the major genes for plant height are acting in a recessive manner.

Table 2. Segregation for dwarfness in the F₂ from 'Kanota' x A.fatua accessions

Accession	Classification no. of plants			Expected ratio	G-value
	tall	dwarf	total		
50	6	49	55	1:15	1.689
286a	15	96	111	3:13	2.167
286b	23	120	143	3:13	0.693
70	8	22	30	1:3	0.044
77	34	83	117	1:3	0.994
92	28	95	123	1:3	0.335
151	30	83	113	1:3	0.143
206	24	83	107	1:3	0.386
463	30	118	148	1:3	1.849
811	28	86	114	1:3	0.012
153	95	26	121	3:1	0.823
169	50	16	66	3:1	0.020
812	93	31	124	3:1	0.000

$$\chi^2_{.05}[1]=3.841$$

a:Tested in 1985, b:Tested in 1987

Data from crosses involving 50,286a and 286b with 'Kanota' indicate digenic inheritance. F₂ distribution for each cross indicated 15:1 or 13:3 genetic ratios, which was completely discontinuous. The F₂ classification of these crosses was quite accurate because the difference in plant height between dwarf and tall was great in the F₂ population. The presence of two distinct height groups in the F₂ along with the parental classes segregating in a 15:1 fashion, would indicate that the dwarf stature in the accession 50 is governed by two independent dominant genes. The two genes had no additive effects or dose-effects on plant height because the dwarf classification in the F₂ showed a single continuous frequency distribution. The accession 286 from Chejudo of Korea had so exceptional frequency distribution in the F₂ populations that is fitted to a expected ratio dwarf:tall = 13:3. Plant height in the F₁s from the cross, 'Kanota' x the accession 286 was intermediate between parents. We verified twice that the segregations of dwarfness derived from the 286 are fitted to the expected ratio in both 1985 and 1987. The results indicate that the dwarfness of the 286 is involving two independent genes acting in both a recessive and a dominant manners.

Data from the cross 'Kanota' x the semidwarf 288 showed continuous frequency distribution in the F₂ population. Classification of the F₂ was not possible.

The frequency distribution for the F₂ of 'Kanota' x 342 (22 normal : 56 intermediate : 27 dwarf) and G test indicated a good fit to a 1:2:1 ratio. This result indicates that the major gene is acting in a incomplete dominant manner.

As shown Table 2 the dwarfnesses for fourteen accessions were controlled by the genetic manners involved all the kinds of major genes ,i.e. 7 single dominant genes, 3 single recessive genes, 2 digenic inheritances, a polygenic inheritance and a incomplete dominant gene. However, allelism is not known yet except three recessive genes. Complementation test was carried out to determine allelism of the three recessive genes for dwarfness, which is shown in Table 3. Diallele crosses were made among the 156, 169 and 812 accessions. Only plants from the reciprocal

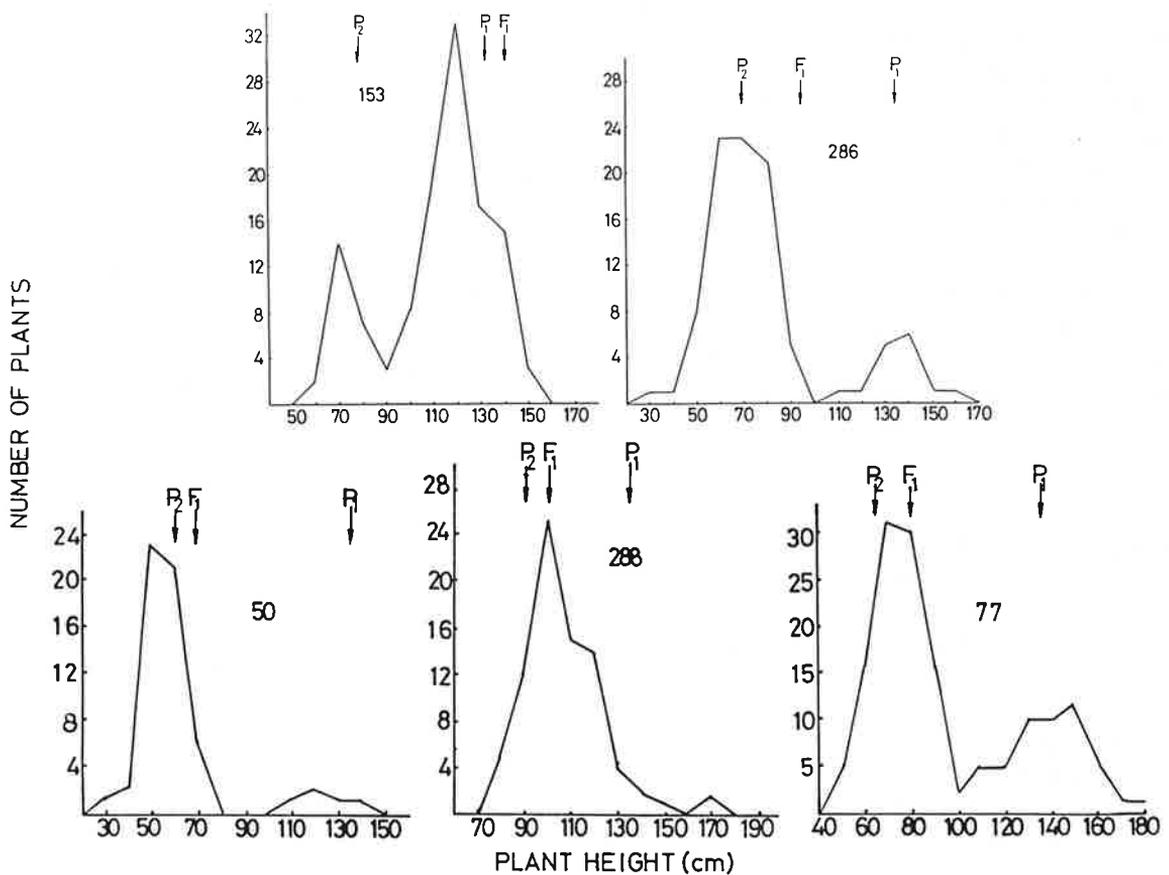


Fig.2. F₂ frequency distributions for plant height in 5 types of dwarf oat crosses with 'Kanota'. Mean height of parents and F₁ hybrids indicated by arrows.

Table 3. Complementation test to determine allelism of three recessive genes for dwarfness in oats

Female	Male		
	153	169	812
153	-	tall	tall
169	tall	-	dwarf
812	tall	dwarf	-

cross 812 x 169 were dwarf. Plants from all the other cross combinations were tall, which means that the dwarfing genes of the 812 and 169 are located at the same locus but that of the 156 is located at a different locus from the others.

According to the list of single-gene dwarfs reported by Pelton(1964), recessive dwarfing gene is much more common in all taxa than dominant one. However, reports of dominance dwarf in oats were quite a few (Simons, et al. 1978). Stanton (1923) reported that dwarfing in progeny of two oat crosses was due to a dominant gene. In natural populations of oats, many dominant dwarf types mostly have been adapting to the crop field in East Asia, which is thought to be the most important gene resources. Furthermore, it is much easier to transfer the dominant dwarfing genes than recessive one from wild oat (*A. fatua*) to cultivated oats. B4F2 generation plants are obtained in the 8 accessions(50,286,70,77,92,151,206 and 811), which have nearly the same genetic background of 'Kanota' in common. Eight homozygous lines have already been extracted from B4F3 generation, which will be useful in plant breeding programs of oats.

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THE HISTORY OF OAT MILLING

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Archaeological evidence indicates that oats were first domesticated as early as the Bronze Age, 1500-500 B.C. It is likely that oats originated in the Mediterranean region and the Near East and were subsequently spread to high altitude and cool climatic regions by nomadic clans. Evidence indicates that the hull-less oats were spread to the east into China and the hulled types moved north into Europe and Scandinavian. These early agriculturalists would plant wheat which was contaminated with weeds such as rye and oats. In certain environments, oats performed better than wheat and were subsequently cultivated for their own merits. Oats were generally used for horse feed. The Greeks are thought to have been the first to recognize the value of oats as a porridge for human food usage.

In Europe, by the Middle Ages, oats were used in rotation with other crops, allowing for an efficient use of the land and providing energy for the horses used to farm the land. By this period, oats were clearly recognized as the best food for horses. French and English soldiers would not eat what had been fed to their horses, however the Germans, Scotch and Irish had eaten oats as a staple for decades. Dr. Johnson defined oats in his famous dictionary as .."being for men in Scotland and for horses in England". This brought forth the Scottish retort that "England is famed for the excellence of her horses, but Scotland is famed for the excellence of her men".

Grain milling is said to be the oldest industry and obviously wheat milling was the progenitor to all other grain milling. Oats were first milled by grinding the grain by hand between two stones. The flour and the meal were then separated from the chaff. The first major advancement in oat milling came with the use of querns which are two round, flat stones about two feet in diameter. The lower stone was held stationery while the upper stone, fitted with a handle, rotated above on a spindle arrangement.

The grain was metered into a hole in the top stone and was milled between the two flat stone surfaces before being directed out to the edges by means of grooves. Again, the chaff was separated from the meal and flour by a winnowing process.

Kilns were introduced during Roman times to dry the grain thus easing the separation of the groats from the hulls. Larger stones were used as time progressed and consequently, animal and mechanical power was employed to turn the stones. The first water mills for oats were developed during the eleventh century. Oat mills proliferated throughout northern Europe, Scandanavia and especially in Ireland and Scotland. As the mills grew in size, the human labor required to lift the raw grain to a level above the mill stones and to relift the ground mixture to a sufficient height for winnowing or sifting became prohibitively laborious. Consequently, the French in the 18th century developed an elevator system to mechanically lift the grain and the milling products, thus providing a major technological advance. The first mill in North America was established in Nova Scotia in the mid 1600's. The first oat mill in the United States was built at Ravenna, Ohio in 1850. Prior to 1875, oat groats were usually ground to meal or flour, or used whole. In 1875, Ferdinand Schumacher developed a groat cutting machine which produced a less slimy porridge preferred by the consumer. In 1881, Schumacher started rolling oats into flakes, which reduced cooking time significantly. Prior to rolling, the oats were steamed to soften them and reduce waste during the flaking process.

Subsequent oat milling improvements were the refinement of the winnowing process of separating the chaff from the meal and flour. Sifting and fanning preceded the development of the gravity table and aspirators.

Cleaning of the grain prior to the milling process was a major enhancement which capitalized on the progress made with the aspirators, gravity tables and cleaning equipment used in the winnowing process. By cleaning and sizing the oats before milling, cleaner finished product and greater mill efficiencies were realized.

The impact dehuller, which was introduced in 1936, effectively replaced the stones in the milling process. By 1963, the first green oat hulling procedures were being used. These procedures do not require the drying of the oats before dehulling. Thus, the term green oats is commonly used. After dehulling and separation, the groats are steamed at 95-100 C for 2-2 1/2 hours to soften the groats, but more importantly to deactivate the lypase enzymes and increase the shelf life of the product.

Instant oats were developed in 1964 simply by using steel cut groats and rolling them very thinly to reduce the effective cooking time. In this era of hurried lifestyles, any time savings in the kitchen are greatly appreciated by the customer. Oat bran was released to the consuming public in 1980 and has subsequently been found to significantly reduce serum cholesterol levels when eaten in conjunction with a low fat diet.

Oat milling has enjoyed a long and illustrious history. The future will surely bring new technological advances which will make the oat milling process more efficient. This will allow the continued development of new and exciting consumer products made from an excellent tasting, healthy, nutritious, high quality grain...oats.

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BREEDING OATS FOR FUTURE USE

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Two major events have rekindled a renewed optimism for the future of oats. The first is that consumers want to return to the consumption of wholesome, whole-grained cereals and this trend has coincided with growing evidence for medical benefits from eating oats and oat products. The second event is not as widely publicized, and will take longer to mature and develop, but may have greater impact on world oat production if successful. It is the development of successful breeding, utilization, storing, grading, marketing and processing programs and procedures for naked oats. The first is important because it equips oats with an advantage based on health which counteracts criticism for lack of food processing functional quality in the grain or flour when comparisons are made with wheats and malting barley. The second event is important because it gives the producer, especially in cool season climates, an opportunity to grow a high energy, good quality protein crop whose grain can substitute for corn and soybeans in feeding animals such as pigs and poultry. It also gives back to the producer the choice of whether to grow oats as a cash crop while satisfying a crop rotation plan, establishing legumes, producing emergency feed or straw, or controlling diseases or weeds. The decline of world oat hectareage over the past 30-40 years has reflected a decline in usefulness of covered-seeded oats. Formerly producers decided on the ingredients in animal diets but now nutritionists, working for feed companies, formulate diets on a "least cost" basis and these diets are used to rear animals in large production units. The oat hull contributes too much crude fibre to diets so covered oats have only been used sparingly, if at all, in diet formulations. This has kept the crop anchored to the farm, reduced its value as a cash crop and gradually decreased the amount of research effort on oat improvement. This result coupled with breeding accomplishments in corn, wheat and barley and entrenchment of corn and soybean meal as the standard of excellence in animal feeding further eroded the case for oat improvement. Fortunately farmers have stubbornly refused to "give up oats" because they still recognize their importance. The genetic removal of the hull thus creates a new crop whose grain energy content is equivalent to corn and this energy is combined with a high quality protein that is in the correct range of concentration for many animal diets. Naked oats are particularly important for "on the farm" feeding because a producer can formulate a diet by adding vitamins and minerals, and possibly some lysine, to naked oats and he has a good diet for pigs and poultry. If enough producers grow naked oats and the production base increases substantially, it could

become the energy and protein grain for cool climates and displace covered-seeded oat hectareage. Food processing companies in Canada (Quaker Oats and Robin Hood Multifoods) have shown interest in naked oats and are now evaluating the variety Tibor (Burrows, 1986a) as a raw material. This interest stems from their dedicated support of oat research and from the fact that oat hulls are now difficult to market and costly to store and transport. Many problems remain in the breeding and commercialization of naked oats but this author believes the resurgence of oats as a feed and food grain is going to be directly tied to the successful development of naked oats.

Naked Oat Breeding

Naked oat breeding has been intermittent over the years and has lacked the long-term committment given to other grains. Many of the old naked varieties possessed low yield, poor straw quality, small seed, low protein content, groat hairiness (trichomes), sprouting susceptibility, and the threshed grain contained a low, but troublesome, percentage of covered seed. Improvements were made, however, and varieties such as Uspek (USSR), Nuprime (France), Rhiannon and Kynon (Wales), Terra and Tibor (Canada), Manu and Caesar (Germany), Coker 82-30 and Pennuda (USA) have been produced and several of these varieties have been used in feeding trials in addition to being grown commercially. Most feeding trials have demonstrated the value of groats used either as a major ingredient, or as the sole source of energy and protein, in grower diets. The mixed linkage B-glucan gum apparently led to reduced intake of feed in very young but not in older animals. Lysine and methionine supplementation may be necessary in some diets to obtain maximum utilization of protein. Improved eating quality (tenderness, juiciness and flavour) has been noted for pork roasts (Friend *et al.*, 1988) and larger egg size was obtained in poultry (Herstad, 1980; Karunajeewa and Tham, 1987; and Cave *et al.*, 1987) when animals were fed diets containing high concentrations of oat groats.

Groat yields will never be high enough to satisfy breeders and producers but raising yields to equal the groat yields of modern covered-seeded varieties, in the same maturity class, have been realized and, in some cases, have been exceeded. In Canada, the variety Tibor (Burrows, 1986) has a tall, strong straw which resists lodging. The seed is large (28-30 mg) and, depending on soil fertility, contains 15-20% protein. Because of the importance of protein and lipid in naked oats, it seems logical to breed new varieties rich in these two components. Fortunately both are, at least in part, under genetic control and genetic stocks are available for breeding. It may not be feasible to raise the globulin percentage in oat protein above that now present in oats (approximately 80%) to improve total lysine content. For some varieties it may be advantageous to raise total protein but there remains the risk of lowering yield potential. For varieties such as Tibor, that are already fairly high in protein, a preferred strategy might be to try to raise lipid levels to make the grain even richer in energy without sacrificing total yield.

Dormancy genes from A. fatua L. have been successfully incorporated into Tibor to prevent pre-harvest sprouting. One selection, PGR 19975 (Plant Gene Resources of Canada Office, Agriculture Canada, Ottawa K1A 0C6) with the parentage 2* Tibor/A. fatua, is quite dormant at harvest time and harvested panicles failed to show sprouting when placed in a rain simulator room for 10 days.

Groat hairiness is a problem because the hairs are liberated into the air at threshing time and each time the grain is handled. They act as respiratory and skin irritants, and their presence on the seed interferes with the easy flow of grain. A search for bald or glabrous parental accessions in the international collection produced two hexaploids (CI 2113 and CI 5558) of which CI 2113 proved to be the best parent for baldness even though it is of poor agronomic type. PGR 8646 and PGR 19976 from the Ottawa breeding program also show promise. None of the accessions are completely free of surface hairs but varieties produced from them may prove to be tolerable to producers. The important point to note here is that genetic variation exists for this trait in hexaploids and advanced germplasm is available at Ottawa.

Covered seed in naked oat grain samples brought about by an incomplete expression of hull-less genes, is a deterrent to food processors because covered seeds must be separated from naked kernels before the groats can be processed. When existing naked-seeded varieties are threshed, approximately 5-10% of the seeds possess a rather tight hull and resemble seeds of A. sativa. The covered seeds are smaller in size than average because they arise at the uppermost positions of each spikelet. There appears to be a gradient within the spikelet in the expression of nakedness with the lower primary and secondary seeds being naked and the tertiary and quaternary florets either being naked or covered in different spikelets of the same panicle. The condition is modified by environmental conditions with cool temperatures during floral differentiation producing a higher percentage of covered seed.

One major (Moule, 1972) and two or three modifier genes (Jenkins and Hanson, 1976) regulate expression of nakedness in A. sativa L. / A. nuda L. hybrids. Nakedness is incompletely dominant and F₁ panicles are structural mosaics. Repeated selection for nakedness in segregating generations has not produced varieties free of covered seeds. One possible solution to this problem became evident at Ottawa when a heavily awned naked line PGR 11980 was selected from a F₅ bulk population derived from a complex hybrid involving parents of diverse origin. It was selected for its novelty and it was hoped that the heavy awns would offer some protection against birds (not proven to date). PGR 11980 was crossed to Tibor and a new improved true breeding awned selection PGR 18877 was isolated. Other studies support the conclusion that PGR 18877 is a naked-seeded fatuoid. The interesting feature is that when hull-less genes combine with the fatuoid complex, the sucker mouth trait is suppressed but there is complete expression of the hull-less genes. The same is true in A. fatua L. / A. nuda L. hybrids where the F₁ is completely naked and non-shattering. PGR 18877 possesses heavy lemma awns on the primary and secondary florets of

each spikelet. Experience has demonstrated that selection within hybrid populations for naked-seeded, awned (both primary and secondary florets) $F_2 - F_4$ plants produces lines whose seed is free of covered seed. *Fatouids* and *A. fatua* may be useful in naked oat breeding programs.

The chevron-type spikelet (Burrows, 1986) offers another means of solving the covered seed problem. In the chevron spikelet (PGR 11621), which may differentiate as many as 12 florets, the uppermost florets usually abort and the lower ranked florets produce naked seed. Seed size is smaller than normal varieties and problems have been experienced in lower floret fertility and shrunken kernels. Both negative traits have been greatly improved in new semi-dwarf, naked-seeded (some awned) hybrid populations and, in a few cases, the yield potential seems to be higher than in normal varieties. The kernels resemble wheat and I am trying to raise the yield potential of oats by combining good tillering capacity and large panicles with spikelets containing many small to average seed size.

It is important to obtain completely naked varieties if cooked whole groats are to be used as a garnish for salads, a rice or potato replacement, an ingredient in soups, or as a stuffing for poultry or fish. Oat groats can now be used successfully for such purposes but covered seeds must be removed before cooking. The toasted nutty flavour of whole grained oats, coupled with their lack of stickiness when cooked, are attractive but the texture of cooked grain is considered by some, but not all, to be too chewy. If food specialists are able to determine if the chewiness is due to the seed coat, the B-glucan gum or to the type of starch that "tightens up" when cooked, then ways could be found to overcome the problem and more healthy oats would reach the dinner table.

The B-glucan content of oats will assume greater importance in the future as evidence mounts for its beneficial effect in human food and its detrimental effect in animal feeds especially for young poultry and pigs. Breeders may wish to breed high B-glucan varieties for human food and low B-glucan varieties for the feed trade providing the required genetic variation can be found in oats. Miller and Fulcher, Plant Research Centre, Agriculture Canada, Ottawa, have established that the cultivar Marion has 5.5 - 6.5% and experimental dormoat (Burrows, 1986b) line OA 516-2 has 3.5 - 4.5% B-glucan in their groats (unpublished data). Food and feed processors may want to identify high and low B-glucan varieties so genetic markers may have to be carefully chosen to satisfy the market place. For example, lemma awns could be chosen to identify naked feed-type varieties and the awnless condition reserved for food-type varieties. Different hull colors could be used to identify the two classes in covered-seeded oats.

It is difficult to predict what new uses will be found for oats and how breeding specifications for new varieties will change. This may be largely determined by scientific innovation in the medical, food

ingredient and food preparation fields as well as in the natural products chemistry field. Dietary fibre is a subject of great interest now and interest will likely continue to grow. Advances in wet processing of oats (US patent 4,435,429) by Burrows *et al.*, 1984) has made it possible to isolate an improved oat bran fraction. Commercial oat bran contains approximately 8% soluble and 8.5% insoluble fibre, whereas, bran from the patented process has been reported (personal communication, D. Paton, Food Research Centre, Agriculture Canada, Ottawa) to contain 19.4% soluble (mainly B-glucan) and 35.6% insoluble fibre. There is also some indication that the quality of the B-glucans extracted from different varieties are of different viscosities indicating possible differences in molecular structure or the degree of degradation caused during extraction.

In spite of the emphasis that has been placed in this report on naked oats, it is not to be interpreted that the author feels that covered oats have outlived their usefulness. On the contrary, covered oats will likely remain in demand especially for milling purposes and in some feeds. However, we must recognize the fact that even though we have had, and still have, excellent covered-seeded varieties, we have witnessed a continual decline in global oat hectareage. Naked oats show the best promise of halting the downward trend and may even reverse the trend. Naked oat breeding should be done within broadly based breeding programs which feature breeding for resistance to major diseases and pests and for specific traits such as dwarfism and semi-dwarfism, winter growth habit, productive forage yields, daylength insensitivity or sensitivity, or good overall agronomic performance.

As an oat breeder it is gratifying to see interest in oats increasing and it is comforting to know that our genetic inventories are rich in unexploited genes and that modern biotechnology is becoming established to create new genetic variation.

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Avena maroccana – a genetic resource used in oat improvement.

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The tetraploid ($2n = 28$) *Avena maroccana* is one among the wild species of *Avena* that is considered to be of great potential value to oat breeding. Not only does it possess wide genetic variability in a number of important characters, but it is also closely related to the hexaploids including the cultivated *Avena sativa*. The A and C genomes of *A. maroccana* is also present in the hexaploid AACCCD complement. Chromosome pairing and genetic recombination is frequent in hybrid material between the two. Interest in this particular species increased when it became clear that it contained very high groat protein content, about 30 %, with a groat size equal to or even larger than that of *A. sativa*. Also its high level of resistance against crown rust disease and good tillering capacity are positive traits of this recently described species.

Interspecific hybridization experiments started in Svalöv in 1980 (Hagberg and Mattsson 1986). The *A. maroccana* accession first used was Cw 525 (received from Paul Rothman, Minn.). In 1985 the author took part in the ECP/GR-IBPGR collecting expedition in the western mediterranean region. The *A. maroccana* populations thus collected in Morocco were increased at Svalöv in 1986 and will hopefully provide a good material for expanding the genetic base of interspecific breeding programs. About 500 genotypes were collected individually from 11 different populations selected to give a representative sample from all typical types of habitats within the limited distribution area of the species. The aim of the evaluation that is now underway is to describe the genetic variability within and between the representative populations of the species. From the evaluation of the IBPGR - ECP/GR material some data on disease resistance, protein content and groat size are presented below.

Among the traits important to Swedish agriculture and oat breeding is resistance against Cereal Cyst nematodes. Resistance was found in all *A. maroccana* populations collected, as is shown in table 1. Only in population M3 was susceptibility a common feature. Resistance reaction varied in the material when it was subjected to crown rust infection, see table 2. Also here population M3 showed susceptibility and in five out of the 11 populations susceptibility was prevalent while M4 showed very good resistance. To evaluate groat protein content and a number of vegetative characters, a randomized complete block trial with 4 replications was sown in 1987. The number of entries was restricted to 10 genotypes from each population. A 12th "population" consisting of the standard hexaploid cultivar "Sang" was added. In each replication each genotype was represented by a single plant. Groat protein content was calculated from Kjeldahl analyses of nitrogen content in dehulled seeds. The distribution of groat protein content

among genotypes is shown in figure 1 with a mean value of 23,0%. The lowest value was 19,8% and the highest 28,0%. The mean groat protein content of the standard variety was 14,5%. Figure 2 shows the relation between protein content and groat size, where the cluster of values at thousand grain weight of 27g and protein content of 14.5% represents the standard cultivar. There seem to be no relation between the two characters. Population means for protein in figure 3 and analysis of variance in table 3 indicate significant differences in protein content between populations.

Hybridization experiments with *A. maroccana* at Svalof started in 1980. The method used was the backcross procedure shown in figure 4 as described by Ladizinsky and Fainstein (1977) and by Thomas et. al. (1978). In comparison to most other diploids and tetraploids, crossing and gene introduction to the hexaploid is readily done because chromosome pairing is regular with high frequency of bivalents with resulting good crossover frequency and genetic recombination. Selection for fertility, cultivated seed type and acceptable plant type began in the BC₁F₂ and BC₂F₂ generation whilst selection for protein and oil content started in BC₁F₄ and BC₂F₄ respectively, using the Near Infrared Reflectance (NIR) method of analysis on flour from seeds. Table 4 shows results from the first replicated yield trial in the program. It was grown in 1987 and bearing in mind that only one backcross has been made, results are interesting. The combination of high protein content and large seed size characteristic of *A. maroccana* has been transferred to *A. sativa* types.

Extreme earliness in ripening is another character that has been transferred from *A. maroccana* to *A. sativa*. Cultivation of oats in the far north of Scandinavia is dependent of this character and now we have been able to expand the variability in the breeding material in this respect.

Figures 5 and 6 describe the distribution of some traits in preliminar trials in the BC₁F₆ and BC₂F₆ generation and in the successive F₇. Plot size is 6,5 m² and the trial has no replications. Selection between the two generations was made with emphasis on both protein content and agronomic characters, while agronomic characters prevailed in previous selection procedures. Population mean for protein was increased relative to the standard cultivar between the two generations. Figure 7 shows the relation between protein and yield in the advanced generation. A weak negative relation seems to be at hand. The negative relation was stronger in a related material with greater variability for protein which was selected for high protein and high oil content. Figure 8 shows the BC-F₆ generation of this material. Low yield and weak straw are, not surprisingly, drawbacks when you go directly for the higher protein levels. However, the ongoing introduction of *Avena maroccana* germplasm into our breeding material including its disease resistance characteristics and the combination of high protein, high oil, and large seed is a promising step in the long term perspective of oat improvement. Accumulation of high quality genes should be possible by intercrossing between

Table 1. Nematode resistance in individual genotypes from 11 *Avena maroccana* populations collected in 1985 in the ECP/GR - IBPGR program. The nematode races used were races 1+2.

Population	resistant	segreat.	susceptible	n
M1	31	7	7	45
M2	13	1		14
M3	13	7	12	32
M4	36	4		40
M5	39	2	1	42
M7	13	6	3	22
M8	21			21
M9	50	3		53
M22	34	3	3	40
M23	39	4		43
M26	48	5	1	54

Table 2. Resistance against crown rust race 331 in individual genotypes from 11 *Avena maroccana* populations collected in 1985 in the ECP/GR - IBPGR program.

Population	resistant	segreat.	susceptible	n
M1	29	11	7	37
M2	1	7	7	15
M3	3	11	21	35
M4	32	1		33
M5	29	6	2	37
M7	12	10	1	23
M8		9	8	17
M9	4	8	30	42
M22	6	12	18	36
M23	20	17	3	40
M26	21	24	4	49

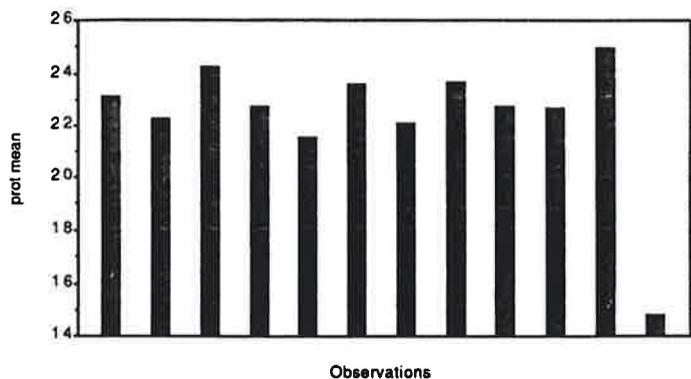


Figure 3. Mean goat protein percentage in 11 *Avena maroccana* populations. The column at the far right represents the standard *A. sativa* cultivar 'Sang'.

Table 3. Analysis of variance table for goat protein content in 10 *Avena maroccana* populations.

Source	df	sum of sq.	mean sq.	F	P
population	9	38.425	4.269	11.70	<0.1%
replication	3	33.890	11.297	30.95	<0.1%
residual	27	9.886	0.365		
total	39	82.181			

L.S.D. = 0.88

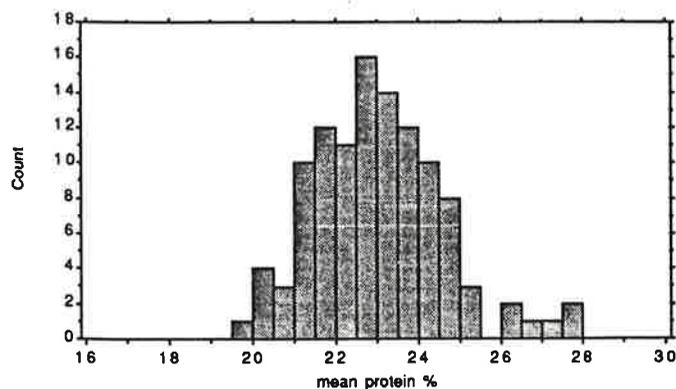


Figure 1. Distribution of goat protein content in 110 *Avena maroccana* genotypes collected in 1985.

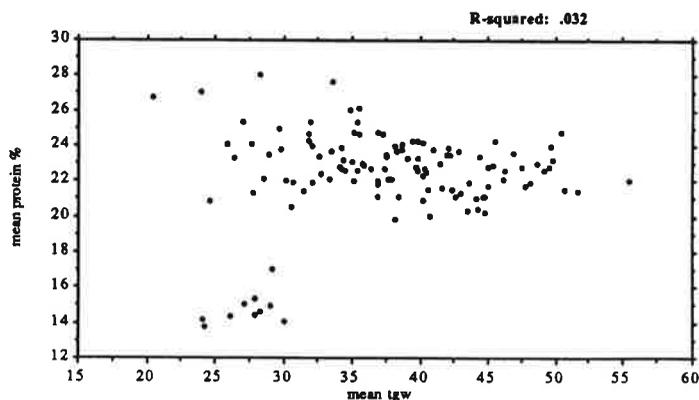


Figure 2. Goat protein content vs. goat size in *Avena maroccana* genotypes. The group of dots at the low left represent the standard *A. sativa* cultivar 'Sang'.

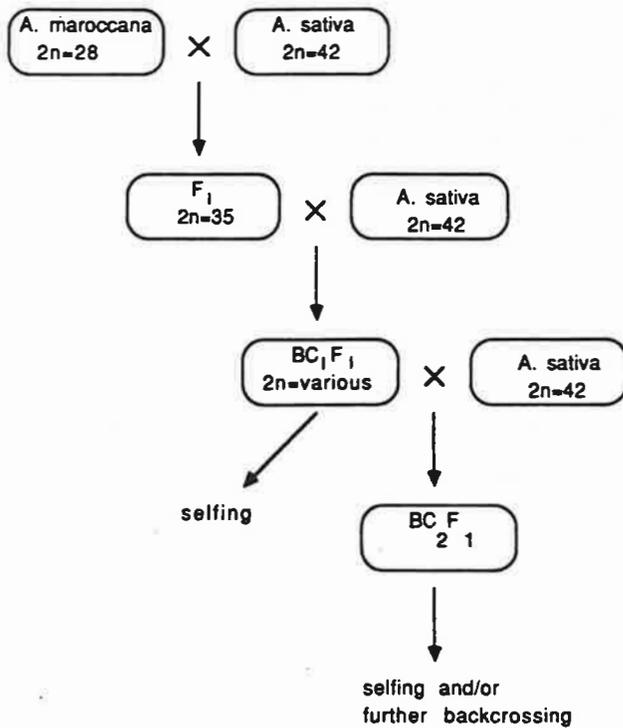


Figure 4. Scheme for gene introduction through backcrossing from *Avena maroccana* into *A. sativa*.

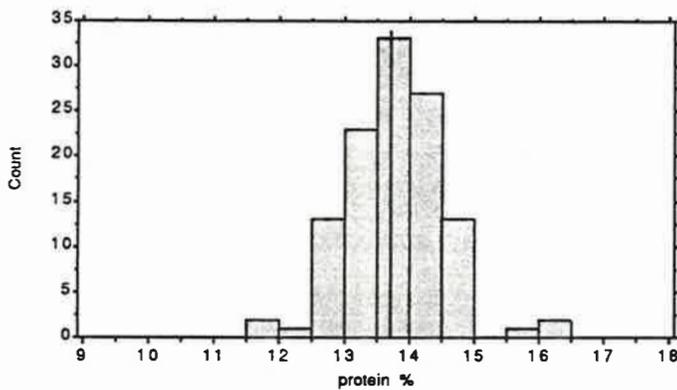


Figure 5. Distribution of grain protein content in BC_1F_6 and BC_2F_6 lines from *A. maroccana* x *A. sativa* crosses selected for good agronomic characters. Population mean = 13,8%. Standard cv Sang mean = 13,7%.

Table 4. Yield trial with BC_1F_8 lines from *Avena maroccana* x *A. sativa*. Plot size: 15 sq m. Number of replications: 4.

Genot. (Cv.)	rel.yield (%)	hlw (kg)	tgw (g)	hull (%)	prot. (%)
Vital	100	54,8	33,75	25,5	11,1
Sv86732	84	50,8	38,0	24,2	11,7
Sv86734	88	53,7	36,5	22,7	11,5
Sv86735	87	53,9	38,0	23,2	11,9
Sang	91	56,1	37,25	22,6	11,7
Sv86736	75	56,1	41,5	21,7	13,1
Sv86737	78	54,1	39,25	22,4	12,5

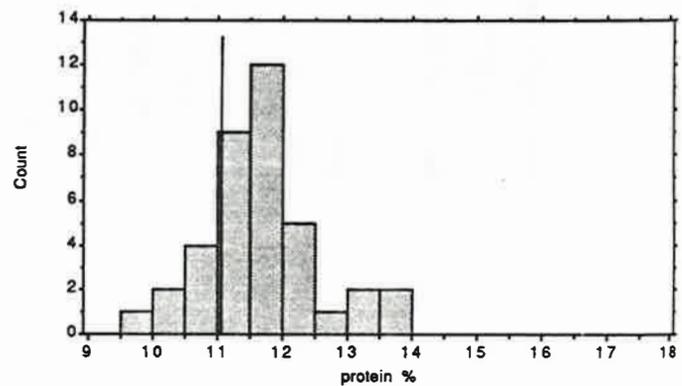


Figure 6. Distribution of grain protein content in selected BC_1F_7 and BC_2F_7 lines from *A. maroccana* x *A. sativa* crosses. Population mean = 11,7%. Standard cv. Sang mean = 11,1%.

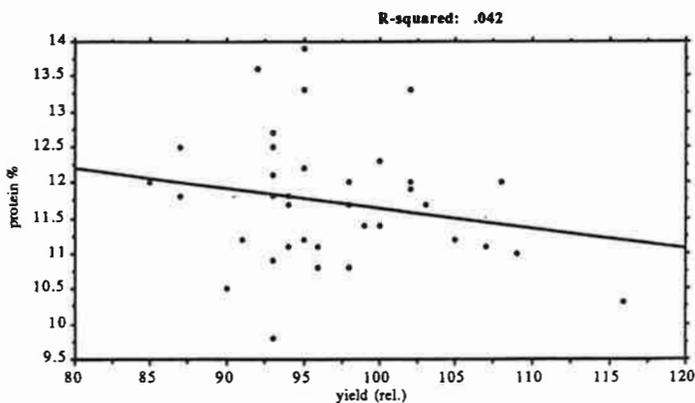


Figure 7. Protein content vs yield in the $BC F_7$ lines in figure 6.

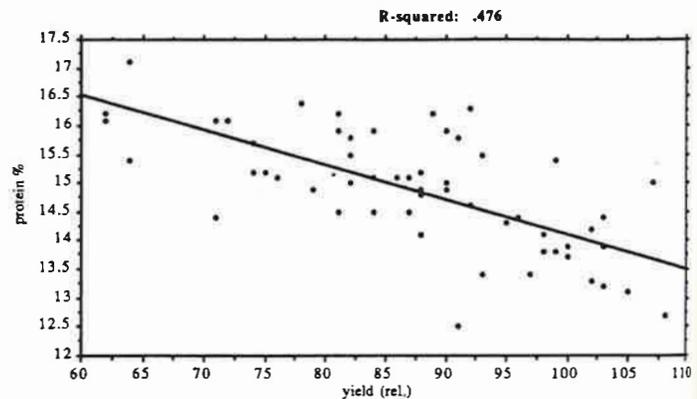


Figure 8. Relation between grain protein content and yield in BCF_6 lines from *A. maroccana* x *A. sativa* combinations selected for wide variability in grain protein content.

breeding lines and additional cycles of backcrossing using selected high quality tetraploid genotypes.

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INTER- AND INTRA-SPECIFIC HYBRIDS INVOLVING THE TETRAPLOID SPECIES
AVENA AGADIRIANA BAUM et FEDAK SP. NOV. ($2n=4x=28$)

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INTRODUCTION

It is generally accepted among oat workers that the cultivated oat Avena sativa L. was derived via hybridisation and chromosome doubling involving a number of steps from the diploids to the tetraploids and finally to the hexaploids. The precise manner in which this progression occurred remains unclear, but the collective data accumulated over the last few years has helped to clarify the picture of the evolution of the genus.

The tetraploid group of Avena is represented by seven taxa whose chromosome number is $2n=4x=28$. These seven taxa can be categorised into groups based on karyotype (where known), morphology and the chromosome pairing of interspecific hybrids. The two main groups are the A.barbata groups which comprises A.barbata, A.abysinica and A.vaviloviana, which share the genomic designation AABB (Rajhathy & Morrison, 1959; Sadasivaiah & Rajhathy, 1968) and the A.maroccana/A.murphyi complex containing the two named taxa which share the genomic designation AACC (Murphy et al., 1968; Rajhathy & Sadasivaiah, 1968; Rajhathy & Sadasivaiah, 1969; Murray et al., 1970; Rajhathy, 1971). The third group contains a single species A.macrostachya which is an autotetraploid perennial oat the genomic constitution of which is unknown.

The fourth group contains the newly described tetraploid species A.agadiriana Baum et Fedak sp. nov., whose genomic constitution is similarly unknown.

From the evidence available, it is clear that the A.barbata group evolved from the A.hirtula/A.wiestii populations of the A.strigosa group of diploid species, and is of near autoploid origin (Ladizinsky, 1973). As Rajhathy & Thomas put it in their 1974 monograph, it is evident from the chromosome pairing of hybrids of this group with the hexaploid A.sativa that these oats did not participate in the evolution of the hexaploid species, but reached their evolutionary climax at the tetraploid level. The A.maroccana/A.murphyi group however, is more closely related to the hexaploids as evidenced by similar morphological attributes and the chromosome pairing of their hybrids (Sadanaga et al., 1968; Ladizinsky, 1971).

Unlike the A.barbata group of tetraploids, no definite progenitor of the A.maroccana/A.murphyi complex has been confirmed. However, the chromosome pairing of triploid hybrids between the available diploid species and A.maroccana led Rajhathy (1971) to propose A.longiglumis as the donor of the A genome of A.maroccana.

Baum et al. (1973) proposed on the basis of morphology (in particular the bidentate lemma tip), the karyotype and geographic distribution, that the diploid species A.canariensis was the probable donor of the A genome of the A.maroccana/A.murphyi tetraploids and hence the hexaploids. Evidence from the hybrids between A.canariensis and A.maroccana (Leggett, 1980) however, did not confirm such a relationship. The only hybrid produced to date between A.maroccana and a C genome diploid (A.eriantha x A.maroccana, Kummer & Miksh, 1977) had such low pairing that the authors suggested that the genomic designation should revert to AAMM as originally designated by Sadanaga et al. (1968).

The dissimilar morphology and lack of chromosome pairing in the A.sativa x A.macrostachya and A.murphyi x A.macrostachya hybrids indicates that only residual homology exists between the chromosomes of these species (Leggett, 1985) suggesting that A.macrostachya was not involved in the formation of the hexaploids species.

The newly described tetraploid species A.agadiriana Baum et Fedak sp. nov., has a very similar morphology to the diploid species A.canariensis and a chromosome count is required to distinguish between them (in fact we collected this species thinking it was A.canariensis). Both A.agadiriana and A.canariensis have a bidentate lemma tip which is a characteristic of the A.sterilis hexaploid species and the tetraploids A.maroccana and A.murphyi. This fact indicated that A.agadiriana may have been involved in the evolution of the hexaploid species.

The remainder of this paper describes the chromosome pairing of some inter- and intra-taxonomic hybrids involving A.agadiriana, and comments on the relationships of the species involved in the hybrids.

MATERIALS AND METHODS

The accessions used in this study were derived from different sources as follows: A.agadiriana Cav7643 and A.canariensis Cav3862 were obtained from Dr Brad Fraleigh, Central Office, Plant Gene Resources of Canada, Ottawa, Ontario, Canada; A.agadiriana accessions M59, M60, M71 and M74, and the A.canariensis accession CS20/24, and the A.atlantica accession M62 were collected by Gideon Ladizinsky, Per Hagberg and the author during a collecting mission sponsored by the International Board For Plant Genetic Resources in the Canary Islands, Spain and Morocco during 1985. The A.barbata accession Cc4897 originated in Algeria, and the A.maroccana was an unclassified accession from Morocco. the A.sativa used in all crosses was the cultivar Sun II. The hybrids were made as indicated in the tables, where the first named accession was the female parent.

In all hybrids, the developing embryos were excised after about 21 days and cultured on Gamborgs B5 medium without 2-4D or kinetin, and incubated at 25°C in the dark until a shoot was established. (This is a procedure I use routinely for interspecific hybrids where the cross compatibility is unknown). The plantlets were then placed in natural daylight at room temperature before being transplanted into soil filled pots in the glasshouse.

For meiotic analysis, immature panicles were taken and fixed in Carnoy's solution (6 ethanol:3 chloroform:1 acetic acid) and anthers at the correct stage were stained in alcoholic hydrochloric acid-carmines according to Snow (1963), and squashed in 45% acetic acid.

RESULTS AND DISCUSSION

Within the A.agadiriana accessions some variation in morphology was observed, particularly in M60 which overall was smaller in all morphological characters, and also in M74 which is larger in most attributes than any of the other accessions. Some variation has also been observed among the M71 population.

I should point out at this juncture that although I have not constructed a full karyotype, I have examined a large number of mitotic cells in addition to the meiotic analyses, and identified three pairs of satellite chromosomes in all but one of the accessions described here. This includes the accession Cav6743 described by Baum & Fedak (1985), who recorded only two pairs of satellite chromosomes. The exception is M74 where I could only resolve two pairs of satellite chromosomes. These differences will be discussed later in relation to the chromosome pairing of the inter- and intra-specific hybrids.

Meiotic metaphase in the four A.agadiriana accessions examined (Table 1) was characterised by the occasional formation of univalents together with a high frequency of rod bivalents, with the exception of M74/25/3 where the formation of rod bivalents was lower. In all these accessions seven bivalents (7II) were formed in at least 81% of pollen mother cells (PMCs).

Two accessions, M71/20 and M59/25 were hybridised with the A.agadiriana accession Cav6743, the latter having been derived from seed obtained from the same accession as the holotype as cited by Baum & Fedak (1985). The chromosome pairing of these two hybrids was similar to the pairing recorded in the parental material, though the frequency of PMCs containing univalents was slightly higher in both hybrids. This indicates that these accessions at least, are A.agadiriana.

Table 1. Mean chromosome pairing of parental accessions and intra specific hybrids of Avena agadiriana

	Mean chromosome pairing per pollen mother cell								
	I	II (ring)	II (rod)	III	IV	V	VI	VII	VIII+
<u>A.agadiriana</u> (M59/25/1/2)	0.43	9.13	-	-	-	-	-	-	-
<u>A.agadiriana</u> (M71/20/5)	0.32	9.46	-	-	-	-	-	-	-
<u>A.agadiriana</u> (M74/25/3)	0.04	12.24	1.74	-	-	-	-	-	-
<u>A.agadiriana</u> (CAV6743)	0.56	8.56	5.16	-	-	-	-	-	-
<u>A.agadiriana</u> x <u>A.agadiriana</u> (M71/29 CAV6743)	1.04	8.60	4.88	-	-	-	-	-	-
<u>A.agadiriana</u> x <u>A.agadiriana</u> (M59/25 CAV6743)	0.60	9.04	4.70	-	-	-	-	-	-
<u>A.agadiriana</u> x <u>A.agadiriana</u> (M74/8 M60/4)	3.56	4.99	6.21	0.37	0.21	0.01	-	-	-
<u>A.agadiriana</u> x <u>A.agadiriana</u> (M74/16 M71/5)	1.90	6.68	5.15	1.33	0.16	-	-	-	-
<u>A.agadiriana</u> x <u>A.agadiriana</u> (M59/20 M71/4)	0.19	11.17	2.73	-	-	-	-	-	-

Of the other intra-specific hybrids, M74/8 x M60/4 and M74/16 x M71/5 showed an increase in the number of univalents and the formation of multivalents, which resulted in a decrease in the number of bivalents formed at first meiotic metaphase. The maximum pairing recorded in the M74/8 x M60/4 hybrid was 12II + 1IV or 10II + 2IV, the minimum was 10I + 9II and the largest configuration observed was a pentavalent. In the M74/16 x M71/5 hybrid, the maximum pairing recorded was 14II or 10II + 2IV, and the minimum was 4I + 12II and the largest configuration was a quadrivalent. The formation of multivalents up to, and including quadrivalents could be due either to the pairing of homologues, or to translocation differences between the accessions. The pentavalent recorded in the former hybrids however, must be due to a chromosome rearrangement. The M59/20 x M71/4 intra-specific hybrid showed very similar metaphase chromosome pairing to the parental M74/25/3 accession, with almost complete and regular bivalent formation. The maximum chromosome pairing observed was 14II and the minimum was 4I + 12II. The largest configuration observed was a bivalent.

From the observations of chromosome pairing in the parental accessions, it is clear that within the genomes of this taxon, there is occasionally partial asynapsis/desynapsis, or lack of homology which leads to the formation of univalents.

Parker (1975) observed a desynaptic mutant of *Hypochoeris radicata* ($2n=8$) where two chromosomes failed to maintain their chiasmata, resulting in two univalents at first meiotic metaphase. He demonstrated that a single recessive gene (ds) was responsible for the desynapsis of chromosome IV and that this gene did not affect any of the other chromosomes in the complement. Such a system might be operative in A.agadiriana giving rise to incomplete synapsis.

Overall then, the chromosome pairing observed in the intra-specific hybrids indicates that although there are differences between some of the accessions, they are closely related.

The A.canariensis x A.agadiriana (M74/7) and A.agadiriana x A.canariensis hybrids both had a high frequency of univalents and multivalents, which resulted in a low frequency of bivalents. The maximum pairing recorded in the

M71/8 x A.canariensis hybrid was 3I + 6III and the minimum was 12I + 3II + 1III, the largest configuration recorded was a decavalent. In the A.canariensis x M74/7 hybrid, the maximum pairing observed was 1I + 6II + 1III + 1V, and the minimum pairing was 10I + 3II + 1V, and the largest configuration was a septavalent (Table 2).

Table 2. Mean chromosome pairing of inter-specific triploid hybrids involving Avena agadiriana

	Mean chromosome pairing per pollen mother cell									
	I	II (ring)	II (rod)	III	IV	V	VI	VII	VIII+	
<u>A.canariensis</u> x <u>A.agadiriana</u> (M74/7)	4.23	0.40	3.53	1.93	0.35	0.16	0.11	0.04	-	
<u>A.agadiriana</u> x <u>A.canariensis</u> (M71/8 CS20/24)	6.63	0.23	2.76	1.87	0.43	0.11	0.05	-	0.02*	
<u>A.atlantica</u> x <u>A.agadiriana</u> (M62 M60/5)	3.80	0.32	3.68	1.96	0.40	0.12	0.08	0.04	0.08**	
<u>A.agadiriana</u> x <u>A.barbata</u> (M71/1 Cc4897)	6.06	0.40	5.04	2.36	0.52	0.20	-	-	-	
<u>A.agadiriana</u> x <u>A.maroccana</u> (M71/8)	19.64	0.01	3.32	0.52	0.01	0.02	-	-	-	
<u>A.sativa</u> x <u>A.agadiriana</u> (Sun II M60)	28.27	-	2.93	0.29	-	-	-	-	-	
<u>A.agadiriana</u> x <u>A.sativa</u> (M74/8 Sun II)	31.52	-	1.68	0.04	-	-	-	-	-	

*Decavalent
**Nanovalent

The triploid hybrid A.atlantica (M62/2) x A.agadiriana (M60/5) also displayed irregular meiotic figures. High frequencies of univalents and multivalents, particularly trivalents were observed. The maximum pairing recorded was 1I + 7II + 2III, and the minimum was 8I + 1II + 2III + 1V. The largest configuration recorded was a pentavalent (Table 2).

The chromosome pairing between the two A.agadiriana x A.canariensis hybrids and the A.atlantica x A.agadiriana hybrid (Table 2) can be considered together since although there is some variation in the frequencies of the various configurations recorded, the overall pattern is similar. It is evident from the bivalent frequency, nearly all of which are rod configurations bearing a single chiasma, that there is some homology between the genomes of the species involved in the respective hybrids. In all three hybrids, trivalent formation could indicate that either homoeologous chromosomes are pairing or that the trivalents are formed due to chromosome rearrangements. Any configuration in excess of a trivalent must be due to the latter. A minimum of three translocations are required to produce the multivalent associations observed in each hybrid, except the decavalent in the A.agadiriana x A.canariensis hybrid involving M71/8 which would require a minimum of four translocations if one assumes that the trivalents arise as a result of the pairing of homologous chromosomes.

The chromosome pairing in the hybrids involving A.canariensis was lower than might have been expected from the similarities in morphology between the two species. This situation however, is not unique within the genus. Ladizinsky (1973) demonstrated that there are at least five chromosome rearrangements between A.prostrata and A.hirtula, which are morphologically similar and are found growing together in mixed stands in the wild.

The chromosome pairing observed in the two tetraploid hybrids was quite distinct. In the A.agadiriana (M71/8) x A.maroccana hybrid, the majority of chromosomes remain unpaired as univalents (Table 2). The maximum pairing recorded was 15I + 5II + 1III and the minimum was 26I + 1II and the largest configuration recorded was a trivalent. The very low pairing in this hybrid indicates that only residual homology between the genomes of the two species remains.

In contrast, the A.agadiriana (M71/1) x A.barbata hybrid has a mean of 6.96 univalents, 5.44 bivalents, 2.36 trivalents, and a low frequency of higher chromosome associations, indicating a much higher degree of homology between the chromosomes of the two species, even though the majority of bivalents formed were rod configurations (Table 2). The maximum pairing recorded in this hybrid was 3I + 5II + 2III + 1IV + 1V and the minimum was 12I + 8II. Once again, the multivalent configurations up to and including quadrivalents could be formed by the pairing of homoeologous chromosomes rather than chromosome rearrangements.

Chromosome pairing in the two pentaploid hybrids A.sativa x A.agadiriana was very limited and not dissimilar to the pairing expected in aneupolyhaploids of A.sativa (Table 2). The maximum pairing recorded was 23I + 6II in the M74/8 x A.sativa hybrid and 22I + 5II + 1III in the A.sativa x M60/11 hybrid. In both these pentaploid hybrids 35I were recorded in several pollen mother cells indicating the complete failure of synapsis. There are two possible explanations for the lack of synapsis: 1) some form of pairing control mechanism is operative thus restricting the number of synaptic events, or 2) the chromosomes of the two species are so dissimilar that only occasionally does synapsis occur between the chromosomes of the two species.

From the evidence available, it seems probable that A.agadiriana has evolved along a similar route to A.barbata and from the chromosome pairing observed in the tetraploid hybrid A.agadiriana x A.maroccana and the two pentaploid hybrids involving A.sativa, it is most improbable that A.agadiriana played any part in the evolution of the hexaploid species of oats.

Finally, the difference in morphology and cytological behaviour of some accessions of A.agadiriana are difficult to explain if they are considered to be taxa of the same species. The greatest differences are between M60 and M74 as demonstrated by the formation of multivalents and univalents in their hybrid, yet when crossed to the hexaploid A.sativa, the chromosome pairing of both hybrids is remarkably similar and quite different to any other tetraploid x hexaploid cross combination. This fact together with the not dissimilar morphology and the similarities of habitat preference and geographic location of wild populations, lend weight to the argument that both accessions belong to the same species.

A plausible explanation for the differences and similarities encountered between these accessions is that one species is currently evolving from the other, or that both are evolving from at least one common parent.

In their work with the wheats, Zohary & Feldman (1962) proposed the concept of polyploid clusters, consisting of one 'pivotal' unaltered genome, which could be traced to a diploid progenitor, and (in the case of tetraploids) a second 'differential' genome which might be derived from intercrosses between the 'original amphidiploids derived from diploid species but sharing the pivotal genome'. If this were the case, then the pivotal genome remains intact, but the differential genome may not be traceable to diploid progenitors as they do not necessarily contain any chromosomes or chromosome segments derived directly from an original diploid parent. If one accepts this credible evolutionary concept, then it provides a further plausible explanation for the chromosomal and morphological differences and or similarities between the various A.agadiriana accessions. It might also be an explanation which can be applied to the chromosome pairing in the hybrids A.agadiriana x A.barbata, A.agadiriana x A.maroccana, and A.agadiriana x A.sativa, as well as the relationships between many other inter-polyploid hybrids.

Further inter- and intra-specific hybrids are needed to test such an hypothesis, and even then it is dubious that any final conclusions can be reached about the differential genome unless a positive progenitor for both genomes can be identified, whence this theory can be dismissed.

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EXPLOITING NEW GERMPLASM IN WINTER OAT BREEDING AT ABERYSTWYTH

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Winter oats account for over half of the UK oat crop. They offer advantages of higher yields, earliness and higher kernel and oil content compared to spring oats. The existence of large areas of winter oats in the UK and France suggest that advantages outweigh disadvantages, such as relatively low winter hardiness and tall straw, in these areas. Moreover, considerable scope exists for the improvement of winter oats for growing within their existing area and for extending their range.

Grain yield

Two recently released varieties, Image and Solva, represent significant advances over previous varieties. In particular, Image (Pendrwm x (Maris Quest/Peniarth), first added to the NIAB Recommended List of Cereal Varieties for 1987, has yielded 7% more than Pennal and 16% more than Peniarth, the most widely grown varieties until this year. Solva ((Pennal x Padarn/Nelson) x Oyster), added to the 1988 List, has yielded 9% more than Pennal and 18% more than Peniarth, with good all-round characteristics. Both Image and Solva serve to illustrate that much of varietal improvement is obtained through inter-crossing the products of previous cycles of breeding.

A third variety, Lustre, contains 25% Cimarron (CI5106). Cimarron, of unknown parentage, originated at Oklahoma as a mass selection of early maturing panicles from a composite of the surviving plants of 30 oat varieties grown in the USDA Uniform Oat Winter Hardiness Nursery grown at Woodward, Oklahoma in 1934-35 (Murphy, 1955). Lustre possesses several interesting characteristics, particularly large grains of high kernel content and resistance or tolerance to barley yellow dwarf virus, (unusual for a European variety) and soil-borne oat mosaic virus (Catherall, Parry and Valentine, 1987; Catherall and Valentine, 1987). These features, but also its deficiencies particularly susceptibility to mildew, almost certainly result from the introduction of Cimarron as a new genetic source. Lustre was added to the NIAB Recommended List for 1987, with a yield 4% more than Pennal and 13% more than Peniarth. The variety's significance may lie less in its short-term commercial value than in its potential for use in further breeding.

Valentine and Middleton, (1986), indicated that the large grain size of 07198CnI/3, a progenitor of Lustre, was associated with lemma non-fluorescence. Segregation for large vs medium grains and lemma non-fluorescence vs fluorescence has now been analysed in two crosses. As Lustre has long grains (Anon, 1987, WPBS unpublished data), grain shape as well as size of well-filled primary grains was used to visually classify progeny for large or medium grains. The presence or absence of fluorescence was categorised using a long-wave (366 nm) UV light source mounted on a dark cabinet. Fluorescence or non-fluorescence is also associated with white or yellow lemmas but is more reliable as immature grains appear yellow (Jones, 1927).

Results are shown in Table 1.

Table 1. Classification of grain size and lemma fluorescence
in F₂ plants from two crosses

	<u>Cross 1</u>			<u>Cross 2</u>		
	Lustre x Solva			78-1Cn3/1 x Lustre		
	Medium	Large	Total	Medium	Large	Total
Fluorescent	116	23	139	94	41	135
Non-fluorescent	26	25	51	20	30	50
Total	142	48	190	114	71	185

Chi-square analysis

Cross 1 3:1 fluorescence = 0.344, P = 0.7-0.5; 3:1 grain size = 0.001, P = 0.98-0.95; 9:3:3:1 joint segregation = 22.01, P < 0.01.

Cross 2 3:1 fluorescence = 0.405, P = 0.7-0.5; 10:6 grain size = 0.010, P = 0.9-8; 30:18:10:6 joint segregation = 3.191, P < 0.01

In each cross, lemma fluorescence/non-fluorescence involved a single segregating gene, either lf-1 or lf-2 (Finkner, *et al.*, 1954, Simons, *et al.*, 1978). In the first cross, Lustre x Solva, results support the hypothesis that variation in grain size is controlled by a major gene or gene block, which in the homozygous recessive state, confers large grains. In the second cross 78-1Cn3/1 (Craig) x Lustre, there was a higher-than-expected proportion of large grains, and the data did not fit a 3:1 ratio. Apart from the possibility that the frequency of large grains has been over-estimated, one possible explanation is the existence of a modifying gene, which when homozygous results in the genotype heterozygous for grain size having large grains. Such modifying genes, in reality, may not be uncommon: their effects not normally being distinguished from the 'blur' of quantitative genetic or environmental variation. Accepting this hypothesis, the data fits the expected 10:6 ratio.

There is a good evidence for grain size and fluorescence/non-fluorescence being linked in both crosses (Table 1). However, the linkage is not close enough for the use of non-fluorescent lemma as a marker gene for indirect selection for large grain size, since using the robust product formula (Mather, 1951), p , the recombination fraction, for the two crosses is 0.30 ± 0.041 and 0.34 ± 0.045 respectively.

Monosomic analyses indicates that the grain size and fluorescent/non-fluorescent genes lie on chromosome IV (H Thomas, personal communication).

That a yield component is simply inherited is perhaps surprising, but is not unique. The semi-dwarf character in wheat conferred by rht alleles increases spikelet fertility.

At the anatomical level, scanning electron-microscopy is being used by B Thomas in the Plant and Cell Biology Department and S Ruffle (Sandwich Student) at WPBS to examine the cause of large grains in Lustre and its derivatives in terms of endosperm cell size and number.

The large grain characteristic may be particularly advantageous in improving grain size in small-grained genetic material which has other useful characteristics. For instance, the winter oat variety S.172, released in 1939 (Griffiths, 1962) and its spring oat derivative Milford released nine years later (Griffiths, 1962), has short stiff straw and compact panicles. Murphy, Petr and Frey, 1958 found that Milford was among the most lodging resistant oats from 5471 accessions examined from the world oat collection. The type of panicle is determined by a single gene, in which the heterozygote of a cross between compact and open panicled types is intermediate; expression of the gene is subject to the action of modifying genes in some crosses and compact panicles are associated with stiff straw (Patterson, *et al.*, 1964). S.172 and Milford therefore share many features with much shorter dwarf lines with compact panicles such as Scotland Club (Patterson *et al.*, 1963) and NC2469-3 (Marshall and Murphy, 1981). Several S.172 (or Milford) type varieties have been produced. S.172 was a parent of Maris Quest, bred in the UK (Jenkins, 1965) and Compact and Walken from Kentucky (Finkner, *et al.*, 1969; Finkner, *et al.*, 1971), while Milford was a parent of Stout and Clintford from the USA (Schafer, *et al.*, 1966) and Mapua (Wright, 1966) and Omihī bred in New Zealand.

Unfortunately, short straw derived from S.172 appears to be accompanied by a reduction in grain yield. This was clearly demonstrated by Lawes, (1968) and Anon, (1970). The advantages of S.172 and Milford generally lie in their resistance to lodging rather than increased yield potential in the absence of lodging.

Table 2. Characteristics of S.172, Lustre and selected hybrid derivative

	Plant height (cms)	1000-grain weight (g)	Grains/ tiller	Tillers/ row	Yield/ row (g)	Total weight/ row (g)	Harvest index
1986							
S.172	117	30.4	64.6	101	200	465	43.3
Lustre	129	43.4	91.2	83	327	618	52.9
81-117Cn2/1(F ₅)	117	37.9	94.4	90	316	622	50.9
S.E.D.	1.9	0.67	5.99	7.2	23.1	40.9	3.20
1987							
S.172	123	32.7	49.5	105	170	422	40.2
Lustre	137	46.8	76.9	62	223	457	48.8
81-117Cn2/1(F ₆)	128	41.6	74.1	72	220	458	48.1
S.E.D	2.4	0.78	2.47	5.9	17.1	34.6	0.86

81-117Cn = S.172 x Lustre

We have examined the yield and other characteristics of S.172 and conventional and reduced height winter oat lines. In 1986 the units of evaluation were single 0.75 m hand-sown drills sown 30 cms apart, while in 1987 four rows were sown and the two central rows harvested. In both years there were two levels of nitrogen but in each case nitrogen and nitrogen x variety interactions were not significant. Line values have accordingly been averaged over nitrogen and blocks.

Table 2 shows that the cause of the reduced yield of S.172 in terms of yield components appears to be small grains and a low number of grains. By crossing S.172 and Lustre, we have been able to isolate a line (81-117Cn2/1) with the compact panicles and short stiff straw of S.172, but with improved grain size and number from Lustre.

Winter hardiness

Major increases in winter hardiness levels are being sought via the introgression of markedly superior germplasm from the USA. In particular, lines from Kentucky and Pennsylvania were identified in the early 1980's as having promising levels of winter hardiness (Finkner, 1981; unpublished reports of the Uniform Winter Hardiness Oat Nursery 1981 and 1982; Valentine and Middleton, 1983; Valentine, Middleton and Jones, 1984; Eagles, Williams and Toler, 1984).

Initial crosses were made in 1980, since when selection has been undertaken in the breeding nursery at Gogerddan and at upland sites for high winter hardiness and good agronomic characteristics, and the best lines crossed with high yielding lines. As well as normal pedigree selection, accelerated pedigree selection (Valentine, 1984), and assessment of random F₃ lines has been used.

Table 3. Winter hardiness and related characters of KY 77-177 and derived material 1988

	Winter hardiness at Tynpynfarch upland site		Crown score	Erectness cms
	Rating	Survival %		
	18.2.88	11.1.88		22.3.88
KY 77-177	6.4	66.9	3.6	14.5
Bulwark	3.8	49.4	1.8	21.2
KY 77-177 x Bulwark	6.4	73.6	2.9	17.1
KY 77-177 x Bulwark	6.0	82.8	3.0	17.4
Peniarth (control)	4.0	50.3	2.5	20.1
S.E.D.	0.49	5.41	0.24	-

Winter hardiness scored 18.2.88 9 = complete survival, no leaf damage
1 = complete kill

Erectness scored 28.3.88

Crowns scored 7 days after freeze treatment (H G Marshall and J Dietz)
4 = 1.9-2.6 cms regrowth, leaves still green but no regrowth of roots
3 = 1.3-1.9 cms of etiolated regrowth, crowns dead after 7 days
2 = 0.6-1.3 cms regrowth, crowns dead after 7 days
1 = only trace regrowth, crowns dead after 7 days

An assessment of progress was made last winter (1987-88). Replicated rows of parents, first and second cycle products and controls were grown at Tynpynfarch. Although the winter was relatively mild in the UK, hard frosts and cold winds in November discriminated between entries, survival between October 1987 and January 1988 ranging from 10.9 to 82.8%. Winter hardiness was also scored on a 1-9 scale on the 18th February 1988. In view of the origin of lines, we also sent the material to Dr H G Marshall in Pennsylvania who tested the material using his crown freezing technique (Marshall and Kolb, 1982). This test has several valuable features, including (1) growing the plants in semi-nutriculture which reduces variability in moisture status; (2) daily fluctuating (rather than constant) hardening temperatures and (3) freezing individual crowns in vials.

Table 4. Winter hardiness and related characters of Pennwin and derived material 1988

	Winter hardiness at Tynpynfarch Upland Site		Crown Score	Erectness
	Rating 18.2.88	Survival % 11.1.88		cms 22.3.88
Pennwin	1.3	10.9	3.4	17.2
Lustre (07198CnI/3/2)	2.8	21.2	3.1	27.0
07198CnI/3 x Pennwin	4.9	59.3	4.3	24.6
Bulwark	3.8	49.4	1.8	21.2
Bulwark x (07198CnI/3/Pennwin)	5.1	80.2	3.4	17.5
Solva	4.1	53.3	1.6	16.9
Solva x (Bulwark x (07198CnI/3/Pennwin))	5.0	78.7	3.0	16.9
" " " "	4.8	81.8	3.0	18.2
" " " "	4.8	75.2	2.1	18.8
" " " "	5.1	81.1	1.3	20.5
Peniarth (control)	4.0	50.3	2.5	20.1
S.E.D.	0.49	5.41	0.24	-

Results are shown in Table 3 and 4. As expected, KY77-177, the main source of winter hardiness from Kentucky, had significantly higher winter hardiness and crown scores than Bulwark, a relatively winter susceptible variety, and Peniarth, representing the best available level of winter hardiness in currently commercial varieties. Moreover, the general level of winter hardiness of KY77-177 has been recovered in the lines from the cross KY77-177 x Bulwark (Table 3).

The picture is less clear for material derived from Pennwin (from Pennsylvania). For some reason, Pennwin appeared winter susceptible last winter. Nevertheless, segregates between 07198CnI/3 (the progenitor of Lustre) and Pennwin, and lines derived from further hybridisation first with Bulwark and then with Solva had higher winter hardiness than Lustre, Bulwark, Solva (parents) or Peniarth (control). Two of the four most introgressed lines (Solva x (Bulwark x 07198CnI/3/Pennwin)) had crown scores lower or not significantly different from Bulwark, Solva or Peniarth, while Lustre had a high crown score. These results fit in with our general experience that

Pennwin is a more difficult source of winter hardiness to utilise, although some derived lines have much better agronomic characteristics than those obtained from KY77-177.

In general there was a positive association between winter hardiness at the Tynpynfarch upland site and prostrate spring growth habit with short leaves at Gogerddan, where there was virtually no kill ($r^2 = 54.8\%$). The association was stronger than that between winter hardiness and crown score ($r^2 = 25.2\%$). An even stronger association was noted when crown scores were entered as a second x variable ($r^2 = 73.9\%$). Two genotypes did not fit this pattern, Pennal (from WPBS), with a lower winter hardiness than suggested by its prostrate habit, and Pennwin, with a higher winter hardiness than suggested by its relatively erect habit. It is not yet known whether the general association is the cause or effect of selection for high winter hardiness and whether it is repeatable in different years, in the face of genotype-environment interactions which as yet we do not understand.

Feeding value

Recent approaches to breeding oats of high nutritional value, including naked oats, have been described by Valentine (1987) who suggested that the feeding value of oats in the UK has been under-estimated. There is a high potential for increasing the yield of energy and protein per unit area drawing on Avena sativa, A. sterilis and A. maroccana germplasm.

Recently a temporary derogation of the germination standard of naked oats to 75% has been granted within the EEC and this should aid the commercialisation of recent winter and spring oat varieties (Kynon and Rhiannon respectively). Two further winter naked oats are presently in National List trials. On the basis of their chemical composition the true value of naked oats has been estimated at £15-17/t above that of wheat and between £16-31/t above barley, depending on whether fed to cattle or pigs respectively (Doyle and Valentine, submitted for publication). In the first instance, their role may be restricted to high-price specialised markets but their real attraction lie in substituting for imported energy and protein. Accordingly we are placing great emphasis in breeding naked (and husked) oats with higher yields of nutrients per unit area.

Conclusions

Very good progress is being made in improving the winter oat crop's 'growability' and 'marketability'. Parallel changes will doubtless be made in spring oats. The challenge lies in combining radical improvements with high yield, resistance to diseases and agronomic characteristics. We are confident that as long as sufficient effort is devoted to the oat crop, the challenge is one that can be met.

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BIOLOGICAL SPECIES AND WILD GENETIC RESOURCES IN AVENA

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One of the aims of taxonomy is to provide a classification which as much as possible expresses the natural relationships among organisms (Davis and Heywood 1973). The species is widely accepted as the basic unit of taxonomy. However, there is no universal definition of this term and the 'species problem' has been a subject of continuous debate and disagreement among scientists. In orthodox classification species delimitation is made according to morphological-geographical criteria. The main disadvantage of the morphological approach is that occasionally different species are fully interfertile with each other and the discontinuous variation between them is simply inherited. In addition, on morphological ground alone it is extremely difficult to separate sibling species from each other. Geneticists, on the other hand, prefer breeding relationships as the main guide line for species delimitation, and consider biological species as a gene pool which is protected by reproductive barriers. The biological species is therefore a more dynamic and evolutionary category compared to the morphological species.

The morphological and biological species are not necessarily mutual exclusive and may even overlap with each other in many cases, because morphology like cytology, ecology and geographic distribution is an attribute of the species gene pool. For greater affinity between the two systems it is useful to apply the nomenclature rules of classical taxonomy also for biological species. When several morphological species are included in the same biological species they can be eliminated or retained as sub species.

Introduction of the biological species concept to taxonomy involves breeding experiments and cytogenetic analysis of the hybrids. This is apparently why it has been applied to a relatively small number of plant's groups, most of them being of economic value. In genera which possess also a crop plants introduction of the biological species concept allows better understanding of the history of the crop plant and the potential genetic resources among its wild relatives.

The genus *Avena* was a subject of taxonomical and genetic studies, particularly in the last 20 years. The first most comprehensive taxonomic treatment of *Avena* was made by Malzew (1930), and a relatively recent monograph was published by Baum (1977). In both treatments the morphological species was adopted even though considerable information has become available on the genetic affinities between some of the morphological species.

The aim of this paper is to present a synthesis between the taxonomical and the genetical information and to apply the biological species concept to *Avena*. It may provide a more natural classification of this economically important genus, and indicate

- 5b. Panicle shattering. (7)
- 6a. Panicle condense; mainly in w. Europe, 2n=14. A.strigosa ssp. strigosa
- 6b. Panicle sparse; mainly in Ethiopia, 2n=28. A.barbata ssp. abyssinica
- 7a. Disarticulation occurs at the basal floret only; 2n=14. A.atlantica
- 7b. Disarticulation occurs at each floret. (8)
- 8a. Callus of the diaspore awl shaped; 2-3 mm long; glumes 25-40 mm long; Panicle usually unilateral; 2n=14. A.longiglumis
- 8b. Callus shorter and round. (9)
- 9a. Stem prostrate; glumes 14-17 mm long; lemma tips 3-5 mm long; 2n=14. A.prostrata
- 9b. Stems erect; glumes 15-30 mm long; lemma tips 3-7 ,occasionally 15 mm long; 2n=14. A.damascena
- 9c. Lemma tips 5-10 mm long; 2n=14. A.strigosa ssp. wiestii-hirtula
- 9d. Lemma tips 2-5 mm long; 2n=28. A.barbata
- 10a. Panicle non shattering; cultivated; 2n=42. A.sativa ssp. sativa
- 10b. Panicle shattering. (11)
- 11a. Disarticulation occurs at each floret; 2n=42. A.sativa ssp. fatua
- 11b. Disarticulation occurs at the basal floret only. (12)
- 12a. Awn inserted at the lower 1/4 of the lemma; 2n=28. A.murphyi
- 12b. Awn inserted at the 1/3-1/2 of the lemma. (13)
- 13a. Spikelet V shaped; 2n=42. A.sativa ssp. sterilis
- 13b. Spikelet widest at the point of awn insertion. (14)
- 14a. Spikelet 20-30 mm long; lemmas extremely hairy; 2n=28. A.magna
- 14b. Spikelet 12-16 mm long; in Canary Islands; 2n=14. A.canariensis
- 14c. Similar to A.canariensis; in Morocco; 2n=28. A.agadiriana

Description, ecology and crossability relation of the biological species

A.macrostachya Bal. ex Coss. et Dur. (2n=28)

Perennial; culms erect and often geniculate, 40-100 cm long. Spikelet (without awns) 20-30 mm long; 3-6 florets, glumes unequal, the lower being about half the length of the upper, 10-25 mm long; all florets disarticulate at maturity; awn inserted at about the upper 1/3 of the lemma; lemmas glabrous with bisubulate tips.

A.macrostachya is found in restricted areas of Mnt. Djurdjura in Algeria, at altitudes of 1500-2000 m, where it is

exposed to severe winter conditions. A. macrostachya has managed to survive the winter in Ottawa, Canada, without any apparent damage to the plants (Baum and Rajhathy, 1976). This species is a cross-pollinating one and set only few seeds upon bagging. Cytogenetically it behaves as an autotetraploid. When ordinary crossing procedures are used, it is cross-incompatible with the annual oats.

A. ventricosa Bal. ex Coss. (2n=14)

Annual; culms erect, 20-60 cm long; panicle flagged or nearly so; spikelets (without awns) 15-25 mm, each spikelet contain two florets; glumes unequal, the lower being about three quarter of the length of the upper one; lemma tips bisubulate; disarticulation occurs at the basal floret only; the callus at the base of the diaspore is shrp, 4-5 mm long.

This wild diploid oat grows in dry habitats on shallow soil which usually form hard crust when dry, but it has been found growing also on calcareous and sandy soils. The habitat is suitable also for A. clauda and the two commonly form mixed populations. It has been reported from Morocco, Algeria, Libya, Saudi Arabia, Iraq and Azerbidjan.

A. ventricosa is cross-compatible only with A. clauda, but the F1 hybrids are sterile because of irregular chromosome pairing at meiosis (Rajhathy and Thomas, 1974). Using embryo culture techniques A. ventricosa can be crossed with the common oat A. sativa, but the hybrids are sterile.

A. clauda Dur. (2n=14)

Annual; culms erect, 20-60 cm long; spikelets (without awms) 15-25 mm; glumes unequal in length, the lower being about one half to one third as long as the upper; lemma tips bisubulate-biaristulate. A. clauda contains two fruiting morphs or sub species, that are considered as separate species in classical taxonomy: in the first type, A. clauda, individual florets serves as dispersal unit, and the second type, A. eriantha Dur. in which all the florets of the spikelet sheds as one unit. The two fruiting types are fully interfertile and the difference in the disarticulation pattern is controlled by a single gene. The two types of A. clauda commonly grow side by side throughout their distributional range. A. clauda is dispersed over a vast geographical area from the Iberian penninsula and the Magreb countries of north Africa to Afghanistan. It usually form small populations and occurs mainly on shallow soil in relatively dry habitats. Occasionally, however, the populations are large and may extend into more fertile habitats.

A. clauda is cross-compatible only with A. ventricosa. With the common oat it can be crossed only by the aid of embryo culture ,but the hybrids are sterile.

A. longiglumis Dur. (2n=14)

Annual; culms 30-150 cm long; panicle equilateral or flagged; spikelets (without awns) 20-35mm; glumes equal in length 25-40 mm long; 2-3 florets which disarticulate individually at maturity; lemma tips biaristulate 6-12 mm long; callus at the base of the diaspore awl-shaped 3-4 mm long.

This species is restricted to sandy and sandy loam soils, mainly along the coastal belt of the Mediterranean sea and adjacent areas. Two interfertile ecological races are known: a mesic, robust type along the coastal belt and a smaller, more delicate type in the deserts bordering the Mediterranean zone.

A. longiglumis is cross-compatible with the diploid species A. prostrata and A. strigosa. The hybrids of the first cross combination are partially fertile but those of the second one are fully sterile. Using embryo culture, A. longiglumis can be hybridized with the common oat but the hybrids are sterile or partially fertile.

A. prostrata Ladizinsky, (2n=14)

Annual; culms prostrate or erect, 10-40 cm long; panicle rather compact, spikelets consist of 2-3 florets, 12-15 mm long; glumes equal in length; lemma tips biaristulate, 3-5 mm long; florets disarticulate individually at maturity.

This species is found in dry habitats on metamorphic bedrock in south-eastern Spain.

A. prostrata belongs to an aggregate of sibling species including A. damascena, A. strigosa and A. barbata, all of which are intercrossed with one another and form highly sterile hybrids. It is cross-compatible also with the diploid A. canariensis, the tetraploids A. magna and A. murphyi and the hexaploid oats but the hybrids are sterile.

A. damascena Raj. et Baum, (2n=14)

Annual; culms erect, 30-90 cm long; spikelets (without awns) 20-26 mm long; glumes equal in length or nearly so, 22-28 mm long; lemma tips biaristulate, 4-6, occasionally 15 mm long; florets disarticulate individually at maturity.

This species was known until recently only from the Syrian desert but apparently grows also in Morocco.

A. damascena is cross-compatible with A. prostrata, A. strigosa and A. barbata but the hybrids are highly sterile.

A. strigosa Schreb. (2n=14)

Includes interfertile cultivated and wild forms that are considered independent species in the taxonomic literature but subspecies rank for the cultivated and the wild forms seem more appropriate.

Annual; culms erect, 50-120 cm long; panicle equilateral or flagged; spikelets consist of 1-3 florets; glumes equal in length or nearly so; lemma tips biaristulate, 5-12 mm long. The panicle

is non shattering in the cultivated forms but the florets disarticulate individually at maturity in the wild types.

Cultivated A. strigosa, ssp. strigosa, is grown mainly in western central Europe and includes also the taxonomic species A. brevis Roth, A. nuda L. and A. hispanica Ard., all of which are interfertile. Among the wild forms of A. strigosa, two main races are distinguished: a mesic robust type, taxonomically known as A. hirtula Lag., and a more delicate, a desert type, A. wiestii Steud., which are fully interfertile. The two taxonomic species considered by Baum (1977): A. lusitanica (Tab. et Mor.) Baum and A. matritensis Baum, apparently belong to the A. strigosa complex as well. The wild members of A. strigosa are dispersed over a vast geographical area from the Iberian peninsula to Afghanistan, and occupy diverse ecological niches and soil types in primary habitats.

A. strigosa can be crossed with most of the Avena species except those having unequal glumes: A. macrostachya, A. ventricosa and A. clauda. It produces partially fertile hybrids only with A. barbata.

A. atlantica Baum et Fedak, (2n=14)

Annual; culms erect, 40-70 cm long; panicle equilateral; glumes equal in length or nearly so, 20-25 mm long; spikelet consist of 2, rarely 3, florets which fall jointly at maturity; lemma tips biaristulate, 3-5mm long.

A. atlantica is a recently described taxon (Baum and Fedak, 1985a). Breeding experiments and cytogenetic analysis of hybrids (Legget, 1987) indicate that this taxon resembles A. strigosa by its crossability relations with other Avena species. Even more significant is the complete chromosome pairing at meiosis in the A. atlantica X A. strigosa hybrids, that may suggests that A. atlantica is another fruiting morph of wild A. strigosa (Leggett, 1987). The final decision regarding the status of A. atlantica as a biological species has to await until more information become available on the fertility of the A. atlantica X A. strigosa hybrids and the genetics of floret separation.

A. barbata Pott ex Link, (2n=28)

This comprises another complex of wild, weedy and cultivated forms which are mutually interfertile. In taxonomical literature they are considered independent species but sub species rank to the cultivated and the wild forms is more appropriate.

Annual; culms erect, 60-150 cm long; panicle equilateral; spikelets (without awns) 20-30 mm long; glumes equal in length or nearly so, 20-30 mm; florets remain intact in the cultivated forms and disarticulate individually at maturity in the wild types; lemma tips biaristulate, 2-5mm long.

The wild form ssp. barbata is dispersed over a vast geographic area, mainly in the Mediterranean basin, and as a weed in other territories where Mediterranean crops are grown. Another

wild form, ssp. yaviloviana (Malz.) Mordv., from Ethiopia is characterized by retaining the lower florets on the panicle for relatively long time after maturity, but this behavior was not observed when the plants were grown elsewhere (Ladizinsky, 1975). A semi cultivated non-shattering type in this complex is ssp. abyssinica Hochst.. Seed non-shattering in this case is controlled by two genes (Ladizinsky, 1975). This oat is restricted to the Ethiopian and Yemaen highlands where it is found exclusively in cereal, mainly barley, fields. The farmers in these regions usually weed out the ssp. abyssinica plants, but may harvest them when the main cereal crop is poor. By the winnowing technique used in Ethiopia, seeds of ssp. abyssinica can not be separated from barley seeds, so they are occasionally sown and consumed as a mixture.

A.barbata is cross-compatible with all the Avena species except those with unequal glumes.

A.canariensis Baum Raj. et Samp. (2n=14)

Annual; culms erect, 20-70 cm long; panicle equilateral; spikelets (without awns) 12-16 mm long; glumes equal in length, or nearly so, 14-17 mm; 2 florets per spikelet, disarticulation occurs at the basal floret only; lemma tips bidentate.

This species is endemic to the Canary Isles; Lanzarote, Fuerteventura, and although rare it is found also in Tenerife. The lemma structure of A.canariensis is similar to that of the hexaploid oats and the tetraploids A.magna, A.murphyi and A.agadiriana with which it is also cross-compatible. A.canariensis is also cross-compatible with the diploids A.strigosa and A.prostrata.

A.agadiriana Baum et Fedak, (2n=28)

Morphologically this taxon is indistinguishable from A.canariensis but is a tetraploid. It was discovered recently in Morocco (Baum and Fedak, 1985b), and independently collected in spring 1985 by oat collecting group supported by the International Board of Plant Genetic Resources.

A.magna Murphy et Terrell, (2n=28)

Annual; culms usually erect, 50-100 cm long; panicle equilateral; spikelets (without awns) 20-30 mm, widest at the point of awn insertion; 2-4 floret per spikelet that are shed as one unit at maturity; glumes equal in length or nearly so, 30-40 mm, lemmas extremely hairy, lemma tips bidentate.

A.magna has been found only in Morocco, and on heavy alluvial soil. The natural habitat of this species is rapidly being converted into farmland and as a result it is under threat of extinction.

Baum (1977) treated this taxon as A.maroccana Gdgr., referring to the type specimen in the herbarium of the Faculty of Science in Lyon, France. Subsequent inquiries about this material

revealed that it is not deposited there and in fact can not be traced. Close inspection of the photograph of the type specimen in Baum's book suggests that it closer to the hexaploid A. sterilis than to A. magna. Further inquiries about the origin of A. maroccana have shown that it was collected by a French botanist, Gandoger, who visited Morocco twice. On his first trip (Gandoger, 1907) he collected three Avena species near Ceuta: A. fatua, A. sterilis and A. longiglumis. On his second trip he visited the Saferinas Islands near Melila, where he discovered A. maroccana (Gandoger, 1908), but referred to Ceuta area as the type locality. In the 1985 survey of the ecological preferences and habitats of A. magna supported by the International Board of Plant Genetic Resources, 12 populations of A. magna were found in the Rommani area, about 80 km south east of Rabat. All were found on heavy alluvial soil. In Ceuta area, on the other hand, no alluvial but sandy and sandy loam soils were found, and no plants of A. magna were found. Thus, on morphological and ecological ground it seems reasonable to reject A. maroccana as the valid name and to retain the name A. magna.

A. magna is exceptionally rich in protein and resistant to rust, and is cross-compatible with most of the Avena species. The meiotic behavior of A. sativa X A. magna hybrids indicates close affinities between the two but can not support A. magna as the tetraploid ancestor of the hexaploid oats.

A. murphyi Ladizinsky, (2n=28)

Annual; culms 50-100 cm long; panicle equilateral; spikelets (without awns) 20-30 mm; 2-4 florets that fall as one unit at maturity; glumes equal in length or nearly so, 30-40 mm; lemma tips bidentate; awn inserted in the lower quarter of the lemma.

This species is found in a restricted area near Tarifa; southern Spain and near Tangier, Morocco. It grows on heavy soil, but the habitat is rapidly coming under cultivation and there is a real threat of extinction of this species.

A. murphyi is cross-compatible with most of the Avena species. Cytogenetically it is more distantly related to the hexaploid oats than is A. magna.

A. sativa L. (2n=42)

This is perhaps the most variable species in the genus Avena, but all types have bidentate lemma tips, share the same chromosome number and are mutually interfertile. It is a complex of wild and weedy forms and cultivated derivatives that have been treated as different species in the taxonomic literature. Under the biological species concept they may be treated as sub species.

The cultivated form ssp. sativa is characterized by non shattering panicles, essentially glabrous lemmas and awns that are rudimentary or absent. The caryopsis is hulled in most of of the ssp. sativa cultivars, but naked types are known and are

characterized by membranous lemmas, relatively long rachillas and 3-4 florets per spikelet.

Among the wild forms of A. sativa two main types can be distinguished: ssp. sterilis, in which all the florets shed as one unit at maturity, and ssp. fatua in which the florets disarticulate individually at maturity. The sterilis taxon is a major component of the annual vegetation in the Mediterranean region and other areas having Mediterranean-like climate. In these regions it is also an aggressive weed in fields and man-made habitats. The fatua taxon is confined mainly to man-made habitats and cultivated fields, in particular in western and central Europe and north America. As a native plant it has been found in a few locations in the Canary Islands.

Wild genetic resources of oats

The rearrangements of of the genus Avena in biological species reflects also the potential wild genetic resources of the cultivated oats. Obviously, the wild forms of A. sativa: ssp. sterilis and ssp. fatua are the most accessible wild material for the breeder since they share the same chromosome number, are fully interfertile with the common oat, ssp. sativa, and are members of its primary gene pool. The contribution of these two taxa to the common oat has been discussed lengthly by Frey (1986). The fatua taxon contributed genes for dormancy, earliness, resistance to seed shattering, and large seed, while ssp. sterilis contributed resistance against crown and stem rust, powdery mildew and barley yellow dwarf, higher content of oil and protein in the groat, and higher biomass and grain yield. Frey's conclusion that ssp. sterilis is a more valuable source of genetic diversity to the common oat than ssp. fatua is compatible with the greater eco-geographic diversity of ssp. sterilis and the effective geographic isolation between this taxon and the common oats that was developed in Europe.

The diploid and the tetraploid wild oats can be hybridized with the common oats directly, or by the aid of embryo culture, but the resultant hybrids are highly or totally sterile. Collectively they can be regarded as the secondary gene pool of the common oat, but gene transfer from them requires special techniques and experimental manipulations which are time consuming.

Irregular chromosome pairing is the main reason for the high sterility of the interspecific hybrids involving the common oats and species of the secondary gene pool. Pentaploid hybrids between the tetraploid species A. magna and A. murphyi, and the common oat can be obtained by common crossing procedure but are self sterile. They may, however, produce a few seeds upon back-crossing with A. sativa pollen (Ladizinsky and Feinstein, 1977, Thomas et al. 1980a). When climatic conditions are favorable, natural back-crossing may occur, and consequently better seed set, by planting these F1 hybrids among plants of A. sativa. This practice may prove

useful also in back-crossing pentaploid hybrids involving A. barbata and A. macrostachya. Doubling of the chromosome number of hybrids between diploid oat species and A. sativa is a common procedure to overcome their sterility, and repeated back-crosses with pollen of the common oat may result the desirable recombinants.

Occasionally barrier to gene flow from species of the secondary gene pool is a result of inadequate chromosome pairing in the interspecific hybrid. Sharma and Forsberg (1977) induced translocation between A. sativa and A. abyssinica chromosomes by irradiation with thermal neutron, that lead to incorporation of gene for crown rust resistance of A. abyssinica in A. sativa. Similar approach was used by Aung et al. (1977) to transfer mildew resistance from A. barbata to A. sativa. A more sophisticated method to overcome poor pairing has been employed by Thomas et al. (1980b). Using the cw 57 A. longiglumis genotype, which promote pairing between homoeologous chromosomes, they transferred a gene for mildew resistance from A. barbata to A. sativa.

Although gene transfer from species of the secondary gene pool is more difficult and time consuming, the merit of this gene pool is diversity which may not exist in the primary gene pool. Some of the examples are most indicative: the highest protein content in the groat is about 20% in the primary gene pool of A. sativa, but 30% and 27% in A. magna and A. murphyi respectively. Winter hardiness has been recorded in the primary gene pool of A. sativa, but A. macrostachya is apparently unique in this regard since it can stand the winter of Ottawa with on obvious damage to the plants.

The present view on genetic resources in oats and other crop plants is derived from crossability relations and availability of methods for gene transfer. Broadening of the genetic resources and shortening the time for gene transfer in oats may be obtained by genetic engineering. The prospects and difficulties with this new technology are obvious. Time will tell us if and how this new technology may offer new diversity and new tools to the breeder.

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POPULATION IMPROVEMENT IN OAT GENE POOLS: GRAIN YIELD

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The concept of population improvement and specifically recurrent selection has been commonly used in cross-pollinated crops for several decades. The basic idea is simple - create a base population, select individuals from it as parents for the next cycle, effect intercrossing among those individuals and repeat the entire process. Because of the anticipated effort required for the intercrossing phase, recurrent selection was not commonly utilized on self pollinated plant species until recently. Now several U.S. programs are using recurrent selection in soybeans, wheat, barley, and oats for several traits including grain yield, disease resistance and various quality components.

Our program was initiated in 1968 with a base population which was created by crossing 12 selected genotypes in all combinations. Our original objective was to produce improved germplasm with higher grain yield potential. We also intended to use these improved plant materials to generate information about genetic variances and combining ability in oats and to learn more about parent-progeny relationships. Finally, assuming that we would be successful in accumulating yield genes and thus increase the genetic potential for grain yield in this material, we wanted to measure how other traits were affected by repeated selection primarily for grain yield. Several other people, including at least one graduate student, have been involved with each cycle of selection.

Our approach, the basic cycle of which is given in Figure 1, requires three years per cycle. Pure line progeny rather than early generation heterozygous individuals are evaluated to take full advantage of any fixable epistatic variance which might be present. Our analysis (8) of the progeny of the base population indicated considerable specific combining ability among pure line progeny suggesting considerable additive x additive genetic variance. To maximize selection efficiency when using hill or microplots for yield evaluation, both among and within cross selection was practiced. Yield testing for parental selection was done in only one environment.

The parental groups from each cycle of selection provide excellent genetic material to ascertain the effectiveness of our selection efforts. In some cases the evaluation has included the parents from every cycle, in others only the original and the most advanced cycle were compared. Usually we have also measured a group of other traits which might be related to yield or agronomic quality to determine the correlated responses for such traits.

The results of several grain yield comparisons are given in Table 1. There was a considerable range in the estimates of gain per cycle of selection, from 1.9% to 11%. As might be expected, the largest values came from evaluations which were most similar to the selection environment, ie, hill plots at St. Paul. Note the values for Pomeranek and Haugerud and contrast them with those from McMullen and from Stuthman. More will be discussed about selection environments later. Of most importance, however, is that all estimates were positive and most would be judged sufficient to warrant the effort needed to execute the

selection program. Further, there is no evidence that the potential for additional gain is any less than that with which we started.

These materials uniquely provide information on the relationship between parental performance per se and progeny performance. Using the information provided in the pedigrees of the parents of each cycle, the percent contribution of each parent to the next cycle can be determined. It is also easy to identify patterns over cycles as well. In table 2 the original 12 parents are divided into several different groups based on their relative grain yield. The frequency with which individual parents appear in the pedigrees of the parents in the next cycle of selection is compared among groups. For example, the six highest yielding original parents constitute about 60% of the pedigrees. Conversely the poorest 6 have contributed the remaining 40%. One parent never advanced to cycle 1 and a second was eliminated before cycle 2. Therefore, the average contribution of each parent in these groups was about 10% regardless of the yield potential of individual parents. The top 1/3 and bottom 1/3 yielding groups are also included. Again the average for both groups is about 10% per parent, since the bottom 1/3 contains one of the non-contributors. Thus, among genotypes with good yield potential, parental performance per se may have limited predictive value of progeny performance.

As indicated earlier we have also measured a number of correlated responses for other important traits. Correlated responses following several successful cycles of recurrent selection primarily for grain yield may be instructive as to changes in either plant morphology or physiology which might produce higher yields. Payne et al (3) and Bregitzer et al (1) measured mainly physiological and morphological traits respectively, in parents from cycles 0 and 3. Payne et al used a growth analysis of multiple hill plots to determine vegetative and grain growth rates as well as partitioning and harvest indices. They found that increases in grain growth rate (measured on a canopy basis) were almost parallel to those for grain yield and phytomass, but vegetative growth rates changed very little (Table 3). Grain growth rate is a composite term which includes all three of the traditional components of yield, number of panicles, number of seeds per panicle, and kernel weight. Of these three, seeds per panicle showed the most increase; however, observations in other environments have shown more increase in another component suggesting an environment specific response because of component compensation.

Days to heading and to physiological maturity were each slightly increased and resulted in a small decrease in the grain filling period (Table 3). Thus, the grain yield increases resulted primarily from increases in growth rate rather than growth duration and specifically grain growth rates rather than vegetative growth rates. Using source-sink terms, it appears necessary to increase sink strength to increase grain yield in this population. Similar results were reported by the Wisconsin program in the most recent Oat Newsletter (1987).

All morphological traits measured ranging from leaf lengths and areas to floret size increased (1). The smallest increase (2.6%) was in floret length while the area of the penultimate leaf (one leaf below the flag) increased 16.5% (Table 4). These larger plant parts resulted in 16% more biomass and 13.5% more grain yield. The somewhat parallel changes in the size of more proximal plant parts are consistent with the concept of allometry and suggest that differential modifications of

individual plant parts may be difficult.

Some of the correlated responses are not in the desired direction. Advanced cycle plants are taller, later, tend to lodge, and may have reduced kernel quality. Radtke and Stuthman (5) attempted to correct the height and maturity increases by employing secondary trait selection. They chose a sib of 9 of the 21 C_3 parents which was either shorter, earlier, or both, and yet similar in grain yield. Stuthman and Haugerud (7) compared progeny from the highest yielding C_3 parents with progeny produced using the sib alternates to measure the effectiveness of the secondary selection. They found only partial correction (greatest success for heading date) which was not sufficient to compensate for the reduced yield gains resulting from using the lower yielding sib as a parent. We are now evaluating the possibility of utilizing genotypes outside of our closed system to effectively correct, or at least, prevent further deterioration in important agronomic traits (4).

Another current effort is comparing C_4 parents with the original parents using row plots at multiple locations. We are interested in changes in lodging and disease resistance and kernel quality as well as any changes in stability of grain yield over a range of environments and plot types. Preliminary results indicate some decrease in yield gains when comparisons are made in row plots rather than hill plots as well as when locations other than the single selection site are included. These decreases have prompted another effort to determine whether early generation bulk progeny grown at two locations would help identify parents that will produce progeny capable of increased yields in a diversity of environments.

In conclusion, recurrent selection for grain yield in oat is an effective breeding procedure to increase the genetic potential for yield in oat. Concurrently some changes in other important agronomic traits have occurred. Secondary trait selection has produced inadequate correction for increases in height and maturity. Genotypes outside the closed system are now being used to produce progeny with better agronomic types. After three cycles of selection all morphological traits measured increased in size. Generally those more proximal to each other had similar increases, which is expected if allometry is operative. A growth analysis of cycle 0 and cycle 3 parents indicated that the increase in grain growth rate (on a canopy basis) was the largest and most important change. This result suggests that the most limiting factor for increased grain yield is grain sink strength. Preliminary results suggest that using hill plot data from one location only to select parents for the next cycle may have reduced effectiveness because of genotype x test environment interaction. Therefore, early generation bulk testing at several locations is also being investigated to help create improved populations which will have high yield potential in different kinds of environments.

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Figure 1. Basic scheme for a cycle of recurrent selection.

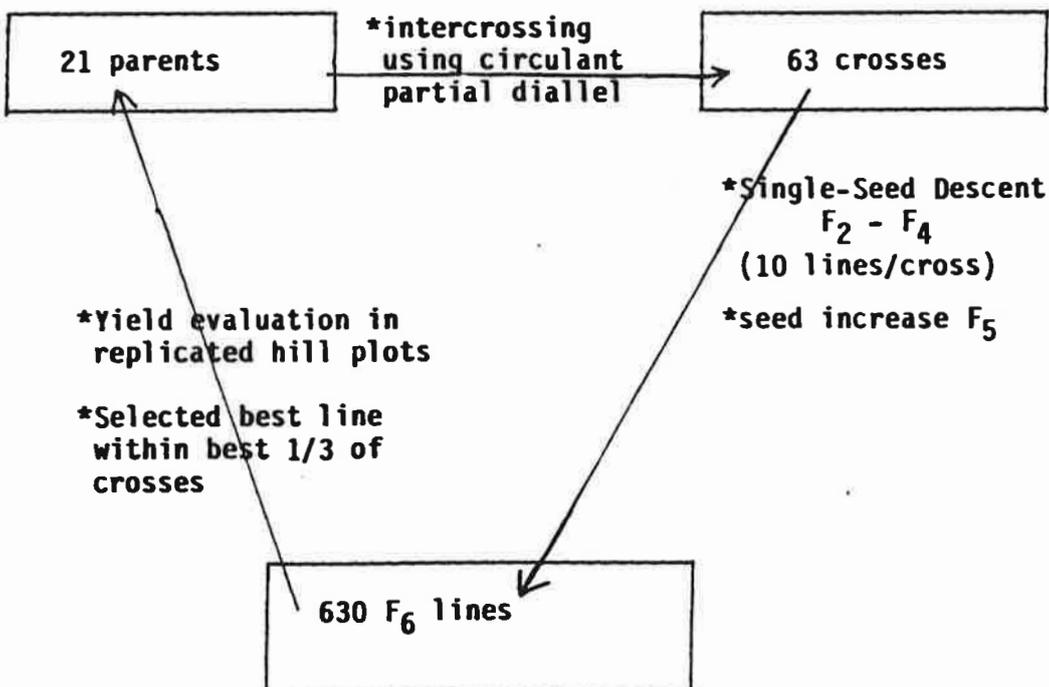


Table 1. Evaluation of grain yield increases from recurrent selection.

Source	% total gain	no. of cycles	Plot type	Location/ Years
Bregitzer (1)*	13.5	3	hills	St. Paul, MN ** Rosemount, MN
Payne (3)	11.5	3	hills	St. Paul, MN **
McMullen (2)	6.5	3	rows	Fargo, ND **
Radtke (5)	15.9	3	hills	Rosemount, MN
Haugerud (7)	28.1	4	hills	St. Paul, MN. Rosemount, MN
Pomeranke (4)	44.0	4	hills	St. Paul, MN
Stuthman (6)	7.5	4	rows	Rosemount, MN Waseca, MN Crookston, MN Brookings, SD

*See references

**Two years

Table 2. Percent contribution to succeeding cycles compared to the grain yield per se of groups of the 12 original parents.

Group	Mean yield	% contribution					
		C ₀	C ₁	C ₂	C ₃	C ₄	C ₅
	g/plot						
Top 1/2(6)	35.7	50	59.6	60.7	61.9	64.9	65.8
Top 1/3(4)	36.3	33	38.2	41.6	38.7	40.2	38.8
Bottom 1/3(4)	32.3	33	30.9	29.8	30.4	28.6	27.5

Table 3. Summary of correlated responses from the growth rate analysis measured in cycle 3*.

Traits	increase		no change or decrease
	>10%	<10%	
Vegetative growth rate			x
Grain growth rate	x		
Days to heading			x
Days to physiological maturity		x	
Grain filling period			x
Harvest index			x
Partition factor		x	
Grain yield	x		
Phytomass	x		

*Payne et al (3)

Table 4. Summary of correlated responses of morphological traits measured in cycle 3*.

Traits	increase	
	>10%	<10%
Flag leaf length		x
Flag leaf area		x
Penultimate leaf length		x
Penultimate leaf area	x	
Panicle width		x
Panicle length	x	
Panicle area	x	
Floret length		x
Photosynthetic area of flag leaf and panicle	x	
Grain yield	x	
Phytomass	x	

*Bregitzer et. al. (1)

RECURRENT SELECTION FOR IMPROVING GROAT-PROTEIN YIELD,
GROAT-OIL PERCENTAGE, AND TEST WEIGHT OF OATS

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INTRODUCTION

The pedigree breeding method has been used almost exclusively for developing oat (*Avena sativa* L.) cultivars. Even though this method has been used successfully, recurrent selection is the method of choice for exploiting and improving breeding populations constructed with genes from many sources. Recurrent selection is designed to concentrate favorable alleles for a selected trait(s) in the breeding population while maintaining genetic variability.

Despite its theoretical advantages (Bailey and Comstock, 1976), the adoption of recurrent selection for breeding autogamous crop species has been slow. Acceptance has been slow because of difficulty (a) in obtaining adequate numbers of hybrid seeds from crossing among selected lines and (b) in producing sufficient quantities of seed to evaluate progenies in replicated field trials. Recently, a recurrent selection plan that eliminates these problems was developed at Iowa State University (Frey et al., 1988). This plan, which is outlined in Figure 1, permits completion of one cycle of $S_{0.1}$ line recurrent selection in 1 year.

Figure 1. Diagram of stages and timing for completion of one cycle of $S_{0.1}$ line recurrent selection with oats in one year (adapted from Frey et al., 1988).

Year and month	Stage of recurrent selection
Year 1, April - July	Evaluation of $S_{0.1}$ lines in C0 (field)
Year 1, August	Selection of elite $S_{0.1}$ lines as C1 parents
Year 1, September - November	Intermating among C1 parents (greenhouse)
Year 1, December - March	Growout of C1 S_0 plants (greenhouse)
Year 2, April - July	Evaluation of $S_{0.1}$ lines in C1 (field)
	ETC.

It makes use of the approach method of crossing (McDaniel et al., 1967; Brown 1980), hill plots for evaluation experiments (Frey, 1965), and specific control of the environment in the greenhouse.

This paper will present results from the use of recurrent selection to increase (a) goat-protein yield, (b) goat-oil content, and (c) test weight of oats. Comprehensive reports on these studies are given in dissertations and a thesis by McFerson (1987), Branson (1987), and Smith (1988), respectively.

MATERIALS AND METHODS

Materials

The genetic materials used to initiate the CO breeding populations of oats were:

1. Groat-protein yield (McFerson, 1987)--
 - a. The high groat yield (HG) line of descent was initiated by intermating 5 $S_{1.4}$ lines with high protein yield due to high groat yield.
 - b. The high protein (HP) line of descent was initiated by intermating 5 $S_{1.4}$ lines with high protein yield due to a combination of high groat yield and high groat-protein percentage.
 - c. The high groat protein yield (HGP) line of descent was initiated from intermating the 10 $S_{1.4}$ lines used in a and b.
2. Groat-oil percentage (Branson, 1987)--The population used to initiate the groat-oil study was obtained via nobelizing selection in a gene pool derived from intermating among hybrids of the type Avena sativa(A) x A. sterilis 2 x A. sativa(B)² where A. sativa(A) and A. sterilis had high groat-oil content and A. sativa(B) had good agronomic traits. The numbers of lines included in these three parental types were 8, 8, and 13, respectively.
3. Test weight (Smith, 1988)--The CO consisted of $S_{0.1}$ lines from double-cross matings among single crosses of the type A. sativa(C) x A. sativa(D), where A. sativa(C) had high test weight and A. sativa(D) had high grain yield. The number of parents in each category was 11.

Field Evaluation

The field evaluations for the groat-protein yield and test weight lines of descent were conducted in randomized complete block designs with two replications at each of three sites. A plot was a hill sown with 20 seeds, and hills were spaced 30.5 cm apart in perpendicular directions. Approximately 300 $S_{0.1}$ lines were evaluated for each line of descent in each cycle. A number of traits were measured on each plot, but only traits pertinent to evaluating success of recurrent selection will be presented herein.

Phenotypic recurrent selection was used for the groat-oil percentage study. For this study, only two growth cycles were used per year; i.e., crossing in the greenhouse and evaluation of S_0 plant in the field. Approximately 4000 S_0 seeds were space-sown in the field for each cycle, and seed lots from ca. 1000 S_0 plants were analyzed for oil percentage.

All field experiments were hand weeded, and the plants were sprayed at anthesis with a systemic fungicide, Bayleton, to preclude foliar fungal diseases. Recommended cultural practices for high oat yields were used at all test sites.

Parental Selection and Intermating

Selection of parental lines was done as follows:

1. Groat-protein yield is the product of groat yield and groat-protein percentage. Groat yield (grain yield x groat percentage) and groat-protein percentages were obtained for bulk seed lots from the two plots of an $S_{0.1}$ line grown at one site, and they were used to compute groat-protein yield. Means of lines across testing sites were used for selection.
 - a. The 50 lines in a cycle of the HG line of descent with highest

groat-protein yields were analyzed to determine what contributions groat yield and groat-protein percentage had made to their groat-protein yields. The 20 lines with the highest groat-protein yield due entirely to high groat yield were chosen as parents for the next cycle.

- b. The 50 lines in a cycle of the HP line of descent with highest groat-protein yields were analyzed as in plan a. The 20 lines with highest groat-protein yield due to both high groat yield and high groat-protein percentage were chosen as parents for the next cycle.
 - c. The 20 lines in a cycle of the HGP line of descent with highest groat-protein yield were chosen as parents for the next cycle.
2. Test weight was measured on a bulk seed lot of the two plots of a line at one site, and grain yield was measured on each plot.
 - a. For the high test weight (HT) line of descent, the 20 $S_{0.1}$ lines with heaviest mean test weight were chosen as parents for the next cycle.
 - b. For the high test weight-high grain yield (HTG) line of descent, the 20 lines with highest index values were chosen as parents for the next cycle. The index values were computed from test weight and grain yield data, with each trait being given 50% weight in the index.
 3. Of the 1000 plants evaluated for groat-oil percentage, 100 progenies with highest percentage were chosen as parents for the next cycle.

For each trait-line of descent combination, a restriction was placed on the actual lines selected as parents so that the means of a group of parental lines for date of heading and plant height could not be greater than the respective means for the cycle population. This restriction was applied to preclude lines of descent from becoming later and/or taller due to random drift or correlated response to selection. The restriction usually reduced the selection differential for the primary trait. Insofar as possible, a group of parental lines never included full sibs.

Intermating among parent lines in a line of descent was done in a systemic design of chain crossing with the restriction that disruptive mating (Frey, 1988) was done for heading date and plant height. In the lines of descent for groat-protein yield and test weight, each parent line was used as a male crossed to five lines as females, which gave 100 matings, and three full sib $S_{0.1}$ lines were evaluated per mating. Each of the 100 parents in the groat-oil percentage line of descent was used once as a male and once as a female to give 100 matings, and ca. 40 S_0 seeds were field sown per mating. For each cycle of each line of descent, the population of lines or plants evaluated had equal contributions of alleles from all parents.

Experiments for Measuring Progress from Selection

For the groat-protein yield and groat-oil percentage studies, four cycles, C0, C1, C2, and C3, were available for evaluation of progress from selection. For each line of descent in the groat-protein yield study, an experiment that included 30 random lines from each of the C0, C1, and C2 and 300 lines from C3, was conducted with two replicates at each of three sites; groat-protein yield was measured on a site basis for each entry. For the groat-oil percentage

study, a similar experiment was conducted with 100 random lines from each of the C0, C1, C2, and C3, and goat-oil percentage was measured on a site basis.

For the test weight study, the experiment to evaluate progress from selection included only C0 and C1 for each line of descent, and each cycle-line of descent combination was represented by ca. 300 oat lines. The experiment had two replications at each of three sites, and test weight was measured on a site basis for each entry.

RESULTS

Goat Protein Yield

McFerson (1987) found that the C0 means for goat-protein yield were similar for HP and HGP and significantly greater than the C0 mean for HG. The C3 means, however, were all significantly different from one another. The rates of gain in goat-protein yield were 21 kg ha⁻¹ per cycle in HG and HGP and 27 kg ha⁻¹ in HP, but all rates of gain were similar (Table 1).

Table 1. Means for goat-protein yield in C0, C1, C2, and C3 for three lines of descent of oats selected for high goat-protein yield (adapted from McFerson, 1987).

Cycle	Line of descent*		
	HG	HP	HGP
	----- (kg ha ⁻¹) -----		
C0	448	492	484
C1	450	500	460
C2	480	555	500
C3	507	569	542
LSD	5	7	3
b	21	27	21

*HG, HP, and HGP are high goat yield, high protein percentage, and high goat protein yield lines of descent, respectively.

These gains translate into 4.6, 5.5, and 4.3% per cycle. Payne et al. (1986) reported a gain of 3.8% per cycle for grain yield of oats and Radtke, (1981) obtained nearly 3.0% gain per cycle. Gouk et al. (1986) increased fruit yield of peanuts (*Arachys hypogoea* L.) by 5.7% per cycle, and for soybeans (*Glycine max* L.), Kenworthy and Brim (1979) and Sumaro and Fehr (1982) obtained increases of 4.0% and 2.1% per cycle, respectively. In general, the rates of gain that McFerson (1987) found for goat-protein yield were as great or greater than those obtained for grain or seed yield in other recurrent selection studies with autogamous crop species when computed on a per-cycle basis. However, when computed on a per year basis, the McFerson (1987) gains were from two to four times greater.

In each line of descent, McFerson (1987) found that the oat lines with highest groat protein yield in C3 generations were from 40 to 80 kg ha⁻¹ greater than were the highest lines in the C0 generations. Genotypic variation for groat-protein yield was not reduced from C0 to C3 in the HG and HGP lines of descent, but in HP it was reduced to 50%.

Groat-Oil Percentage

In the study done by Branson (1987), groat-oil percentage was increased 0.9% ± 0.1% per cycle. The increase in mean oil content from C0 to C3 was 2.8% of groat weight. The cumulative increase over the C0 percentage was one-third after three cycles of selection (Table 2).

Table 2. Means for groat-oil percentage and grain yield in the C0, C1, C2, and C3 of a line of descent of oats selected for high groat-oil percentage (adapted from Branson, 1987).

Cycle	Groat-oil (%)	Grain yield (Mg ha ²)
C0	8.5	3.01
C1	9.9	3.06
C2	10.6	3.18
C3	11.3	3.04
LSD (0.05)	0.3	ns
b	0.9	0

The genotypic variance for groat-oil percentage was reduced 30% from C0 to C3, but the reduction was not significant. Realized heritability for groat-oil percentage was 0.68 (Branson, 1987). Recurrent selection, in theory, should increase the population mean and produce individual lines with even greater performance. Branson (1987) found that, after three generations of recurrent selection, the frequency distributions of oat lines showed little overlap. The highest line in C0 had ca. 11.0% groat-oil, whereas in C3, it had ca. 14%. Of especial interest to Branson (1987) was that grain yield did not change over the three cycles of recurrent selection for higher groat-oil percentage.

Test Weight

Smith (1988) found that selecting oats for either test weight solely (HT) or an index (HTG) that included both test weight and grain yield increased test weight significantly (Table 3).

Table 3. Means for test weight and grain yield in C0 and C1 for two lines of descent of oats selected for high test weight or a selection index (adapted from Smith, 1988).

Line of descent	Cycle	Test weight	Grain yield
		kg m ⁻³	kg ha ⁻¹
HT	C0	412	2940
	C1	426	3440
HTG	C1	422	3540
LSD (0.05)		10	10

The increases were 14 and 10 kg m⁻³, respectively, which represents gains of 3.4 and 2.4% per cycle of recurrent selection. The highest C1 lines were 20 and 10 kg m⁻³ greater in test weight than the highest C0 lines for the HT and HTG lines of descent, respectively.

The increases that Smith (1988) found for grain yield were 500 and 600 kg ha⁻¹ in the HT and HTG lines of descent, respectively. These gains, which represent 17 and 20%, respectively, of the C0 mean were not expected. The phenotypic correlations between test weight and grain yield ranged from 0.35 to 0.43 and all were highly significant.

The genotypic variances for test weight and grain yield were unchanged by one cycle of selection. Therefore, continued progress from selection is expected for both traits.

CONCLUSIONS

In the Iowa studies conducted by McFerson (1987), Branson (1987), and Smith (1988) on oats, recurrent selection was found to be an effective method for increasing breeding population means and the performance of individual lines. The traits improved were groat-oil percentage, test weight, and groat-protein yield, all of which are quantitatively inherited, and with heritabilities of 0.90, 0.67, and 0.50, respectively. Rates of gain per cycle for these traits were ca. 11, 3, and 5% per cycle, respectively. These results corroborate findings previously reported for soybeans, peanuts, and oats, but what is unusual about the Iowa results is that the gains per cycle also represent gains per year. Most studies on recurrent selection require from 2 to 4 years to complete a cycle, whereas the Iowa studies completed one cycle per year (Frey et al., 1988).

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BIOTECHNOLOGY APPLICATIONS IN OAT BREEDING IN THE U.S.

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Techniques for genetic analyses and manipulations at the cellular and molecular levels represent biotechnological tools now becoming available to plant improvement programs. These tools are valuable both for understanding gene structure, function, regulation and for allowing specific gene transfer and selection. In this paper we describe two recent studies in oats, one involving tissue culture and one molecular genetics, and list several others to illustrate how techniques in these two major areas of plant biotechnology are being developed for oat improvement in the U.S.

Tissue culture approaches. The study to be described to illustrate tissue culture approaches in oat improvement research is an attempt made in our laboratory to promote stable integration of alien genetic material by passage of interspecific oat lines through tissue culture. In 1976 the regeneration of plants from tissue culture in cultivated oats (*Avena sativa*) was first reported from the University of Minnesota (Cummings et al., 1976). Even in this initial work cytogenetic abnormalities were noted in several of the recovered plants. In an extensive follow-up study, McCoy et al. (1982) documented a high frequency occurrence of chromosome breakage in oat tissue cultures with detectable interchanges present in about 6% and partial chromosome loss present in about 22% of 803 regenerated plants meiotically analyzed. The frequency of the recovered cytogenetic aberrancies due to chromosomal breakage was influenced by oat genotype and by length of time in culture before plant regeneration. A hypothesis for a role of late replication of heterochromatic DNA as a cause of this frequent chromosome breakage was proposed (McCoy et al., 1982) and evidence supporting this hypothesis has been obtained (Johnson et al., 1987). Utility of this high frequency chromosome breakage induced by tissue culture was suggested by McCoy et al. (1982) in that it might provide an alternative to radiation or special genetic mechanisms for promoting interspecific recombination or translocations in interspecific oat hybrids. To test the feasibility and potential efficiency of such an approach for facilitating introgression of alien genetic material, the following study was made (Bullock, 1986).

A monosomic alien substitution (MAS) line ($2n = 40 + 1 + 1'$) containing a pollen non-transmitting gene for crown rust (*Puccinia coronata* Cda.f.sp. *avenae*) resistance carried on a substituted *A. strigosa* chromosome was obtained from Dr. R. Forsberg, University of Wisconsin. Sharma and Forsberg (1977) had previously identified, among 47 MAS lines subjected to ionizing radiation, two lines with a high frequency of pollen transmission of the rust resistance trait. They interpreted the conversion from pollen non-transmission to transmission of the rust resistance gene as being the result of a radiation-induced translocation. The initial objective of Bullock's study was then to try to obtain similar translocations via passage of a non-transmitting MAS line through tissue culture. The proposed scheme is illustrated in Fig. 1. In this scheme, if there is no pollen transmission of the dominant resistance gene, then progeny of selfed plants should segregate at a ratio of approximately 1 resistant:1 susceptible (1R:1S) and all resistant plants will be heterozygous. If there were conversion via a translocation to full pollen transmission of the resistance gene, then progeny of selfed plants should segregate at a ratio of 3R:1S and one-third of the resistant progeny should be homozygous and breed true for rust resistance.

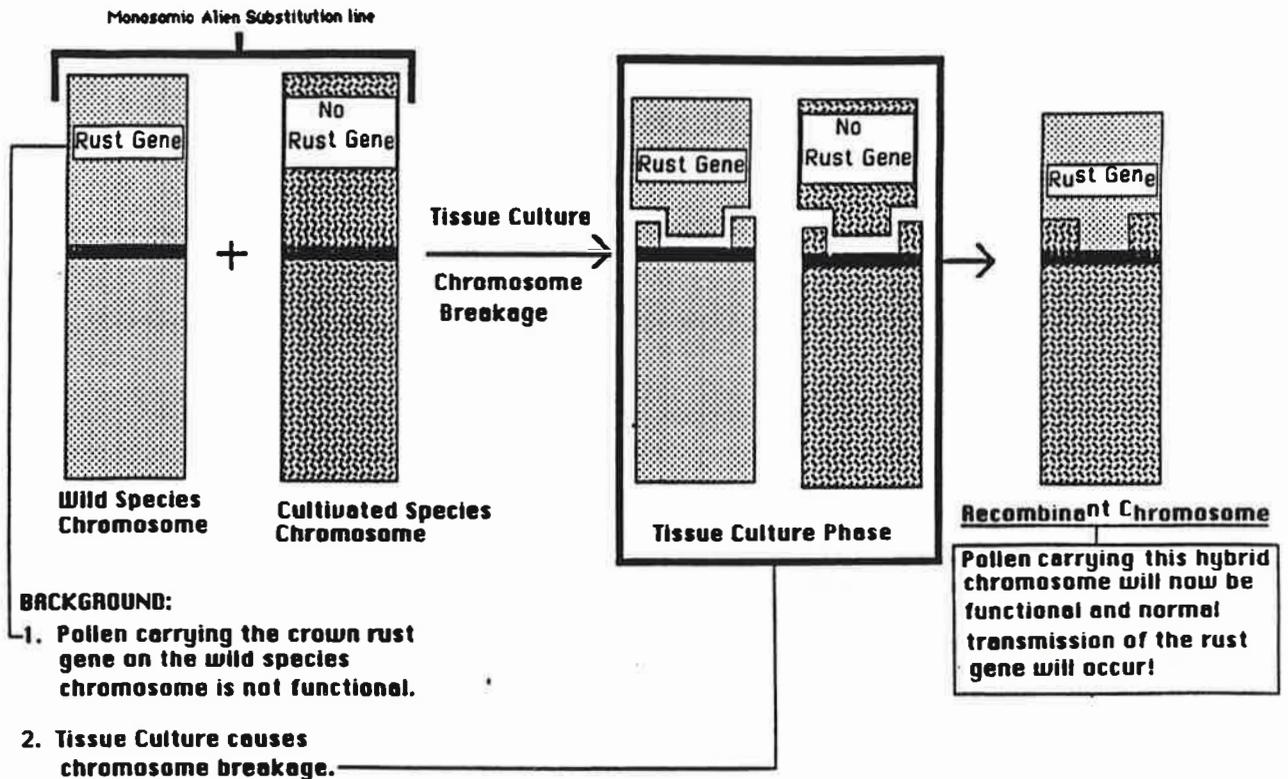


Fig. 1 Proposed scheme for inducing translocations through tissue culture to transfer an alien chromosome segment with a gene for crown rust resistance onto a pollen-transmitting cultivated oat chromosome.

In the study, 345 progeny populations derived from plants regenerated from tissue cultures initiated from verified MAS lines were tested for deviations from the expected 1R:1S pattern of transmission of crown rust resistance. The rust tests were conducted in the greenhouse on progeny population sizes of 20 or more seedlings per population using crown rust race 264B. The parent plants had been regenerated over a range of culture ages from 4 months to 40 months following culture initiation. In most cases the proportions of resistant progeny did not exceed that expected for 1R:1S segregation pattern; however, one progeny population of 47 seedlings contained 82% resistant seedlings. This ratio may have been reflective of a 3R:1S pattern, as would be expected in a progeny population from a plant with the desired translocation. Unfortunately, no plants were rescued from the population to test this possibility. In addition to this putative translocation population, six progeny populations among the 345 tested contained no resistant progeny. In these situations, progenies from sister plants from the same tissue culture lines still segregated in the expected 1R:1S ratio. The apparent loss of the resistance gene during the tissue culture period for these six regenerated plants might have resulted from either gene mutation, or perhaps more likely, chromosome breakage and loss of the chromosome segment carrying the resistance gene. Because of the inherent highly aberrant meiotic behavior of the MAS lines, even in the absence of radiation treatment or tissue culture, Bullock (1986) concluded that it would be difficult to verify in this system that any observed changes in rust resistance transmission frequencies were indeed caused by either radiation or tissue culture.

The approach, and to a degree the outcome, of our study was similar to an earlier reported attempt at the Welsh Plant Breeding Station to use tissue culture to integrate into the A. sativa genome a gene for resistance to powdery mildew (Erysiphe graminis f. sp. avenae) from a pair of A. prostrata chromosomes carried in a disomic addition line (King et al., 1986). Passage of the addition lines through tissue culture failed to produce the desired translocation in the 21 regenerated plants and their progeny that were analyzed; however, there was evidence for frequent changes in chromosome structure and for somatic instability and preferential loss of the A. prostrata chromosomes in the regenerated plants.

Although neither in our study nor in the one at the Welsh Plant Breeding Station was the desired stable integration of alien genes into the A. sativa genome demonstrated, changes in gene transmission were observed in both cases. Also, Larkin et al. (1988) have preliminary findings of altered transmission patterns in tissue culture regenerants for introduced alien traits in wheat MAS lines. These results plus direct cytological evidence from C-banding by Lapitan et al. (1984) for several wheat/rye chromosome interchanges produced in plants regenerated from tissue cultures of wheat/rye hybrids indicate that tissue culture does have potential for facilitating interspecific chromosome exchanges.

Examples of other approaches involving oat tissue culture techniques that are being investigated in the U.S. include the following. Heritable resistance to the phytotoxin produced by the fungal pathogen Helminthosporium victoriae was obtained by Rines and Luke (1983) in oat plants regenerated from toxin-selected cultures. Nabors (1983) obtained regenerated plant progenies which were much more salt tolerant than controls following selection in tissue culture. Dahleen et al. (1988) recently reported in oats positive as well as negative non-selected tissue culture-induced variability in several agronomic traits including yield, plant height, heading date, seed number, seed weight and protein content. Bregitzer et al. (1987) have developed an improved oat tissue culture type of friable, embryogenic callus which should facilitate the development of the technology for introducing specific foreign genes by microinjection (Bregitzer et al., 1988) or other gene transfer methods.

Haploid oats have value in the identification and selection of recessive mutants, in producing aneuploid stocks for cytogenetic analyses, and as a source of doubled haploids as "instant homozygous lines" for genetic and breeding studies. Genotypes producing high frequencies of callus from cultures of oat anthers have been identified, but only one haploid oat plant has been recovered by this technique (Rines, 1983). However, haploid oat plants have recently been recovered by rescue of oat embryos following pollination of oat florets with maize pollen, presumably involving elimination of maize chromosomes from early-stage hybrid embryos (Rines and Dahleen, 1988). These various studies involving tissue culture approaches represent one major area of biotechnology being investigated as a tool for oat improvement.

Molecular genetics approaches. The example presented in this paper to illustrate molecular genetic analysis as an approach in oats is recent work at Minnesota to characterize ribosomal DNAs (rDNAs) of oats as to chromosomal location, structural organization, and sequence polymorphism among oat genotypes and species (Jellen, 1988; Jellen et al., 1988). This work also represents an initial step toward generating a DNA molecular genetic marker system for oats. The molecular genetic approaches often entail the use of cloned DNA segments as specific probes for detecting homologous DNA segments via DNA-DNA hybridization.

The DNA clone used as the source of the hybridization probe for our studies was the 17S/26S ribosomal DNA (rDNA) repeat from maize (*Zea mays* L.) and was obtained courtesy of Dr. I. Rubenstein of the University of Minnesota. The 17S/26S rDNA repeat of maize is like that of other species in consisting of two main parts, a highly conserved transcribed region including the 17S, 5.8S, and 26S rDNA genes and a partially conserved spacer region (Phillips et al., 1988). The nucleotide sequence of the transcribed region of the 17S/26S rDNA repeat tends to be highly conserved across species, whereas the intergenic spacer region may be variable both in sequence and in length. The 17S/26S rDNA repeats usually occur in tandemly repeated units of a few hundred to several thousand copies in various species and are localized to the nucleolus organizer regions (NOR) of the genome.

In order to determine the number and location of 17S/26S rDNA loci in cultivated oats, *in situ* hybridizations of a ³H-labeled 17S/26S rDNA maize probe were made to root-tip chromosome squashes of the cultivar Sun II. These *in situ* hybridizations revealed localization of the probe to secondary constriction sites present on six of the 42 oat chromosomes (Jellen, 1988). These six chromosomes correspond to three chromosome pairs, indicative of three loci for 17S/26S rDNA in *A. sativa* hexaploid oat. When root-tip chromosome squashes from plants monosomic for satellited chromosomes including Monosomic VIII of Sun II and Monosomics 2 and 3 of 'Kanota' were probed with this sequence, only five distinct clusters of hybridized labeled probe were seen. These results confirm that each of these oat monosomic lines is missing a chromosome carrying 17S/26S rDNA genes.

In Southern blot analysis (Southern, 1975) of oat DNA isolated from Sun II seedlings and digested with the restriction enzyme *Eco* RI, three distinct bands were present upon hybridization with the ³²P-labeled maize 9.1 kb 17S/26S rDNA repeat (Fig. 2). These bands corresponded to fragment lengths of about 10 kb, 7.5 kb, and 2.6 kb. In contrast, *Eco* RI digests of two plants of Sun II nullisome VIII (lacking chromosome 2) each were missing the 10 kb band and had only the 7.5 kb and the 2.6 kb bands. These results were interpreted to mean that the 17S/26S rDNAs in oats are organized in repeat units of about 10.1 kb with repeats located on chromosome 2 containing only a single *Eco* RI digestion restriction site per repeat while repeats located on the other two oat SAT chromosomes each contain a second or internal *Eco* RI digestion site, as illustrated in Fig. 2. Furthermore, additional Southern blot analyses using probes from subclones of the maize 9.1 kb probe showed that the 7.5 kb and 2.6 kb *Eco* RI fragments corresponded roughly to the conserved transcribed and the intergenic spacer regions, respectively (Jellen, 1988).

The maize 9.1 kb 17S/26S rDNA probe was then used to test for possible restriction fragment length polymorphisms (RFLPs) for 17S/26S rDNAs as a means to examine relatedness among oat cultivars, genomes, and species. Nine of ten *A. sativa* cultivars, chosen to represent a diversity of parentage and geographic origin, displayed identical fragment patterns in *Eco* RI restriction enzyme digests (Fig. 3), indicating a high degree of homogeneity among *A. sativa* cultivars. Only 'Black Mesdag', a dark-hulled oat introduced from France in the late 1800s, displayed a variation in pattern. This variant was a slightly faster-migrating, smaller band corresponding to the spacer region fragment. A lack of restriction fragment polymorphism between *A. sativa* cultivars 'Noble' and Sun II was also found with this probe in digests employing several other restriction enzymes (Jellen, 1988). In contrast to the homogeneity of restriction fragment patterns among *A. sativa* cultivars, extensive polymorphism was found among the five accessions of *A. sterilis* (shown in Fig. 3), seven of *A. byzantina*, and six of *A. fatua* examined (Jellen, 1988). The various tetraploid and diploid *Avena* species also displayed a high degree of polymorphism with this rDNA probe.

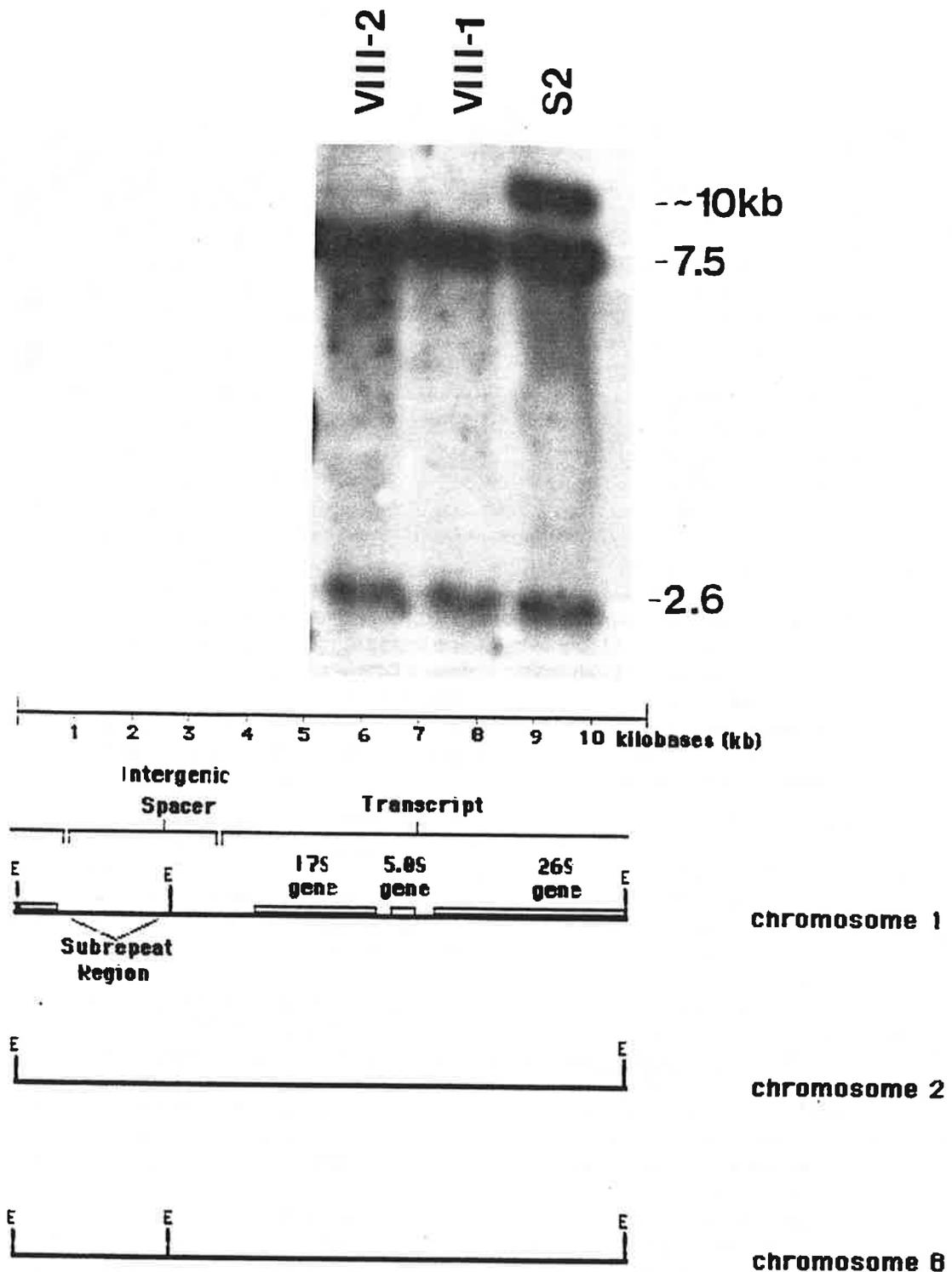


Fig. 2 The upper portion is a Southern blot autoradiogram of DNA from Sun II (S2) and two different plants nullisomic for chromosome 2 (VIII-1 and VIII-2) digested with the enzyme Eco RI and probed with the ^{32}P - labeled maize 9.1 kb 17S/26S rDNA repeat. The lower portion is a diagrammatic interpretation of the structure of oat 17S/26S rDNA repeats on SAT chromosomes 1, 2, and 8. Plants nullisomic for chromosome 2 presumably lack those rDNA repeats without the internal Eco RI site that separates the other repeats approximately into 7.5 kb transcribed regions and 2.6 kb spacer regions.

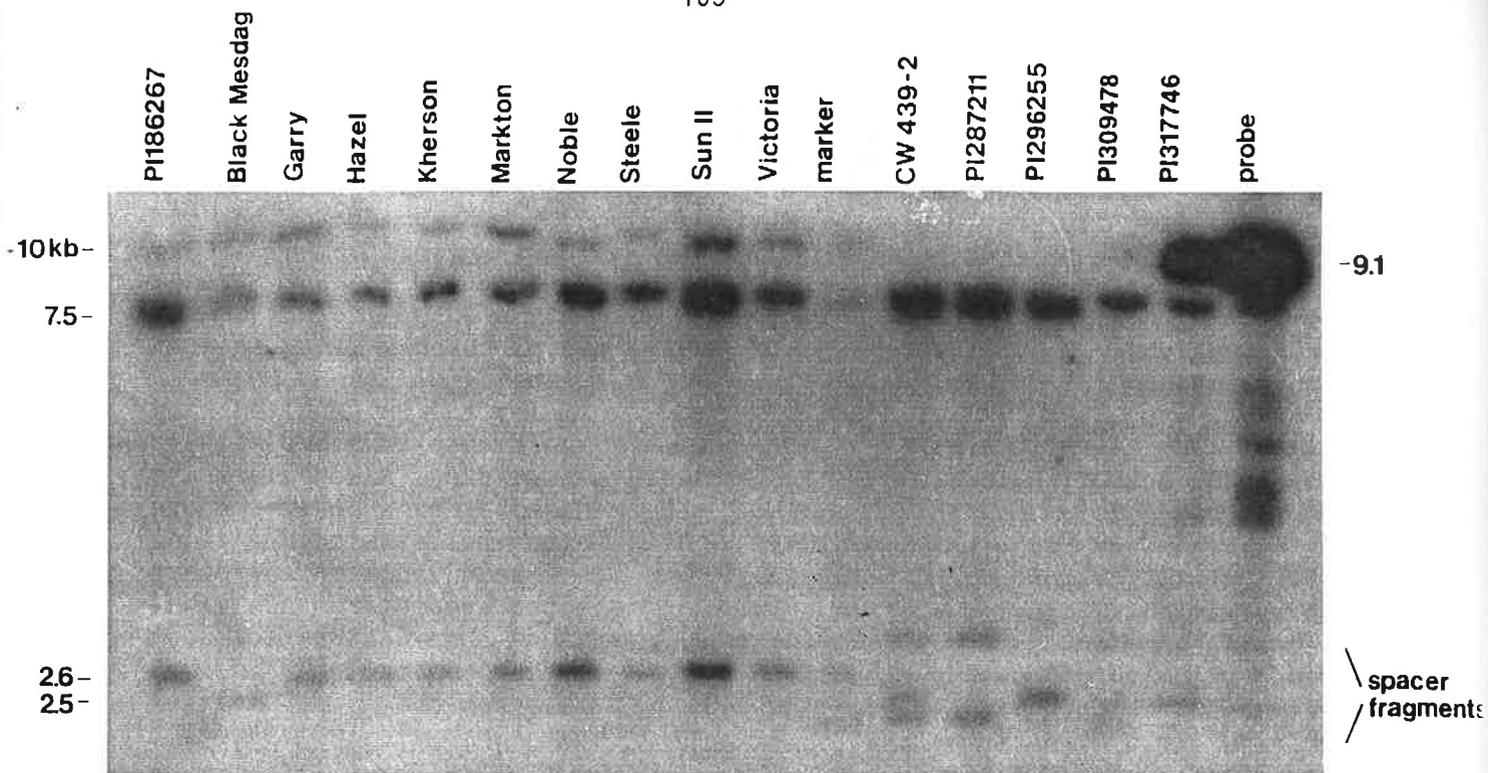


Fig. 3 Restriction fragment pattern of DNA from ten *A. sativa* and five *A. sterilis* lines digested with *Eco* RI and hybridized with the maize 9.1 kb rDNA probe. The *A. sativa* lines, run in the lanes to the left of the marker lane, are highly monomorphic in spacer fragment sizes; whereas the *A. sterilis* lines, in the lanes to the right of the marker lane, are highly polymorphic.

One notable difference between the *A. sativa* and the *A. sterilis* patterns is the absence of a 10 kb fragment in the *A. sterilis* lines (Fig. 3). Presumably each of the 17S/26S repeats of these lines contain the 'internal' *Eco* RI site discussed earlier while the repeats on chromosome 2 of the *A. sativa* cultivars are lacking it. In the *A. byzantina* and the *A. fatua* lines, some had the 10 kb fragment and some did not (Jellen, 1988). Another striking difference in fragment patterns among the hexaploid oat species is the heterogeneity of bands corresponding to the spacer fragments in *A. sterilis* lines compared to the single 2.6 kb band found in 9 of the 10 *A. sativa* cultivars (Fig. 3). *A. byzantina* and *A. fatua* entries also displayed heterogeneities in these fragments with up to three distinct bands in this region. Determination of whether the three distinct spacer region fragments reflect portions of three distinct repeat sequences, each located on a different SAT chromosome, will require further analyses involving crosses with monosomic and nullisomic tester stocks.

The molecular genetic analyses of the 17S/26S rDNA repeat described here illustrate some of the potential for use of this tool in oat genetics and improvement. DNA sequences recognized by specific probes can be mapped to chromosome using aneuploid oat stocks. Alternatively, polymorphisms in these sequences can be used as molecular markers to establish genetic linkage relationships, either to other molecular markers or to any genetically variant trait. Such molecular markers have the advantage of being codominant, environmentally insensitive, phenotypically neutral, potentially unlimited in number, and fairly readily monitored. Techniques for assaying these molecular markers are constantly being improved. Also analyses of structural organization and polymorphism patterns of cloned DNA sequences can provide a powerful means for examining relatedness among genotypes and species as a tool in germplasm development and breeding. The use of molecular markers for RFLP-based studies

in oats will require the generation, characterization, and mapping of a large number of locus-specific probes. Also, the 17S/26S rDNA system described here has many tandemly arranged repeats at each locus, making the molecular analysis fairly simple. Improved DNA isolation and detection techniques may be required to work with single copy sequences. Efforts to generate and characterize the needed probes and to characterize their RFLP patterns among oat genotypes are currently underway with our group at the University of Minnesota, at the USDA-ARS National Small Grains Germplasm Research Facility in Aberdeen, Idaho (D. Hoffman, personal communication), and at Cornell University in Ithaca, New York (M. Sorrells, personal communication).

The techniques of molecular genetics also have made possible the nucleotide sequencing of cloned genes to reveal their structure and potential mechanisms of regulation, as well as to monitor their expression at the RNA levels. Oat genes of potential interest to oat improvement that have been cloned and at least partially sequenced to date in the U.S. include genes for the following: phytochrome, the light signal receptor protein (Hershey et al., 1987); alpha and beta tubulins, protein components of microtubules essential to cell division and growth (Mendu and Silflow, personal communication); and globulins, a storage protein fraction in large part responsible for the favorable amino acid balance of oats (Walburg and Larkins, 1985; Shotwell et al., 1988).

A final potential contribution of molecular genetic technology to oat improvement is the capability to assemble specific DNA constructs that may be needed to develop efficient methods of genetic transformation; i.e., the engineered introduction and integration of new or alien source genes. By the same token, some form of regenerable oat tissue culture may be needed as receptor tissue for the transforming DNA. Thus, it is in the realm of genetic transformation of oats that the two areas of biotechnological research described in this paper, tissue culture and molecular genetics, may together make possible the full potential of biotechnological genetic manipulations in oat improvement.

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GENETIC ENGINEERING OF OATS: REGULATION OF PROTEIN SYNTHESIS IN ENDOSPERM DURING EMBRYOGENESIS

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Abstract

Since the prolamin:globulin proportions are reversed in wheat and oat these genes are being used as a model system to find the regulatory DNA sequences which are responsible for this differential gene expression in cereals. In oats, 75-88% of the grain protein is composed of salt-soluble globulin while the synthesis of the alcohol-soluble prolamins is stopped at 10-15%. This is in sharp contrast to the Triticeae, where prolamins form 60-70% of grain protein. Our laboratory has sequenced a cDNA clone for a 16,000 molecular weight avenin where the predicted NH₂-terminal domain is unique and interestingly the COOH-terminal domain shows homology to globulin. Such a "chimeric" storage protein should exhibit amphipathic solubility characteristics. The available cDNA sequences for oat prolamin and globulin can be used to generate predicted secondary structures for the corresponding messenger RNA molecules to test whether steric hindrance of ribosome attachment may explain the differences in their translational efficiencies during grain development.

Introduction

Cereal breeding programs will continue to develop higher yielding cultivars with increased disease and stress resistance. Biotechnology research programs can explore the possibility of adding specific genes to elite cereal cultivars, thus giving them additional economic and agronomic advantages. Grain quality improvement (e.g. kernel hardness) offers a striking example of how farmers have benefited from aggressive crop improvement programs. A prime goal of agricultural biotechnology is to help develop successful **gene-transfers** in experimental and elite cultivars, thus aiding and **accelerating** the cereal breeding program.

The cereal-based industries rely on a steady supply of high quality grain. New improved cultivars have allowed grain producers to participate in this growing market area. New cultivars, however, take 15 to 20 years to develop using conventional plant breeding methods. Recombinant DNA techniques have the potential to speed up this process: a) by identifying new genetic resources through DNA screening using cloned genes, b) by isolating and transferring single genes coding for useful proteins or enzymes, or known to enhance or suppress the expression of particular genes. The milling and food processing industries, in turn, will be in an advantageous position to develop new processes and new products for the agri-food markets. A striking example is wheat, where the improvement of bread-making quality by the gene-transfer of specific "good" glutenin genes is underway. Wheat glutenin genes have been isolated and both the gene and the wheat protein have been expressed specifically in the endosperm tissue of foreign host plants (1,2). It is clear that biotechnology of grain quality will undoubtedly have a most positive impact on the cereal-based industries together with the excellent breeding programs already in place.

Therefore, the genetic engineering of cereals may, in the future, involve (a) changing the number of copies of a certain gene in a cultivar, (b) altering DNA sequences which regulate gene transcription into messenger RNA or its translation into protein or enzyme, and, among many other possibilities, (c) inserting genes from other species. Understandably there is a need for oat breeders also to have access to cloned single genes for use as probes and promoters in their crop improvement programs.

Grain Quality Improvement

To increase knowledge of cereal gene control mechanisms, two seemingly "on-off" systems in oats have been studied. One model system is the lipase gene which actively makes enzyme in oats in large quantities while this gene-product is virtually absent in wheat, barley and rye (3,4,5). The second model system studies the abundant proteins in grain, the storage proteins. In wheat, for example, allelic variation at the Glu-1 loci which code for High Molecular Weight subunits of glutenin (HMW) is responsible for cultivar variability in the dough elasticities of flour (6). In general the tribe Triticeae contains three main groups of homologous seed proteins: the HMWs, sulfur-rich (S) prolamins and S-poor prolamins (7). Amino acid sequences of a number of these grain proteins have been determined directly and by deduction from cloned DNA sequences (1,2,8-11). Similar work has been progressing on the analysis of storage protein gene expression in other monocots as well as dicots (12,13).

Oat Storage Proteins

Through the characterization of these same storage protein groups in oats (Avena sativa), more genetic "light" might be shed on these important grain proteins. We found common oat cultivars of different protein content to exhibit molecular weight and charge heterogeneity of their prolamins similar to wheat but the level of expression is greatly reduced (14). Instead of forming 60-70% of grain protein as in other cereals, oat prolamins synthesis is stopped at 10-15%. The genetic expression of the glutenin fraction in oat is virtually shut down completely (15). Even the residual protein, left in the extracted flour after removal of all the Osborne fractions, we have now found to consist of insoluble globulin by Western immuno-blotting techniques (16). Therefore, rather than consisting of mainly alcohol-soluble proteins as in the Triticeae, 75-88% of oat grain protein is composed of salt-soluble globulin instead (17,18,19). The protein and developmental characteristics of oat are unique enough so that the oat model system might be treated as a "mutant" cereal system.

Differential Expression of Prolamins and Globulins

To better understand these genetic differences, the genes being transcribed during grain development were studied at the level of polysomes (20) and mRNA (21). The 40 kDa and 20 kDa subunits of oat globulin were shown to be disulfide linked in unreducing conditions suggesting that the 60,000 molecular weight (60 kDa) dimer is homologous to pea legumin and other 11S storage proteins. This was confirmed by direct in vivo labelling (22). Transported to protein bodies, preproglobulin is proteolytically cleaved to form the dissociable α - β dimer respectively (23). This striking evolutionary conservatism between dicot legumes and monocot cereals was corroborated by DNA-DNA hybridization (Southern blotting) using a cDNA clone for pea legumin (24) and it showed direct homology to a Hind III fragment of oat chromosomal DNA (Matlashewski, G.J. Ph.D. Thesis, University of Ottawa 1983). ¹²⁵I-labelled antibodies, raised against both oat 12S globulin holoprotein and the acidic 40 kDa α -subunit, gave positive signals in Western immuno-blots

against globulin extracts from wheat, barley, rye, corn and rice (25). The legumin (i.e. globulin) levels were low except in rice. We analyzed each rice fraction by Westerns and found that all rice glutelin polypeptides cross-react, thus confirming that the legumin gene is actively expressed in rice (26,27,12). Oat protein also contains the vicilins characteristic of legumes (28). Oat glycosylates its vicilins in a similar manner (29). Antibodies against oat 3S and 7S vicilins, used to challenge extracts from wheat, rye, barley, rice and corn showed that polypeptides antigenically related to pea and oat vicilins do occur in the globulin fractions of all cereals (30). Another important finding concerns relative proportions. In the oat globulin fraction, the legumin:vicilin ratio is about 7:1 whereas in the members of the Triticeae it is about 1:8, almost the reverse, another example of differential gene expression among cereals (31).

Translational Control

We studied wheat mRNA and translated it in vitro showing that the 60 kDa legumin polypeptides also arise from a precursor message (32). The bulk of the mRNA, however, codes for prolamins. Fractionating oat mRNA carefully on sucrose gradients, we were surprised to find that the bulk of it corresponds to the same size class of mRNA as in wheat (33). When translated in vitro, the major peaks of oat mRNA (12S and 15S) yield prolamins-like polypeptides. Prolamins, however, only constitute 10-15% of oat protein as detailed above. Only a minor peak of oat mRNA, 18S in size, was found to code for the globulins (i.e. legumin), the abundant protein constituting 75-85% of oat protein (33). This suggested that 18S mRNA is preferentially translated by oat ribosomes and that some form of translational control may be responsible. We therefore started to investigate how prolamins mRNA translation might be blocked in oat endosperm. Our simple reconstitution experiments showed that polysomal protein factors do influence the translational specificity of the 18S oat globulin poly A⁺ mRNA relative to the more abundant prolamins mRNAs present (34). ³²P-in vivo labelling indicated that there are also differences in the phosphorylation states of certain ribosomal proteins between oat endosperm and leaves (35). Another possibility might be that the 5'- and 3'-untranslated regions (UTR) of the prolamins or globulin mRNAs may differ. One could now test specific gene constructs of hybrid (prolamins/globulin) mRNAs in both in vitro and in vivo systems. This may show more clearly which cereal DNA sequences influence protein synthesis in grain.

To further elucidate translational controls in cereal endosperm we must determine mRNA levels as well as 5'- and 3'-flanking region signals using standard S1 mapping techniques and specific mRNA transcripts. The molecular genetics of these major grain protein genes may help to explain the complementarity of genes for high grain protein content seen in A. sativa x A. sterilis experiments (36). During barley germination for example, gibberellic acid somehow increases the amount of translatable mRNA for α -amylase (transcriptional control?) and probably exerts translational control also to increase the relative amount of α -amylase synthesized from the increased amount of mRNA. Recent work on two barley α -amylase gene families (isozymes A & B) shows they are regulated differently in the aleurone cells (37), type B genes being relatively more active transcriptionally than A upon hormone stimulation.

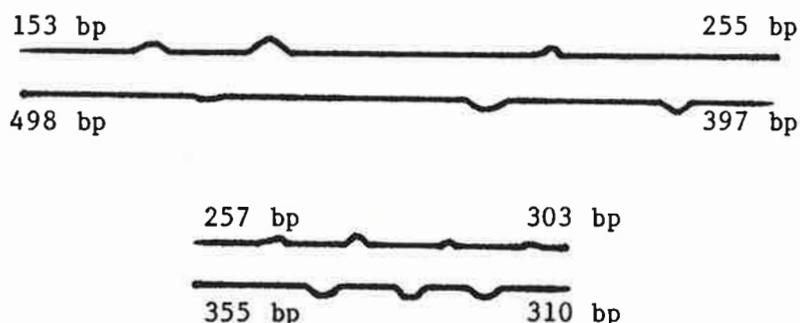
The translational efficiency of maize storage proteins (zeins) has been studied using a pDS-6 cell-free system. The translation of zein zA₁ mRNA is blocked because of hybrid formation between two inverted repeats. When the IR sequence was spliced out of the 3'-UTR, the hybrid clone directed the synthesis of at least 50 times more zein than the original message (38). Varying the length of the 5' leader also affected translational efficiency.

Representative cDNA Clones from Oat

Oat endosperm RNA was cloned in both pBR322 and λ gt 10 to form several cDNA libraries. Screening with 12S (prolamin) or 18S (globulin) end-labelled mRNA on plaque filters, we have isolated both 12S RNA-specific and 18S RNA-specific clones coding for prolamins and globulins respectively. Our prolamin cDNA clone, p3B3, has been used to probe for the expression of this gene during grain development by Northern blotting (39). Similarly we have used it to probe the DNA from 21 species of *Avena* (diploids, tetraploids, hexaploids) to look at how prolamin gene copy number and chromosomal rearrangement vary with ploidy level (40). The p3B3 cDNA insert is 780 nucleic acid base pairs (bp) long and codes for a 16 kDa prolamin (11). This oat prolamin sequence is homologous to the cDNA sequence for oat globulin (41) at the COOH-terminal ends of these two proteins. In fact, the 3'-untranslated flanking sequences are also very similar, but not identical, raising the possibility that differences in the 5'-untranslated leader sequences of their mRNAs may be more likely to contribute to the higher synthesis of globulin over prolamin. Such molecular differences may play a role in the differential expression of grain protein genes. Genomic libraries have been constructed and screened with our oat prolamin (p3B3) and globulin (pLL-2) cDNA probes to isolate the complete 5'-leader sequences of respective clones, so that their regulatory effects on protein synthesis can be tested.

Secondary Structure of mRNAs

The available oat prolamin cDNA sequence (11) was searched for intramolecular Watson and Crick base-pairing, using the FOLD program (University of Wisconsin Genetics Computer Group). Two long stretches of potential RNA-RNA duplex (snap-back hybridization) appear within the mRNA, which are about 75% complementary.



These double-stranded regions, if formed, would perhaps be difficult for the ribosome complex to dissociate or "melt", and might impede translational efficiency.

In general, the secondary structure of eukaryotic mRNAs is one of the features that affect translational efficiency (44,45), with much elegant proof available for the 5'-leader. Less information is available for the role of 3'UTRs, but recent work has uncovered differences in mRNA stability between oncogene transcripts and their normal cellular homologues (46). An 51 bp AU-rich element engineered from a human GM-CSF gene into the 3'UTR of rabbit globin mRNA caused high metabolic instability in transfected cells. And now B2-RNAs in mouse are thought to associate in an "anti-sense" complement at the 3' ends of mRNAs to increase the stability of the mRNA by protecting it against intracellular nucleases with specificity for such single-stranded AU-rich elements (47). Changes in the composition of the B2-RNA population might differentially regulate the susceptibility of individual mRNAs to nucleolytic degradation in the cytoplasm.

Such "countertranscripts" may also be operating in plants. The naturally occurring co-existence of RNAs in oat endosperm cells, which are complementary to oat prolamin or globulin mRNAs, could be tested for by probing Northern blots. Labelled RNA (from pGEM3,4 riboprobe vectors) of the same polarity as the prolamin (p3B3) or globulin (pLL2) mRNAs may detect transcripts of various lengths in polyadenylated or non-polyadenylated RNA tracks if such countertranscripts exist during the differential synthesis of these proteins during embryogenesis. This technique has been used recently to pick up two "anti-sense RNAs" for murine L27'rp mRNA (48), and RNA complementary to α -amylase mRNA has been reported for barley (49).

Transient Expression in Protoplasts

The need to determine the various controls operating during cereal protein mRNA translation becomes more pressing as the genetic engineering of cereals becomes a reality (50). The successful transformation of maize plants obtained from protoplasts treated with Agrobacterium T-DNA containing neomycin phosphotransferase (NPT II) next to the 35S promoter region of CaMVirus has been reported (51). Transgenic plants of rye have been reported to be obtained by the direct injection of DNA into the base of young inflorescences (52). Exciting progress with other monocots such as rice and yams is also occurring with respect to gene-transfer (53,54). While Agrobacterium co-cultivation and protoplast regeneration techniques are further developed for these and other cereals, elegant systems are already available to study monocot gene expression in the laboratory. Walbot's lab at Stanford has developed electroporation of monocot protoplasts to introduce both DNA constructs and RNAs for either transcriptional studies or as a tool to study eukaryotic mRNA translation (55). For example, this allowed the testing of several versions of the 35S CaMV promoter attached to transferase marker genes for transient promoter (transcription) activity in maize and tobacco protoplasts (56). One plasmid, pMP1, contained a shorter 5'-untranslated leader sequence in the transferase mRNA as well as a TTCGCATG \rightarrow AGACAATG change at the start of the coding region. This results in a 5-fold increase in the marker enzyme activity in embryogenic cell suspension culture protoplasts of maize (51). Using deletion mutants of a dehydrogenase mRNA (Adh1), the Stanford lab has shown that a cap structure is essential, the poly (A) tail is very important, and that an intron in the 5'-leader can result in a profound increase in product levels (57). In a similar way, but using oat aleurone protoplasts instead (58), wheat α -amylase promoter constructs have been assayed in transient expression experiments to test for effects of gibberellin regulation (59).

Summary

Prolamin and globulin genes from oat are being further characterized to see how their final levels in grain are controlled by their molecular genetics. The isolated genes will be also used to transform cereal protoplast cultures, to test the feasibility of engineering the DNA sequences which modulate both the functional (e.g. viscoelasticity) and nutritional (e.g. globulin content) properties of oat flour.

To increase our knowledge of crucial flour components, we need to better understand gluten and globulin gene(s) behaviour. Studying the translational activity of specific mRNA sequences may allow molecular designs for increased flour strength and nutritional value in oat, and in other cereal breeding lines as well.

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A MALE-STERILE HEXAPLOID OAT

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Two spontaneous male-sterile oat plants were found among F_2 progeny of a complex-pedigree oat cross in the greenhouse at College Station, Texas, in 1985. The cross producing the sterile plants was 83SA79/83SAT139. An abbreviated pedigree for 83SA79 (entry 79 in the 1983 Quaker Oat "International" Oat Nursery) is 74C8014/3/'TAM 0-301'/2/CR cpx/SR cpx. 74C8014 is a breeding line developed by the Texas Agricultural Experiment Station (TAES); its pedigree is 68JHG19/4/'Egdolon 26'/'Norwin'/3/65C308/2/'Ora'/P.I. 295919. JHG19 was a TAES breeding line (short, large-seeded selection) derived from a cross of 'Suregrain' with two promising "forage-type" TAES selections. P.I. 295919 was a crown-rust resistant *Avena sterilis* selection from Israel, and 65C308 was an experimental selection from the backcross Suregrain*5/'Abda'. The "CR cpx" and "SR cpx" parents represent a series of crosses made to transfer or improve resistance to crown rust (CR) and stem rust (SR), respectively. Pedigrees of these crosses were unwieldy, and these abbreviated forms were substituted. C.I. 9221 was the original source of stem rust resistance in the "SR cpx" crosses, while various crosses among TAM 0-301, 'TAM 0-312', 'Coker 227', and 'Coker 234' were designated "CR cpx" crosses. F_2 plants exhibiting the highest level of resistance to crown rust or stem rust were used in more complex crosses such as the one producing 83SA79. The other parent, 83SAT139, was from a panicle selection in the 1983 oat nursery at Guaiba, Brazil (selection 4, Row 1698). It came from an early-maturing plant with good resistance to crown rust; unfortunately, its pedigree is not known.

The male-sterile oat plants were discovered during routine emasculation of F_2 plants previously found to be resistant to crown rust and/or stem rust. Both plants were quite attractive, agronomically (relatively short, strong straw, large florets, nice panicle type). The plants were well-tillered, and appeared entirely normal in overall plant morphology. However, when florets were opened for emasculation, it was immediately obvious that the anthers were sterile. They were small, pale, and had the "arrow-head" shape typical of anthers of male-sterile wheat and barley plants. Anthers from these plants were broken on a microscope slide, and stained with aceto-carmin. Pollen grains were found, but they were completely "hollow", and devoid of starch. Subsequent examination of microsporogenesis of sterile plants derived from crosses to the original sterile plants showed normal behavior through the "tetrad" stage of development, but no viable pollen was produced.

Crosses were made between the sterile plants and a "normal" parent, the cultivar 'H-833'. All male-sterile plants subsequently used as parents in this study derive from these original crosses. F_1 plants from crosses of the two "original" male-sterile greenhouse plants with the pure-line parent were grown in the field at Aberdeen, Idaho, in the summer of 1985, and in the

greenhouse at College Station in the spring of 1986. All F_1 plants from these crosses appeared normal, and the hybrid plants were fertile. F_2 populations from these crosses were first grown in the greenhouse at College Station in 1986 (only small populations from two 1985 Aberdeen F_1 plants), and a small number of sterile progeny were used for backcrosses to H-833, and for crosses with 82C6023, subsequently released by TAES as the cultivar 'TAMO 386'. Unfortunately, we do not have records of the frequency of sterile F_2 plants in these populations. However, F_2 populations from eight of the 1986 greenhouse F_1 plants from the original cross (sibs of the 1985 Aberdeen plants) were grown at Aberdeen in the summer of 1986 (40 F_2 plants from each F_1). Only eight completely sterile plants were observed, while 53 plants were rated partially sterile (some of which might have been male-sterile with unusually good outcrossing); 216 plants were judged to be fully fertile. Three plants in this population appeared to be aneuploids (small, weak plants), and 40 plants were missing (failed to emerge in the field).

F_2 populations from the "2nd-generation" sterile x fertile crosses, made utilizing sterile F_2 's from the "original" fertile x sterile crosses as female parents and H-833 and TAMO 386 as pollinators, (9 crosses, 36 F_1 plants, 16 F_2 plants per population observed) were subsequently classified for fertility in the 1987 greenhouse season at College Station. The frequency of sterile plants was 12.6% (47 of 372 plants), and was relatively consistent for the nine crosses.

Since the frequency of sterile plants was low (approximately 3% for the F_2 populations from the original crosses and 13% for the "2nd generation" crosses), it appeared likely that more than one gene might restore fertility. Our next strategy was to cross sterile plants with fertile "sib" plants to try to eliminate restorer genes. We hoped to produce at least some populations in which the inheritance of fertility was simplified. We produced 78 such crosses in the greenhouse at College Station in the spring of 1987, and grew 1-8 plants from each cross at Aberdeen, Idaho, that summer. Thirty four of these crosses segregated for fertility, producing a total of 81 fertile and 75 sterile plants (a good fit to the 1 : 1 ratio expected if a single, heterozygous-dominant gene locus conditioned fertility in the fertile parent plants). Although the F_1 family population size was limited, even a population of 4 plants should identify segregating populations with approximately 95% accuracy, assuming 1 : 1 segregation.

We next classified F_2 populations from fertile F_1 plants from the families exhibiting the 1 : 1 segregation pattern, in the 1988 greenhouse season at College Station. All such F_2 populations would be expected to segregate 3 fertile : 1 sterile, as all these fertile F_1 's should be heterozygous for a single, dominant gene for fertility restoration. An acceptable fit ($P > .10$) to the expected 3 : 1 ratio was obtained for 15 of 20 F_2 families (1-4 fertile F_1 plants per family, 18 F_2 plants per F_1). However, the overall ratio of 497 fertile : 139 sterile plants does not give a very good fit to the expected 3 : 1 ratio ($.10 > P > .05$). Removing two of these families would improve the fit to $.40 > P > .30$ (the remaining distribution would be 400 : 120).

Since it appeared that many of the families were producing a

"clean" 3 : 1 segregation, we again sib-mated sterile F_2 plants from these families with fertile F_2 sib plants. These crosses were grown at Aberdeen, Idaho, in the summer of 1988. Sterile segregates were found in 37 of the F_1 families, while the remaining 16 families produced only fertile plants (an excellent fit to the 2 : 1 ratio expected if a single, dominant gene conditions fertility restoration, and heterozygous and homozygous fertile plants used as parents were, therefore, present in the 2 : 1 ratio). "Segregating" families (those having sterile plants, 1 to 10 surviving plants per F_1 family) generally produced fertile and sterile plants in the 1 : 1 ratio expected if they resulted from crossing a heterozygous fertile (male) plant with the homozygous recessive female (single-gene hypothesis). A total of 126 fertile plants : 106 sterile plants : 11 partially sterile plants were observed. The ratio of fertile : sterile plants gives an acceptable fit (Chi-square probability .20 - .10) to the expected 1 : 1 ratio. If partially sterile plants (which may have been "sterile" plants with unusually high outcrossing) are included with the sterile group, the ratio of 126 fertile : 117 sterile gives an excellent fit ($.60 > P > .50$) to the expected 1 : 1 ratio.

The 1987 and 1988 results from sib matings of sterile and fertile plants make us confident that we have been successful in "simplifying" the inheritance of male-sterility in these hexaploid oats. By using plants with known 42-chromosome constitution (root tip counts) for crosses, it appears we also have reduced the minor degree of aneuploidy noted in the original crosses. The only question that remains to be answered is whether there is any cytoplasmic component involved in conditioning the male-sterility. All crosses observed until this time have had the cytoplasm of the sterile parent, so a cytoplasmic component cannot be ruled out. However, we are observing F_2 populations from crosses of known heterozygous plants (those that produced segregating F_1 families when crossed with sterile sibs) with several "normal" pure-line parents in the greenhouse in the spring of 1989. The heterozygous plants were used as the male parents in these crosses; therefore, any frequency of sterile plants (probably lower than 3 : 1, based on previous experience with "sterile x normal" crosses) will give proof that cytoplasm is not involved. We believe that these crosses should provide the last piece of missing information concerning this male-sterility in oats. At present, however, all other available evidence supports the hypothesis that sterility is conditioned by a single, recessive gene pair.

Although the recessive inheritance of sterility will limit its usefulness, we hope that it will be of some value as a tool in plant breeding research (perhaps to produce random-mating populations for recurrent selection programs). However, it seems likely that outcrossing under field conditions may be quite limited. We obtained only 2.3% seed set on sterile plants at Aberdeen, Idaho, in 1987 (42 of 1840 florets examined), and the same low frequency (107 of 4618 florets) in the field at College Station in 1988. Relative humidity was quite low in each instance; hopefully, more humid conditions might significantly increase natural outcrossing. Female fertility of male-sterile plants appears to be normal (seed-set >70% for most greenhouse crosses); it is not likely that the low degree of outcrossing is caused by any abnormality in female reproductive parts of these plants.

THREE-LOBED STIGMAS IN OATS

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'H-833', a commercial cultivar of "winter" oats developed by the Coker's Pedigreed Seed Co. (Hartsville, South Carolina), was found to have a high frequency of three-lobed stigmas. This discovery was made in 1986, when we were making routine greenhouse emasculations to cross the new cultivar with crown rust and stem rust resistant experimental lines in the oat breeding program at College Station. H-833 is a desirable agronomic type (short, strong straw, good winterhardiness, attractive grain); we were using it extensively in crosses designed to improve cold-tolerance in our breeding material.

Although we had observed a very small number of abnormal three-lobed stigmas in making oat crosses over the period 1965-1985, the frequency of such stigmas almost certainly was less than one per thousand florets (no records kept). We were surprised to find that the new cultivar had a much higher frequency of stigmas with an extra "lobe" or branch. Subsequent examination of a number of taxonomic descriptions showed that the oat floret is described as having an ovary with a bifid style (dictionary definition: divided into two equal lobes or parts by a median cleft). Obviously, this definition is not appropriate for florets having the three-lobed stigma trait.

We first determined the frequency of three-lobed stigmas in H-833 by examining primary, secondary, and tertiary florets from a number of panicles from the greenhouse, and from field plants growing in our experimental nursery at College Station. In greenhouse plants, 22.7% of primary florets (172 examined) 42.6% of secondary florets (68 examined), and 28.6% of tertiary florets (only 7 examined) had the three-lobed trait. Field plants showed a lower frequency of three-lobed stigmas; 6.3% of primary florets (252 examined), 21.0% of secondary florets (252 examined) and 26.5% of tertiary florets (68 examined) had the abnormal stigma morphology. In contrast, field-grown panicles of 'Coronado' oats had no three-lobed stigmas in 100 primary, 100 secondary, and 52 tertiary florets we examined. The differences in frequency of three-lobed stigmas in greenhouse and field plants, as well as different frequencies for the different floret "classes" (note the higher frequencies of three-lobed stigmas in secondary and tertiary florets than for primary florets for both greenhouse and field plants) led us to believe that environmental factors might influence the "penetrance" of this trait.

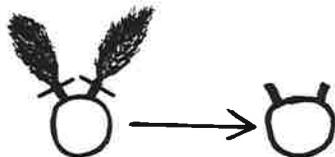
We were interested in learning whether the "extra" stigma lobe could function in the pollination-fertilization process. We designed a number of treatments to determine the relative efficiency of "normal" and "extra" stigma lobes in producing seed-set by the approach crossing method. Previous observations had shown that seed-set appeared to be normal when three-lobed stigmas were allowed to self-pollinate. Floret treatments for 1987 are shown in the following diagram. All florets (only primary florets were utilized) were emasculated, with subsequent

pollination by the approach crossing method. This method has been utilized exclusively for making oat crosses at College Station since 1966; generally, excellent seed set percentages are obtained with this crossing method at this location. In some treatments, stigma lobe(s) were removed by cutting through the style with very high-quality scissors designed for cornea-transplant surgery. We attempted to remove all the "feathery" stigmatic tissue in this process. "Check" florets were normal (two-lobed stigmas) with both stigma branches left intact. In one of the treatments, one of the two stigma branches in "normal" florets was removed. In another treatment, the two "outside" stigma branches (those in the normal positions on the pistil) were removed in florets having three-lobed stigmas, leaving only the "extra" stigma lobe (located midway between the "normal" lobes) to function. In the final treatment, both lobes of normal stigmas were removed to determine whether removing all stigmatic tissue would prevent fertilization.

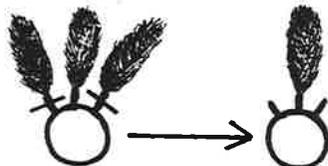
Greenhouse Treatments Involving Stigma Removal



Two-Lobed Stigma,
One Lobe Removed



Two-Lobed Stigma,
Both Lobes Removed



Three-Lobed Stigma, Two
"Normal" Lobes Removed

Different floret treatment "classes" were identified by tying a loop of sewing thread (different color for each treatment) around the pedicel of treatments in which stigma branches were removed. Similar treatments also were made in 1988 (greenhouse study at College Station); however, a treatment in which florets with three-lobed stigmas were emasculated, but in which the abnormal stigmas were left intact was included. The treatment in which both stigma lobes of normal florets were removed was not repeated.

Results of these studies are given in the following tables:

1987 Greenhouse

Stigma "Treatment"	Number florets	Number seed	Percent seed set
"Intact" 2-lobed	112	79	70.5
2-lobed, one removed	20	14	70.0
2-lobed, both removed	20	0	0.0
3-lobed, two removed	22	5	22.7

(26 of 178 primary florets on panicles used in 1987 study had three-lobed stigmas = 14.6%).

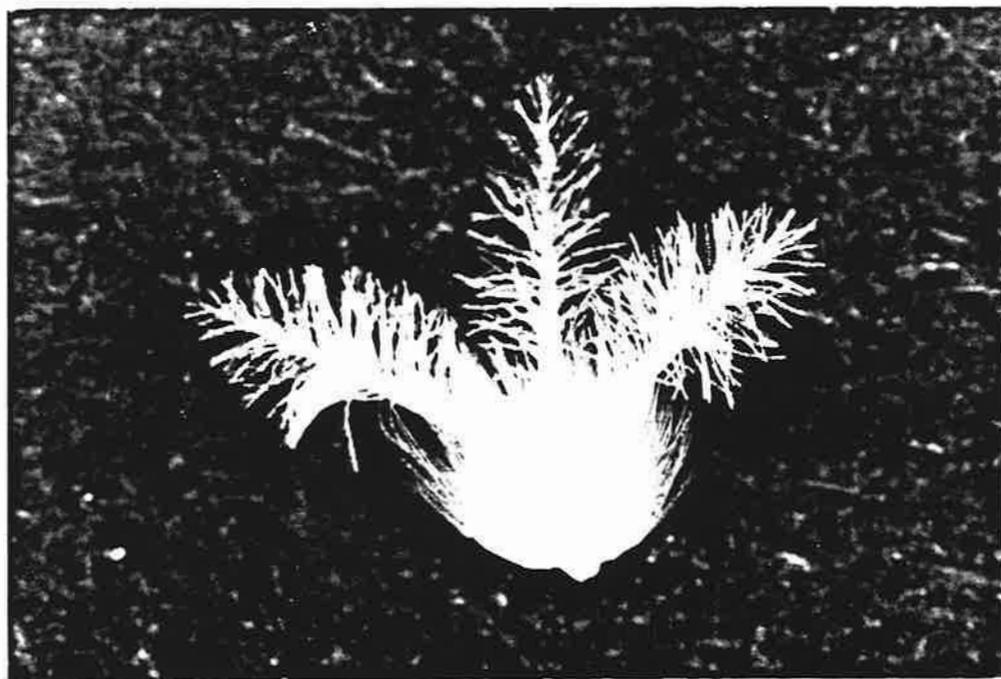
1988 Greenhouse

Stigma "Treatment"	Number florets	Number seed	Percent seed set
"Intact" 2-lobed	209	153	73.2
2-lobed, one removed	26	14	53.8
3-lobed, two removed	29	8	27.6
"Intact" 3-lobed	31	19	61.3

(60 of 295 primary florets on panicles used in 1988 study had three-lobed stigmas = 20.3%).

In both years, the treatment in which two stigma lobes of three-lobed stigmas were removed produced a lower seed-set percentage than did the treatment in which one stigma lobe was removed from "normal", two-lobed stigmas. Although this probably indicated that the third stigma branch is not as efficient in the overall fertilization process, the seed set percentages of 22.7 and 27.6 for this treatment in 1987 and 1988 demonstrate conclusively that the third stigma lobe can function, to some degree. Since no seed-set was obtained on the treatment in which both stigma branches were removed from normal florets (1987 study, only), we are confident that all treatments involving stigma removal were effective in eliminating all functional stigmatic tissue, and that fertilization of such florets had to be accomplished by the remaining stigma branch in these florets.

The frequency of primary florets having the three-lobed stigma trait in the 1987 study was 26/178 = 14.6%; in 1988, it was 60/295 = 20.3%. One panicle used in the 1988 greenhouse study had 17/19 of primary florets (89.5%) having the three-lobed trait. In 1989, we will observe F_1 and F_2 plants from reciprocal crosses between H-833 and Coronado to attempt to determine the mode of inheritance of the three-lobed stigma trait.



Oat pistil with 3-lobed stigma

COMPARISON OF TWO SELECTION STRATEGIES FOR THE DEVELOPEMENT OF HIGH-YIELDING OAT VARIETIES IN BRAZIL

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INTRODUCTION

The potencial grain yield productivity of small grains crops, including barley, wheat and oat has not yet been reached, especially in areas with agroecological conditions different from those of their major center of adaptation. Yield advances can be achieved by two breeding strategies which are conceptually different: The first depend on increasing the genetic potential for yield by modifying yield-enhancing plant traits, so-called morphophysiological traits; the second strategy removes or reduces constraints that interfere with the yield potential of cultivars (Johnson, 1986). This strategy is sometimes caled defect elimination, such as susceptibility to diseases. These two concepts of breeding have been discussed with some emphasis in the 1970's after the publication of Donald's (1968) paper about plant ideotypes. He stated that in the past plant breeders were most often working in the defensive, trying to correct the susceptibility of the cultivars for most diseases. His ideotype concept stressed the "ofensive" approach and the selection of theoretically more efficient plants. Several examples of traits obtained by the use of the latter approach were described for several crops by Frey (1971).

High grain yield is the expression of the good adaptation of the genotype to the environment and the breeding strategies may vary from place to place due to the interaction genotype x environment. In the south of Brazil environment, several factors have been pointed out as responsible for the low yield obtained with the currently used cultivars of small grains. However, most reports give special emphasis to disease problems as the main cause for low yield. Thus, it is not surprising that in the majority of the breeding program of small grains in the southern Brazil the primary selection criteria is resistance to disease (Camargo, et al, 1986; Doto et al, 1978; Floss et al, 1986; Osorio, 1982). Consequently, the prevalent breeding strategy applied has been the defensive one.

Small grains are grown in the southern states of Brazil. The breeding for high-yielding genotypes of oats is recent in this environment (about 15 years). There are two main breeding programs at University of Passo Fundo (UPF), at Passo Fundo, and University Federal of Rio Grande do Sul (UFRGS), at Porto Alegre. Since 1979, the oat nurseries with advanced breeding lines from each program have been organized by these two Universities, and they are grown in five to eight locations in the states of Parana, Santa Catarina, and Rio Grande do Sul.

The main source of genetic variation for the two breeding programs is the Quaker Oat International Nursery sent to south Brazil every year by the University of Wisconsin and the Texas A.M. University. Analysis of the genotype x environment interaction for oat grain yield did not show any significant of genotypes x locations effects (Carvalho et al., 1982). Which suggested that selection at the breeding sites of these two universities, should give equivalent gains, unless different selection criteria are applied at each place.

However, the selection strategies are completely different in the two programs.

At Passo Fundo the main objective is the selection of cultivars resistant to the diseases ("defensive") prevalent in the region (Floss et al. 1982); and at Porto Alegre the main emphasis has been placed on the selection of a theoretically more efficient plant ("ofensive") (Carvalho et al. 1982).

Since 1982 twelve different varieties have been released by each University, which provides a unique situation for comparing selection strategies because the same base population of breeding materials has been used at each place. Comparisons of cultivars released from the same Quaker Oat International Nursery (QOIN) for the two selection program may help to decide which is the best strategy for selection of high-yielding varieties for southern Brazil.

It is difficult to compare two breeding strategies without bias and to find out which is the most appropriate for a specific environment target. In this paper we describe an empirical approach of assessing two selection strategies by comparing the varieties selected and released to oat growers in Brazil.

MATERIALS AND METHODS:

Comparisons for mean yield were made between the varieties released at Passo Fundo and at Porto Alegre selected from the QOIN prior of 1975, 1976, 1977, 1978 and 1979 (Table 1). All data utilized for this analysis were taken from the official records of the Reunião Conjunta de Pesquisa de Aveia for each year and it represents all the data obtained where the varieties were grown in the same experiment for several years. Trials were grown in a randomized block design in several locations per year. For these locations an analysis of genotype x environment interaction with twenty oat varieties showed that the genotype x location interaction was not significant (Carvalho et al., 1982).

For the first set of varieties UPF 1,2 and UFRGS 1,2,4 data were obtained for the years 1979 to 1987. In 1986 and 1987 three replication of the oat nursery were sprayed with a fungicide (propiconazole) to prevent the occurrence of crown rust and three replications were not. These experiments were grown at four locations each year.

For the QOIN of 1976 and 1977 comparison were no made because no varieties were selected from those nursery at Porto Alegre, and at Passo Fundo, respectively.

Varieties UPF 7,8 and 10 were selected from the QOIN of 1978. For this set of varieties data was obtained for the 1985, 1986 and 1987 seasons.

Data for the three last years were used to compare the varieties UPF 9 and UFRGS 8, which were selected from the 1979 QOIN. Others varieties were selected in this material but they were grown in different experiments.

Mean values for other traits including plant height, days to anthesis and harvest index were available only from the experiments grown at Porto Alegre.

RESULTS

The comparison of the UFRGS 1,2 and 4 with the varieties UPF 1 and 2, for different seasons are in the Table 2. Until 1982 season the UPF varieties were resistant to the prevalent races of crown rust, providing an environment free of disease. With a shift in the pathogen population in 1982, both set of varieties became susceptible. The data in Table 2 showed that, until 1982, the advantage for the UFRGS varieties was more than 500 kg/ha. That was expected since they were selected for a theoretically more efficient plant type. An unexpected results was observed in the years after 1982 when the presence of disease should favor the UPF varieties or be randomly distributed. However, the data in Table 2 shows that the UFRGS varieties outyielded the UPF varieties in all comparisons, but one, by 398 kg/ha or 22%, ($T=1.64$ $P=0.12$). The mean number of days to anthesis was 97 and 110 and the mean plant height was 110 and 135 cm for the UFRGS and UPF, respectively. However, the mean to crown rust infection in the last five years was similar for the two set of varieties. The harvest index of the UFRGS varieties

superior showing better partitioning of the total biomass produced by the oat plant (Table 2).

For the QOIN of 78, comparisons for the two set of varieties are in Table 3. The UFRGS varieties outyielded the UPF varieties in all comparisons. The mean advantage of UFRGS varieties was 508 kg/ha or 22%, but a T-test for the means was not significant ($T=1.49$ $P=0.12$). The mean plant height and heading time were lower for the UFRGS varieties, the harvest index was better for the UFRGS and the UPF varieties had a lower incidence of crown rust (Table 3).

In the Table 4, are the data for the UFRGS 8 and UPF 9 varieties, which were grown in the same experiment in the seasons of 1985, 1986 and 1987. The UFRGS 8 outyielded the UPF 9 in the average of all environments by 31% ($T=1.96$ $P=0.09$). UFRGS 8 was shorter, early and it has a better harvest index than the UPF 9 (Table 4). The mean values for crown rust were higher for UFRGS 8 in most of the environments.

The application of fungicide in three replications of the 1986 and 1987 nurseries provided two different set of environments: one where the presence of crown rust was prevented (high yield) and another with the presence of crown rust (low yield). Data presented in Table 2, 3, and 4 showed that from twelve comparisons the UFRGS varieties outyielded the UPF varieties by 531 kg/ha or 26% ($T=2.19$ $P=0.04$).

DISCUSSION

The comparison of different breeding strategies is very difficult to make, and specific conditions are necessary for preventing the bias of the data for one or another procedure. The "offensive" and "defensive" breeding strategies have been suggested for different environments, and for specific conditions. For those environments where disease epiphytotics are severe, the majority of plant breeders adopt the "defensive" strategy. However, shifts in the pathogenic population break down the resistance for some diseases in very short time; for the conditions of this study, in four years or less (Rosito, 1976).

In southern Brazil the conditions are ideal for comparing the two strategies because epiphytotics are present and different strategies have been used for the breeding of high-yielding oat varieties. In addition, it is very difficult to find any significant differences in selection ability among breeders with some experience (Townley-Smith et al. 1973).

The data presented in this paper clearly show that selection for a theoretically more efficient plant resulted in varieties that had a better performance even in the presence of severe epiphytotics. In addition, the results of this study suggests that the emphasis in the resistance to disease could limit the advances in grain yield by preventing the selection of more efficient types. Also, it suggests that for environments where epiphytotics are frequent, the emphasis in the breeding programs may be shifted to a offensive approach. Only after a better agronomic type is reached, the selection for resistance to disease should be the main objective.

Because the data of this study was obtained in a relatively low yielding environment, the results maybe not applicable for environments with high yielding potential. Attention also should be given to the fact that the breeding programs being compared have started only recently and the results may apply only for this condition. However, these results may have applications for those species that are bred in environments different from that of their major center of adaptation and for those breeding programs that are in the beginning.

The results obtained in this study did not stands against the selection for resistance to disease, it clearly shows, however, that selection of a theoretically more efficient plant with some tolerance to disease is better than the selection of varieties with immunity to disease but with a poor agronomic type. We suggest that selection criteria to be applied in segregating

populations be first for good agronomic types, and secondly for resistance to disease.

Finally, the results showed that the selection of a theoretically more efficient plant as pointed by Donald (1968) was efficient even in environments with usually low grain yields. Thus, selection with basis in an ideal model may be of considerable importance even if some of the assumptions for the proposed model are not meet.

CONCLUSIONS

A ofensive selection strategy gave better results for oat grown in the environments present in southern Brazil;

The selection criteria for these conditions should be for best agronomic type (reduced plant height, early and high harvest index), and after this goal is reached for some tolerance to diseases;

The main emphasis to disease should be adopted only when an efficient type of plant has been reached; or if the population size are adequate for multiple trait selection.

More efficient plants had a better yield also in the presence of severe epiphytotics, and a theoretical model should be taken in account even if assumptions are not completely meet.

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TABLE 1. Varieties selected from the Quaker Oat International Nurseries at Porto Alegre (UFRGS) and at Passo Fundo (UPF).

QOIN	UFRGS	plant height	number days anthesis	UPF	plant height	number days anthesis
1975	1,2,4	110	97	1,2	135	110
1976	-	-	-	3,4,5,6	-	-
1977	5,6	-	-	-	-	-
1978	7,9,10	110	98	7,8	130	111
1979	8,11,12	115	95	9,10	131	113

TABLE 2. Mean yield (kg/ha) of UFRGS 1,2 and 4 with UPF 1,2 grown in several locations during the years of 1979 and 1987.

Year	UFRGS, 1,2,4			UPF 1,2			diference
	n	mean	s.d.	n	mean	s.d.	
1979	18	1994	945	12	1624	608	370
1980	18	3242	651	12	2604	910	638
1981	18	3476	830	12	2544	830	932
1982	27	1629	865	18	1492	621	137
1983	33	1957	1555	22	1742	1151	215
1984	27	1994	965	18	1622	707	372
1985	18	2207	896	12	1690	838	517
1986 ¹	15	1309	546	12	1117	612	192
1986 ²	12	2179	441	8	1541	649	638
1987 ¹	18	1897	870	12	1933	910	-33
1987 ²	12	2690	500	8	2289	822	401
mean yield		2234			1836		398
heading (days)		97			107		-10
plant height		110			135		-25
harvest index		0.39			0.24		-0.15

¹ experiments without fungicide

² experiments with fungicide

TABLE 3. Mean yield (kg/ha) of UFRGS 7,9,10 with UPF 7,8 selected from the 1978 QOIN and grown in several locations during the years of 1985,1986 and 1987.

Year	UFRGS 7,9,10				UPF 7,8				diference kg/ha
	n	mean	s.d.	cr% ³	n	mean	s.d.	cr% ³	
1985	18	2570	645	20	12	2339	859	0	231
1986 ¹	15	2189	351	25	10	1784	568	0	405
1986 ²	12	2765	487	10	8	2357	733	0	408
1987 ¹	18	3289	1005	25	12	2376	1175	30	913
1987 ²	12	3421	772	20	8	2841	768	20	580
mean yield		2847				2339			509
plant height		112				128			-16
heading (days)		99				112			-13
harvest index		0.41				0.26			-0.15

¹ experiments without fungicide

² experiments with fungicide

³ crown rust

TABLE 4. Mean yield (kg/ha) of UFRGS 8 and UPF 9 selected from the 79 QOIN grown in several locations and years.

Year	UFRGS 8				UPF 9				diference kg/ha
	n	mean	s.d.	cr% ³	n	mean	s.d.	cr% ³	
1985	6	2459	541	10	6	2196	855	0	263
1986 ¹	5	1853	585	25	5	1496	497	0	357
1986 ²	4	2492	468	25	4	2341	366	20	151
1987 ¹	6	3098	1171	20	6	1768	953	40	1330
1987 ²	4	3388	802	20	4	2354	371	40	1034
mean yield		2658				2031			627
plant height		115				130			-15
heading (days)		96				113			-17
harvest index		0.42				0.28			-0.14

¹ experiments without fungicide

² experiments with fungicide

RECURRENT SELECTION IN OAT BREEDING

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The improvement of grain yield in oats is getting more and more difficult. So we have to look for new breeding methods or to adapt methods which are mainly used in other fruits.

Recurrent selection methods are often used to improve quantitative traits of cross-pollinating crops. In a recurrent selection scheme the progenies of genotypes of population A are tested, the best ones selected and intermated to get an improved population A' with which the next cycle can be start.

In self-fertilizing cereals and especially in oats the crossing, an important step in recurrent selection, is very laborious in the field and practicable on a small scale only. Therefore in a favourable recurrent selection program the number of crosses should be low. This can be done either by reducing the number of parents or by reducing the number of crosses for each pair of parents. We tried to find out the best combination of these two possibilities with regard to a character like grain yield.

Therefore we started three recurrent selection programs (Fig. 1).

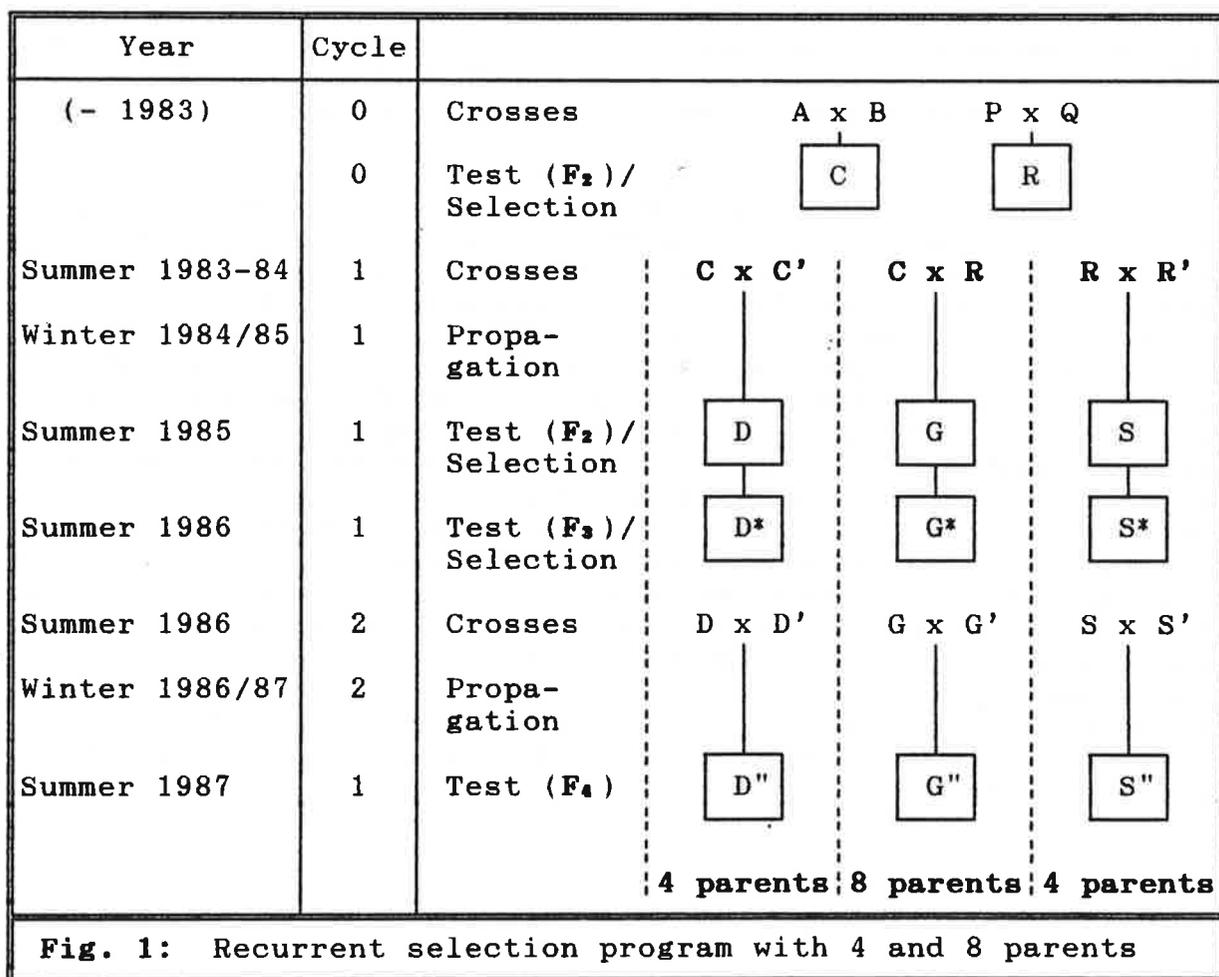


Fig. 1: Recurrent selection program with 4 and 8 parents

We got the initial plant material from the company v. Lochow-Petkus. It consisted of the homozygous lines A ('Saladin'), B ("LP7765"), P ('Trafalgar') and Q ("LP7770") and the F_2 -single-plant progenies in F_5 (C_1 - C_4) selected from the crossing of A and B and also the progenies R_1 - R_4 from the crossing of P and Q. The progenies C_i and R_i were used for two recurrent selection programs with 4 parents each and also in combination for a program with 8 parents. The selection schemes in detail with 4 and 8 parents are shown in Figure 2.

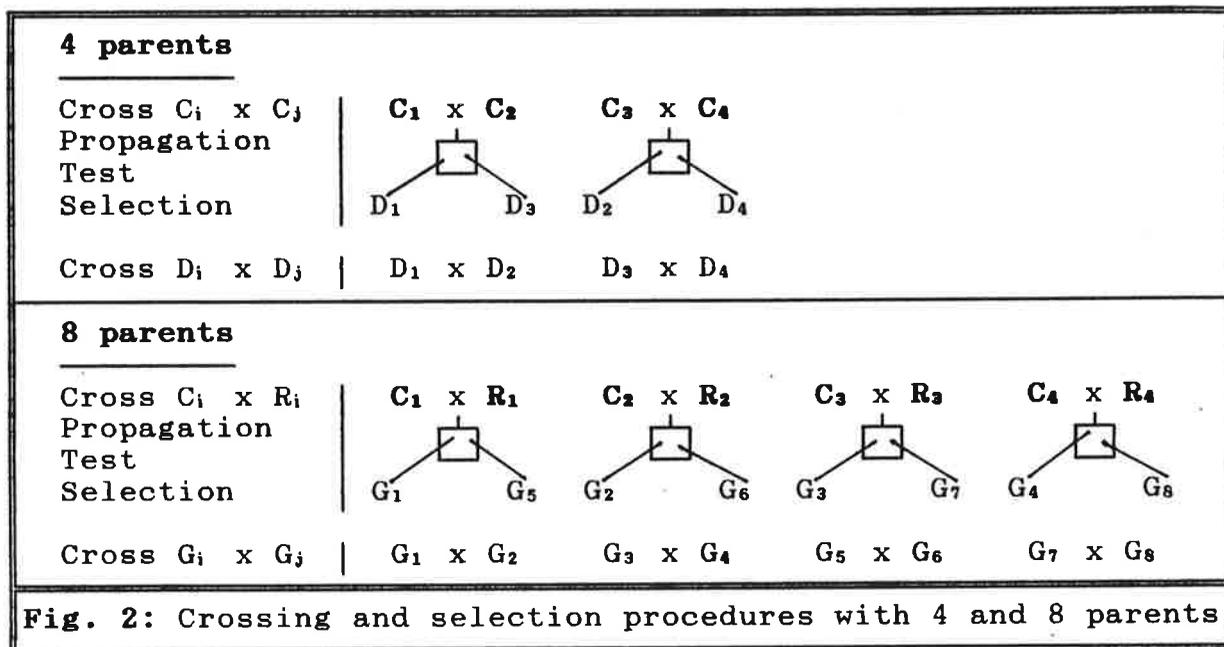


Fig. 2: Crossing and selection procedures with 4 and 8 parents

For the crosses the first florets of 5 spikelets from one panicle were used only. During the crossing periods 1984 and 1986 temperature and relative humidity were recorded. The comparison of the temperature curve and the seedset rate shows that the success of crossing was very low when the temperature was high as it was from the 7. to 13. of July in 1984 (Fig. 3).

We received the same results for 1986. The correlation between temperature and successful crosses was -0.6 . The reason for this is probably the low relative humidity when the temperature is high. Because of the very thin wall the pollen dries up very quickly and can not germinate any more.

For the first test, that means the F_2 -generation, we had only a small amount of seed and so we used two-row-plots (Tab. 1). On the basis of these results we made the first selection. The aim of this selection was to show whether a selection in such an early generation is useful or whether the breeder has to do one additional propagation before testing.

The same material was tested in F_3 and in F_4 for another selection on the basis of the results of larger plots (Tab. 1) and to check the selection decisions.

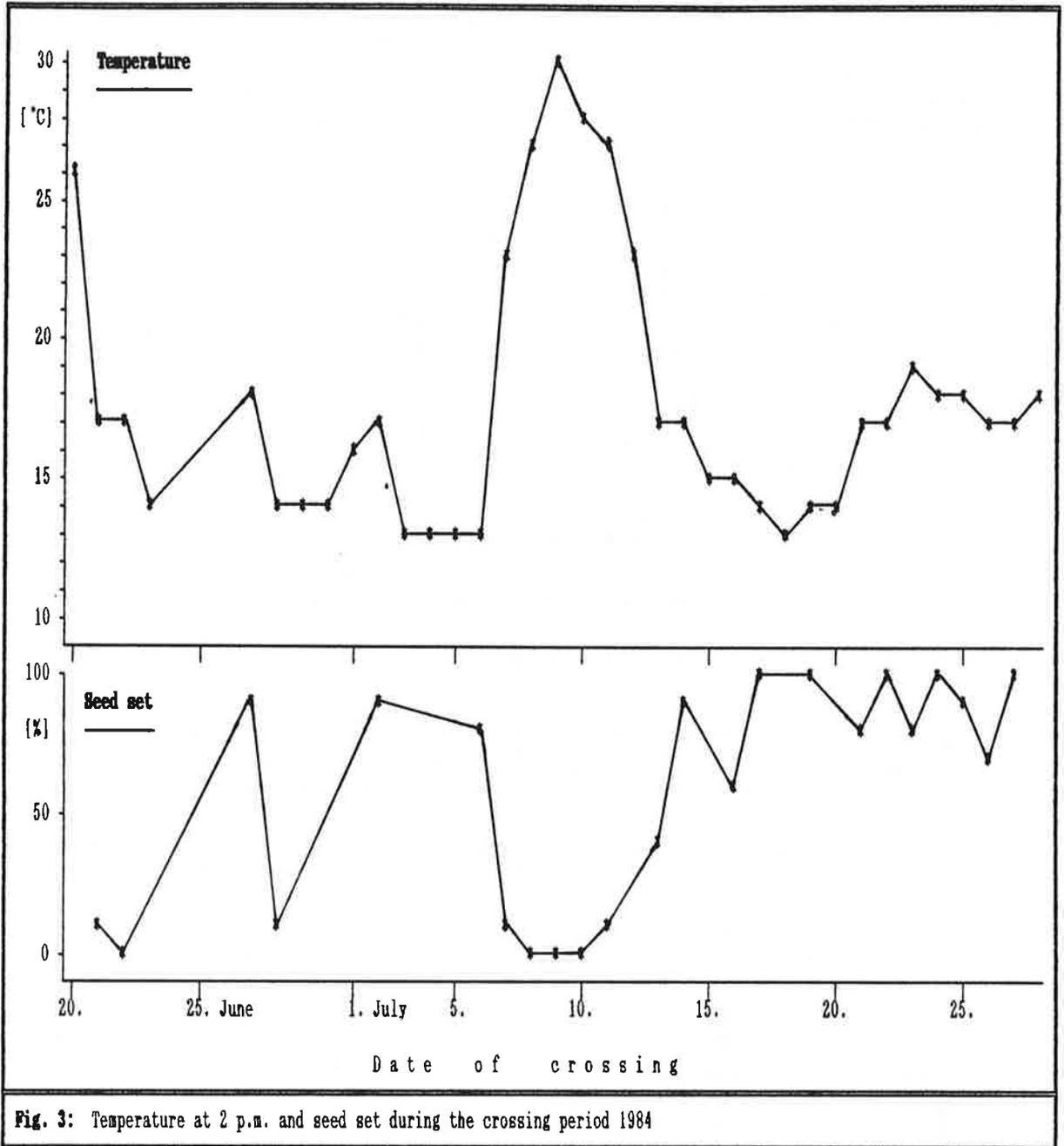


Fig. 3: Temperature at 2 p.m. and seed set during the crossing period 1984

Tab. 1: Dimensions of the tests for the F_2 , F_3 and the F_4 generation

Gen.	Location	Replications	Plot size
F_2	1	2	2 rows
	2	1 - 6	2 rows
	3	1	1.4 m ²
F_3	1	2	4.4 m ²
	2	2	4.4 m ²
	3	2	2.1 m ²
F_4	1	2	4.4 m ²
	2	2	4.4 m ²

In the field trial with two-row-plots (F_2), the variation was large even in the control variety 'Flämings vita'. The coefficient of variation CV for grain yield was even greater in the control than in the F_2 (Tab. 2). For TKW the variation was clearly smaller but the coefficients of variation for the control and for the F_2 were not much different.

Tab. 2: Mean, coefficient of variation (CV) and number of plots for grain yield and TKW of the control variety and the F_2			
1 9 8 5		Control	F_2
Grain Yield [g/pl]	mean	4.77	4.65
	CV[%]	25.48	21.88
	n	280	1830
TKW [g]	mean	35.02	32.92
	CV[%]	5.27	5.55
	n	283	1854

The correlation coefficients between replications, locations and generations are shown in Table 3.

Tab. 3: Correlation coefficients between replications, locations and generations for grain yield and TKW			
Gener.		Grain yield	TKW
F_2	betw. rep.	0.137 ***	0.414 ***
	betw. loc.	0.124 ***	0.588 ***
F_3	betw. rep	0.183 ***	0.409 ***
	betw. loc	0.108 **	0.611 ***
F_4	betw. rep.	0.087 *	0.606 ***
	betw. loc.	-0.001	0.646 ***
F_2/F_3 F_2/F_4 F_3/F_4	betw. gener.	0.075 0.077 0.252 ***	0.686 *** 0.657 *** 0.804 ***

For the grain yield the correlation was significantly positive but very low for practical use. For the TKW the correlations were much higher with 0.414 between replications and 0.588 between locations. In principal the results of the F_3 and F_4 field trials with larger plots confirmed these correlations. In spite of the larger plots the improvement was not clear but the correlation between F_3 and F_4 was closer than the correlation between F_2 and other generations.

Selection

With a recurrent selection program genetic gain in early generations is only possible if there is a high correlation between generations for the trait to select on. For the grain yield this correlation was low and therefore the grain yield depends more on environmental factors than the TKW. The correlation between the two traits was negativ but very low.

Beyond the selection for grain yield or TKW only, a selection was made with a selection index as a product of standardized values for grain yield ('GY') and 1000-kernel-weight ('TKW'). The results of the different selections are shown in Table 4.

Tab. 4: Improvement of grain yield (GY) and TKW in % by selection on GY, TKW and selection index (SI='GY'*'TKW').
{General mean for GY = 68 dt/ha and for TKW = 32.2 g}

Sel. on	Check year	Generation of selection			
		F ₂		F ₃	
		GY	TKW	GY	TKW
GY	1986	+2.5	+1.2		
	1987	+0.5	+0.1	+2.5	-2.1
TKW	1986	-2.4	+4.0		
	1987	1.6	+3.5	+2.2	+2.1
SI	1986	+2.1	+2.1		
	1987	+1.6	+1.0	+3.0	+1.7

Selection in F₂

The selection on grain yield increased this character by 1.5% (mean of the tests in F₃ and F₄). The TKW was nearly not changed. Based on the results of the field tests in F₃ and F₄ the selection on TKW improved the TKW by 4.0 and 3.5% and decreased the grain yield only by a small amount (0.4%). The selection on the index increased the grain yield by 1.8%. That is nearly the same amount found for the direct selection on grain yield. But the TKW could be improved by 1.6% at the same time.

Selection in F₃

By the direct selection on grain yield in the F₃ this trait increased by 2.5% but because of the small negative correlation between TKW and grain yield the TKW decreased by 2.1%. The selection on TKW in the F₃ improved the TKW by 2.1%. The grain yield was also improved by 2.2%. This had not been expected because of the negative correlation between grain yield and TKW and cannot be explained. The selection on the index resulted in an increase of the grain yield by 3.0% and of the TKW by 1.7%.

For a comparison of the selection in F₂ and F₃ the realized selection gain was checked with the data of the F₄ only. For grain yield the gain of selection in F₂ was with 0.5% clearly less than the gain of selection in F₃ with 2.5%. For the TKW the selection gain was even greater in F₂ than in F₃. These results conform the

expectation. The selection gain should be dependent on the plot size only for the grain yield but not for the TKW.

Comparison of the 4-parent-scheme with the 8-parent-scheme

Up to now the results were presented without discriminating the different parent-schemes mentioned in the beginning. For a comparison of the different programs the amount of work must be the same. For each pair of parents 2 progenies were selected. So the total number of progenies in an 8-parent-scheme has to be only 1/2 of the progenies in a 4-parent-scheme. The selection gain was checked with the data of the F_4 field test.

Tab. 5: Gain of selection [%] on grain yield and TKW with 4 and 8 parents checked with the data from the F_4 -test

in F_3 selected on	Crossing	Selection gain (F_4 -test)			
		Grain yield		TKW	
		4 par.	8 par.	4 par.	8 par.
Grain yield	$C_i \times C_j$	+2.25		-0.65	
	$R_i \times R_j$	-0.31		-1.93	
	mean	+0.97	+2.96	-1.27	-2.64
TKW	$C_i \times C_j$	-1.10		+3.14	
	$R_i \times R_j$	+2.78		+1.18	
	mean	+0.84	+0.62	+2.17	+0.56

The largest selection gain for the grain yield was received when using the 8-parent-scheme (Tab. 5). But for TKW the 4-parent-scheme was more successful.

The results of our experiments have shown that:

A recurrent selection scheme must be constructed with only few crosses per cycle (laborious crosses in the field).

The correlation between F_3 and F_4 is better than between F_2 and other generations (plot size).

As a consequence of low heritability for yield, tests are not useful before F_3 (seed shortage in F_2).

No clear answer can be concluded from the filed experiment to optimal number of parents (one cycle only).

Recurrent selection seems to be promising in the long term (results from computer simulation).

Recurrent selection is useful to improve the gene pool with respect to quantitative characters. On every step of the program it is possible to select breeding material for example to develop lines or varieties. On the other hand it is possible to integrate new genetic material into the recurrent selection program by replacing some of the parents of a new cycle. In this way a breeder can create an individual recurrent selection scheme that is optimal for his breeding tasks.

The valuable donors for quality improvement in oat breeding

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One of the main source of protein in the feeding balance of the USSR is cereal crops, among which oat protein is of the greatest value due to the high balancing of amino acids content.

Due to the comparatively high nutritional value of the cultivated varieties the breeding towards quality improvement was not paid much attention to, though there are good possibilities for that.

In the content of grain starch is dominating, the average protein content is 11,0 - 12,0 %, lysine 3,4 - 4,0 %, metionine 2,0 - 2,5 % and tryptophane 1,5 - 2,0 %. At the same time the average figures do not show the varietal differences and varieties reactions on growing conditions.

The reaction of oats in the world collection of VIR showed a wide amplitude of changeability of protein content (7 - 26 %), lysine in protein (2,3 - 5,0 %) and fat (3 - 16 %) in case of different varieties and kinds that enables to carry out purposeful breeding work in that direction.

Of recommended Soviet varieties the following have higher protein content: Jakutski, Gerkules, Severjanin, Sibirjak.

Among the collected samples of oats the varieties with the protein content of 19 - 20 % were found out. Among them are Ryhlik Khersonski (USSR), breeding lines (k-11951, 11954, 11961, 11962, 11969, 11972, 11978) and the varieties Clintland, Clintland 64, Goofield, Dal (USA), local samples of Equador and Peru (k-12026, 11787, 11808), Reima (Finland), Hird (Denmark), Fel (Sweden), Perablanc (FRG), etc. and also samples of wild strains (k-13, 14, 90, 112) with the protein level of 24 - 26 % (for a hulless grain).

High protein forms are usually characterized by lower yield and the wild kinds by shattering and high chaff content but the genetic research shows that there exists the possibility to break these relations.

Samples with higher lysine content (more than 4 %) have been found out - Artemovski 107 (USSR), Nos Weiss (FRG), Goldschatz (GDR), Regina (France), Schleiter (Austria), Bambu (Sweden), Patterson (USA). Varieties uniting higher protein and lysine content deserve special attention, as they guarantee high concentration of lysine in the grain (770 - 870 mg/100 g); among them are - old local varieties of Kirov oblast (k-6060) and the Ukraine (k-8258, 8261), Belyi mazur (White mazur) and Slandski ranni (Slandski early ripening) from Poland, Reha from France, Alba from Italy, Fullgrain and Holden from USA.

In the course of the last years hullless oats have become considerably interesting, as the protein content of the grain in that case is by 6-10 % higher than in hull varieties and their fat content is nearly twice as high as in hull varieties. So high indices of protein and energetic components in complex with higher vitamin (B₁, B₆, etc.) content and insignificant amount of fibre make this crop very valuable from the feeding and eating point of view.

The lack of hulls in oat grains simplifies the process of producing food concentrates and increases the outcome of final product by 30 - 40 % in comparison with hull grain. Thus the use of hullless oats in industrial poultry and pig farms has become especially important. According to the data of UzNIIZh the piglets growth rate increases by 10 % while introducing hullless oats into feeding ration. Specialists in the field have raised the question of the necessity to breed varieties of that crop even then, if their yield is lower than that of the hull varieties. However, until recently hullless oats have not spread widely because of their lower yield in comparison with the best varieties of hull oats and also due to their higher requirements to growing, harvesting and storing conditions. Low usage of hullless oats is also due to the fact that until recently no systematic work in that field has been done.

The first records of breeding that crop date back to the middle of our century, when in Canada the varieties Nacota, Liberty, Brighton, Torch and Vicar were bred by crossing hullless forms with hull ones. In a slight degree hullless oats were bred in our country (VIR, Verhnjatchskaja, Tulunskaja, Narymskaja stations, UraINIISHoz etc.).

At present hullless oats are bred in the USA, France, Belgium, FRG, Poland and other countries. The yield of the Polish hullless oat variety Pulawski Nagi is not less than that of the hull varieties. An analogous positive estimation can be given to the varieties Nos Nackt (FRG), Nuprime (France) and a number of others.

The VIR collection of hullless oats includes more than 80 samples from different geographical locations. Among them the forms with different lengths of growing period and resistance to diseases have been found out. Quicker ripening forms were found among Soviet (Narymski 164, Kamalinski 133), local samples of Korea Peoples Republic and Mongolia (k-1926, k-4075). From among the collection of hullless oats the genetic sources for resistance to crown rust and smutty head were found out. Among them are Canadian varieties Torch, Vicar.

Characteristic of all hullless oats is higher tillering that compenstates its sparseness. Specially known for that quality are the local oat from Korea PR (k-11012) and breeding forms of the USA (k-7776 and 7976).

Among hullless oats long-leaf samples were found out - the local one from Yugoslavia (k-6950) and Nahy from CSSR (k11213). The length of their leaves is by 7 - 14 cm longer than that of the varieties Zolotoi dozhd (Golden Rain) and Pobeda (Victory).

The spike length of hullless forms varies from 15 to 25 cm and is in the average bigger than in case of hull varieties. The greatest number of grains per spike (68 - 77 grains) is in case of local samples from Korea PR (k-1930) and Yugoslavia (k-6950). Soviet samples (k-1996, 2301, 8641, 10759, 11278) have the biggest grains (28 - 30 g); the samples of the Asian countries have the smallest ones.

The research of hullless oats in the system of VIR experimental stations enabled to find out the most productive forms with higher protein and fat content for North-West zone - k-11680 (Finland), Nos Nackt (FRG), Nuprime and Reha (France), Nacota (Canada); and for South-East - Uspeh (USSR), Pulavski golyi (Pulavski hullless) (Poland), Nahy (CSSR) Manu (FRG), the yield of which is not less than that of the hull standard varieties.

The highest protein content (20-30 %) was in small-grain samples k-2122 (France), k-1926 (North-Korea), k-2468 (Mongolia), k-1766, k-1799 (USA); high fat content (7 - 8,7 %) was found in the samples k-1998 (USSR), Nos Nackt (FRG) and Nacota (Canada).

The genetic sources of higher quality grain found in VIR are included in the work programs of several breeding centres of our country.

By crossing a hull oat variety Victoria (USA) with a local hullless oat from Perm region in VIR and by selecting more productive varieties with bigger grains in UzNIIZh later a new hullless variety Uspeh with higher protein and lysine content in grain was bred and recommended for cultivation in irrigated zones of Uzbekistan since 1981.

In Siberian NIISHk a variety Omski kormovoi I (Omski Fodder I) was bred in the way of individual selection from the variety Clintafe (Canada). Omski kormovoi I has high protein and lysine content in grains and green mass and it was recommended for cultivation for green fodder in Omsk region in 1978.

It must be taken into account that the main criterion of varieties is the productivity potential that determines the outcome of full-value protein and the sum of essential amino acids from an area unit. Thus while selecting the source material for breeding side by side with the quality indicators of a plants productiveness is necessary, as that in its turn determines the level of a variety's productivity.

CONTRIBUTIONS MADE BY THE BREEDING PROGRAM TO PRODUCE HIGH QUALITY MILLING AND FEED OATS.

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A. INTRODUCTION.

Oats was introduced into México by the Spaniards. However it was an unknown crop in this region, the High Mountain Valleys of Chihuahua, until 1922-1924 when German speaking immigrants from Canadá seeded Canadian varieties here. Since then oats has become one of the principal crops of which 115,000 hectares (3) are seeded annually and now the region is considered to be "The Largest Concentrated Oat Growing Region in the Western Hemisphere" which produces 80 percent of the oats grown in México. On the average - - - 80,000 tons (1,121 kg/ha) (3) of oat grain and 400,000 tons (3,364 kg/ha) - (3) forage are harvested annually. Twenty percent of the grain is used for seed by the farmers and oat meal production by the four local oatmeal plants as well as by Quaker Oatmeal Company. The rest, oat grain and forage, is used principally as dairy and beef cattle feed.

Since 1922-1924, until the present time various methods, from the simplest variety selection to actual plant breeding, have been used to improve oats. This paper will relate the results these methods have had on obtaining high quality milling and feed oats by overcoming the environmental condition that limit high yield, high quality grain and forage oat production.

B. ENVIRONMENTAL CONDITIONS LIMITING HIGH QUALITY OAT PRODUCTION.

1.- The Short Growing Season.

a). Rainfall

The growing season generally begins July 10 when the rainy season begins, which table 1, indicates, but as can also be noticed, the rainy season occasionally begins late in July or even in August (Table 1) (1). Before the rainy season begins there is insufficient rainfall and humidity in the soil for oat growth.

TABLE 1. DATE OF FIRST SUMMER RAINFALL (1).

AVERAGE DATE	YEARS	DATE IN
July 10	1964 - 1986	1965 - July 18 1970 - July 27 1976 - July 13 1978 - July 25 1980 - Aug 17

b). Autumn Frost.

The autumn killing frosts usually occur at the end of October, but they also occur during the first week of this same month (Table 2) (1).

TABLE 2. FIRST AUTUMN KILLING FROSTS (1).

AVERAGE DATE	YEARS	DATE IN
Oct. 31	1964 - 1986	1965 - Oct. 3 1970 - Oct. 5 1976 - Oct. 9 1978 - Nov. 10 1980 - Oct. 29

There are 104 frost free days (growing period), from the first of July until the first killing frost in October (Analysis of 37 year data) (2). However, as the data from the tables 1 and 2 indicate (1), there are years when the growing period is less than 104 days (table 3). Since the frost free period ranges from 77 to 108 days it is obvious that it is necessary to develop early varieties that mature in 90 days or less for the years when the rainy season begins late in July or early August (1).

TABLE 3. FIRST SUMMER RAINFALL AND FIRST FALL KILLING FROST IN 1965, - 1970, 1976, 1978, 1980.

YEAR	DATE FIRST SEASONAL RAINFALL	DATE FIRST FALL KILLING FROST	DAYS WITHOUT FROST
1965	July 18	Oct. 3	77
1970	July 27	Oct. 5	70
1976	July 13	Oct. 9	88
1978	July 25	Nov. 10	108
	(Because of the late seeding date the crops matured very slowly).		
1980	Aug 17	Oct 29	66

2.- Irregular Rainfall.

The 37 year rainfall analysis indicates that in two out of ten years, it is less than 261 mm, in six out of ten years it is from 261 mm to 446 mm and the other two years it is over 446 mm (2).

Table 4 indicates that the precipitation is also variable from month

to month.

TABLE 4. AVERAGE MONTHLY RAINFALL 1964 - 1987 (1).

	M O N T H				TOTAL
	JULY	AUGUST	SEPTEMBER	OCTOBER	
Average per month (mm)	115	114	88	28	345

Generally there is good rainfall in July and August with less rainfall in September and very little in October when the oats is ripening. Table 5 indicates that the rainfall can be very irregular during the -- whole growing season and therefore tolerance to drought also has to be bred in to oats for good yield and quality.

TABLE 5. RAINFALL DURING 1968, 1969, 1976, 1985 GROWING SEASONS (1)

YEAR	JULY	AUGUST	PRECIPITATION DURING THE FOLLOWING MONTHS		TOTAL
			SEPTEMBER	OCTOBER	
1968	243	178 (Rainfall good during the whole season)	59	32	512
1969	157	34 (Very little rainfall after August 15)	14	17	222
1976	156	61 (Very little rainfall in August)	146	6	359
1985	60	45 (Little rainfall all the growing season)	105	30	240

3.- Diseases.

In seasons with continuous rainfall and temperatures the third problem arises: Disease infestation especially stem rust.

The yield of Páramo was severely reduced by the high rust infections in 1986, as can be noted from Table 6, when farmers suffered heavy crop - losses from rust. Páramo is rust susceptible, but is escapes serious damage when the rainfall is low and the rust infections occur late in the season as they did in 1985 and 1987.

TABLE 6. YIELD AND STEM RUST SUSCEPTIBILITY COMPARISON OF RARAMURI IN 1985-1987.

VARIETY	YEAR	YIELD KG/HA	REACTION TO STEM RUST
Rarámuri	1985	2,139	15 MS
	1986	2,451	29 MS
	1987	2,193	5 MS
Páramo	1985	1,882	40 S
	1986	1,372	50 S
	1987	2,002	39 S

Therefore, stem-rust resistance is being incorporated into oats to improve its grain and forage quality.

4.- Other Problems.

Besides the problems mentioned above, there are the general problems of lodging and shattering which affect yield and cause yield loss. Resistance is also incorporated for these characteristics into new oat varieties.

C. PLANT BREEDING METHODS USED IN:

1.- 1922-1940. Beginning of Oat Production.

The German speaking Canadian immigrants brought their oat seed variety Gold with them from Canadá (1922 to 1924) to México. However, they soon discovered that it was too late for the environment here. Therefore, they went to the United States of America in search of earlier oats. Their objective was to obtain high yielding forage oats earlier than they had imported from Canadá. The variety Burt, which they found in Texas, and there fore named Texas, filled their requirements. This was the first step in producing quality milling and feed oats.

2.- 1950-1960. Oat Meal Production - Quaker Oats Company.

In the 1950's the Quaker Oats Company opened its oat meal plant in México City. It obtained oats from this region to produce oat meal. However, the oats grown in this mountain valley of Chihuahua was Burt which produces small kernels and a small groat. Therefore, the Quaker Oats Company together with the Mennonite Central Committee seeded observation plots with foreign varieties to select high yielding, early oats with large groats. The American varieties Newton and Clintland had these characteristics. The seed of these varieties was increased and released to the farmers.

3.- 1961-1988. INIA, México.

Since 1961, the National Agricultural Research Institute through its experimental farms has been improving oat varieties. Since the aforementioned varieties were not being accepted by the farmers, further selections were again made from foreign varieties whereby the U.S.A. varieties AB-110, AB-177 and Nodaway were released. In 1967 two oat varieties, Cuauhtémoc - and Chihuahua, were released from selections made from crosses made in México. However, all the varieties released until this period were still too late for the weather conditions mentioned under "Problems Involved in Oat Improvement." Therefore oat lines were selected from crosses made with American varieties from which the early varieties Guelatao, Páramo and Tarahumara were obtained. For example Guelatao is a selection of the cross Curt-Nošaway. Páramo, which since 1980, has become the main variety seeded, is a selection of the cross AB177² - Curt x Curt-Nodaway² - AB177². Until -- this period no grain quality analysis had been made, except for visual assessment.

Since 1975 the Oat laboratory in México City has analysed all the oat varieties developed in México. The analysis indicated that all the varieties developed in México before 1976 have a high hull content. Emphasis had been put primarily on high yield, earliness, lodging and shattering and disease resistance. Recently five new lines with high groat and protein, high kernal weight, good yield, earliness and good stem rust resistance have been developed of which three will be released as varieties. They probably are Babícora, Rarámuri and Papigochi.

D. Results.

Since oat improvement began when new varieties were selected primarily on the basis of yield and earliness, now there are early high yielding; lodging, shattering and moderate stem rust resistant varieties with large kernels which have high protein and groat percent.

(Table 7, with new varieties and Páramo)

The grain and forage yield, rust resistance protein and groat protein percent will continue to be improved. The fatty acid oil content of the kernel and the protein content of the forage will also be analysed.

TABLE 7. CHARACTERISTICS OF THE VARIETIES SELECTED BY THE GRAVIMETRIC BULK AND PEDIGREE PLANT METHODS COMPARED TO PARAMO. (5 STATION YEAR AVERAGE).

VARIETY	YIELD KG/HA	PERCENT OF CHECK	DAYS TO MATURITY	HEIGHT CM	REACTION TO P. g. a.	WEIGHT 1000 KERNALS GMS.	GROAT PROTEIN	PERCENT PROTEIN	LODGING
Papigochi	2,384*	130	96	100	14MS	35.8	63.2	18.05	1.0
Rarámuri	2,285*	125	88	95	17MS	33.2	66.7	20.46	0.0
Cusihuiríachic	2,248*	123	84	80	12MS	28.6	66.1	22.86	0.0
Pampas	2,154*	118	91	95	17MS	34.4	63.1	21.10	0.0
Babícora	2,116*	116	90	100	21MS	36.0	68.4	20.15	0.0
Páramo (Check)	1,828	100	87	90	44S	35.8	59.0	18.90	6.6

DMS AT 5% FOR YIELD = 301.38 kg/ha C.V. 19.01% General Mean 2,169.256 kg/ha

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Protein and lipid quantity and quality in Swedish oats

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Oats is the second largest cereal crop in Sweden. The acreage about 450.000 ha is two thirds of that of barley but fifty percent higher than that of wheat. The annual total yield of oats and wheat are the same about 1.5 million tons. The annual mean yield per ha in oats vary from 3.1 to 4.5 tons. Premium for protein in wheat started in Sweden more than fifty years ago. Individual payment to farmers for protein content in each delivery was introduced in wheat in 1984, in barley in 1986 and in oats in 1987. The premium for oats in 1987 was two percent per percentage point, starting from 12% protein on dry matter basis. From 1988 the premium was changed for both barley and oats to 1.6% and starting from 11% protein.

The mean protein content in official trials in Sweden is about 12% for most cultivars of oats. The maximal difference between cultivars is about two percentage points although most cultivars are within one percentage point.

In an inventory in 1968-78 with samples of oats from farmers' fields the mean protein content each year was about 12% or 13.5% (Table 1). The protein content in the south and the west regions of the country was each year very similar but in the east region up to two percent higher. The differences were not greater in years with high protein level.

The two years 1987 and 1988 with individual protein payment has shown extreme conditions. In 1987 the protein content was extremely low in all cereals and in 1988 very high in comparison to normal years in the eighties. The variation in protein content in 1968-69 and 1987-88 in samples from farmers' fields is shown in Table 2. The protein content and variation in 1988 was normal considering that the dominating cultivar Vital is having about 0.5% lower protein content than most of the cultivars in the inven-

tory period 1968-78. During the period 1968-78 there was a very good correlation between grain yield and protein yield. The protein yield in 1987 was in comparison to grain yield very low due to wet climatic conditions, poor nitrogen uptake and oxygen deficiency in the soil.

In most cereals there is a negative correlation between lysine content in protein and total protein content. In oats however the lysine content is almost constant. The following regression equation has been calculated from 48 samples representing eight cultivars and seven localities in south and middle Sweden the same year:

$$\text{lysine mg/g sample} = 0.354 \times \text{protein content in dry matter} + 0.123.$$

The decrease in lysine content in the protein is only about one percent in the interval of ten to fifteen percent protein.

Lipid content and fatty acid composition was investigated in a wide collection of oats from Sweden, Denmark, USA, Mexico, Canada, Australia, Wales and Soviet Union all grown in Svalöv in 1981 (Table 3 and 5). The variation in total, free and bound lipids was 5.6-10.8, 3.5-8.9 and 0.7-3.4% respectively. Several lines as CI 2868, CI 2875, PI 174573 and PI 259868 contained 50% more lipids than our modern Swedish cultivars. The lowest amount of total and free lipids in the whole collection was found in Selma. Sang had about 15% higher amount of free and total lipids. Selma and Sang were during a decade the dominating cultivars in Sweden. Four mutants of the old cultivar Sol II had about 10% higher content of free and total lipids. The content of free and bound lipids in dehulled oats was between 8-10% in Swedish cultivars but 12-13.5% in the lines with high fat content. The correlation coefficient between content of free lipids and content of free+bound lipids was 0.87. The content of total lipids (free+bound) could be estimated from the following equation: $0.76 \times \text{content of free lipids} + 3.79$.

The variation between years in free and bound lipids in the two cultivars Selma and Sang are shown in Table 4. The content of free

and total lipids were 20 respectively 10% lower in 1972 and 1981 in comparison to 1973 and 1982 (Johansson 1975 and 1976).

Fatty acid composition in free and bound lipids in oats from the collection grown in Svalöv 1981 are shown in Table 5. The variation in free lipids was for palmitic acid 10.4-17.5%, for oleic acid 38.7-52.4% and for linoleic acid 32.1-43.1%. The content of stearic acid and linolenic acid was about 1%. The variation in bound lipids was for palmitic acid 15.4-22.6%, for oleic acid 23.0-40.4% and for linoleic acid 39.0-54.2%. The content of stearic acid and linolenic acid was as for free lipids about 1%. The cultivar Selma had in the free lipids in comparison to the cultivar Sang more palmitic acid and in the bound lipids less oleic acid but more linoleic acid. The mutants had a fatty acid composition similar to Sol II.

The content of palmitic acid and linoleic acid was higher in the bound than in the free lipids. The greatest difference in fatty acid composition between the two lipid components was observed in oleic acid. The content in the free lipids was one third higher than in the bound lipids. The highest content in the free lipids of the essential linoleic acid was observed in Selma, Sang, CI 2723 and CI 2875. Selma and Sang had a low content of oleic acid. The correlation coefficients in the free and the bound lipids between content of oleic acid and content of linoleic acid was -0.86 and -0.88 respectively, between content of oleic acid and content of linolenic acid -0.80 and -0.67 respectively and between content of linoleic acid and content of linolenic acid 0.61 and 0.71 respectively. The correlations between content of palmitic acid and content of any of stearic, linoleic or linolenic acid were weak. The correlation coefficients between content in free and bound lipids were for palmitic, oleic and linoleic acid 0.17, 0.75 and 0.69 respectively.

The fatty acid composition in Selma and Sang was compared in 1973, 1981 and 1982 (Table 6). Both Selma and Sang had in 1982 in comparison to 1981 less stearic+oleic acid in the free lipids but more palmitic acid and stearic+oleic acid in the bound lipids. The decrease in linoleic acid in the bound lipids was quite consider-

able. In 1973 the content of palmitic acid and linoleic acid in the free lipids was higher but the content of stearic+oleic acid lower than in both 1981 and 1982 (Johansson 1975 and 1976). In the bound lipids there were only minor differences.

Wild oats (three collections of Avena fatua) had in comparison to cultivated oats (cultivar Sang) higher content of both free and bound lipids (Table 7). In both the free and the bound lipids of wild oats the content of oleic acid was higher and of linoleic acid lower. The nutritive quality in lipids of cultivated oats is therefore better than that of wild oats.

Litteratur:

Johansson, H., 1975. Lipid content and fatty acid composition in cereals. In Quality problems in cereals. A Swedish Soviet Symposium at Svalöv p. 27-28.

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Tabell 1. Protein content in oats from different regions of Sweden 1968-78 and 1987-88.

Year	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1987	1988
Region of Sweden													
South	11.7	12.3	12.5	11.5	11.3	12.5	11.4	12.9	12.7	12.4	11.9	10.4	11.3
East	12.1	14.6	13.6	13.2	13.2	14.4	12.5	13.3	13.5	11.6	12.1	10.2	12.3
West	11.1	12.5	11.8	11.4	10.7	12.2	11.9	12.8	12.4	12.7	11.4	10.3	11.9
Whole country	11.9	13.5	13.0	12.1	11.9	13.7	12.3	13.4	13.4	12.0	11.7	10.2	11.9

Tabell 2. Variation in protein content in oats in 1968-69 and 1987-88.

Protein content %	7	8	9	10	11	12	13	14	15	16	17	Mean	Number of samples
	% samples												
1968				4	25	31	25	11	4	1		11.9	167
1969				2	7	15	17	24	14	21		13.5	208
1987		2	12	34	30	14	6	2	0.5			10.2	454
1988			0.1	7	16	33	26	13	3	1	0.1	11.9	713

Table 3. Free and bound lipids in oats from field trials in Svalöv in 1981.

Cultivar	Lipid content %		
	Free	Bound	Free+Bound
Selma	3.5-4.2	1.6-2.2	5.6-6.1
Sang	4.4-4.8	2.0-2.1	6.5-6.8
Sol II	5.5	1.6	7.1
Sol II mutants (n=4)	5.7-6.1	2.0-2.3	7.7-8.3
Foreign lines and cultivars n=39	3.5-8.9	0.7-3.4	6.8-10.8

Table 4. Variation between years in free and bound lipids in the two cultivars Selma and Sang.

Cultivar	Year	Lipid content %		
		Free	Bound	Free+Bound
Selma	1972	3.6	2.3	5.9
	1973	4.4	2.1	6.5
	1974	4.4-4.8		
	1981	3.5-4.2	1.6-2.2	5.6-6.1
	1982	5.0	1.5	6.5
Sang	1973	5.4	2.2	7.7
	1974	5.0-5.4		
	1981	4.4-4.8	2.0-2.1	6.5-6.8
	1982	5.6	1.7	7.3

Table 5. Fatty acid composition in free and bound lipids in oats from fields trials in Svalöv 1981.

Cultivar	Palmitic acid %	Stearic acid %	Oleic acid %	Linoleic acid %	Linolenic acid %
<u>Free lipids</u>					
Selma	16.1-17.5	1.0-1.2	38.7-41.8	38.5-42.5	1.1-1.5
Sang	15.1-15.9	1.3-1.4	40.0-41.7	40.1-42.6	1.0-1.2
Sol II	15.2	1.7	41.9	40.0	1.2
Sol II mutants	14.3-15.9	1.5-1.9	41.1-43.8	38.9-40.2	0.9-1.4
Foreign lines and cultivars, n=39	10.4-17.5	1.0-1.6	40.0-52.4	32.1-43.1	0.5-1.3
<u>Bound lipids</u>					
Selma	18.2-19.9	0.8-1.4	23.0-27.1	51.3-54.2	1.7-2.1
Sang	18.4-19.5	1.1-1.3	27.4-28.1	49.8-51.5	1.4-1.6
Sol II	19.3	1.7	26.7	50.6	1.8
Sol II mutants	17.0-20.5	1.5-1.8	27.4-30.7	46.0-51.5	1.4-2.0
Foreign lines and cultivars, n=39	15.4-22.6	0.9-3.0	23.7-40.4	39.0-54.2	0.9-2.1

Table 6. Variation between years in fatty acid composition in free and bound lipids in the two cultivars Selma and Sang.

Cultivar	year	Palmitic acid %	Stearic+Oleic acid %	Linoleic acid %	Linolenic acid %
<u>Free lipids</u>					
Selma	1973	19.6	35.7	43.5	1.2
	1981	16.1-17.5	39.7-43.0	38.5-42.5	1.1-1.5
	1982	16.8	38.3	42.5	1.6
Sang	1973	18.9	37.6	42.2	1.4
	1981	15.1-15.9	41.3-43.1	40.1-42.6	1.0-1.2
	1982	16.8	39.6	41.4	1.4
<u>Bound lipids</u>					
Selma	1973	20.7	25.1	51.7	2.5
	1981	18.2-19.9	23.8-28.5	51.3-54.2	1.7-2.1
	1982	20.9	30.2	45.5	1.5
Sang	1973	20.8	28.8	48.5	2.0
	1981	18.4-19.5	28.5-29.4	49.8-51.5	1.4-1.6
	1982	20.1	32.9	44.0	1.3

Table 7. Comparison between wild and cultivated oats in lipid content and fatty acid composition.

	Lipid content %	Palmitic acid %	Stearic acid %	Oleic acid %	Linoleic acid %	Linolenic acid %
<u>Free lipids</u>						
Cultivar Sang	4.4-5.6	15.1-16.8	1.3-1.4	37.0-41.7	40.1-42.6	1.0-1.6
Wild oats (<u>Avena fatua</u>)	5.4-6.1	15.1-21.2	1.2-1.7	46.8-51.5	24.9-35.6	0.6-1.1
<u>Bound lipids</u>						
Cultivar Sang	1.7-2.1	18.4-20.1	1.1-1.3	27.4-31.7	44.0-51.5	1.3-1.6
Wild oats (<u>Avena fatua</u>)	2.5-2.8	20.1-24.6	1.1-1.4	34.1-36.8	37.3-41.0	1.3-1.4

THE QUALITY OF DIFFERENT OAT VARIETIES AND INDUSTRIAL OATS
(1984-87) IN WEST-GERMANY

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Variety trials:

In the last years the European and German oatmills had a great demand for high quality milling oats. To get more information about the quality of German oat varieties for oat milling purposes we investigated oat samples of the variety trials performed by the Agricultural Board of Schleswig-Holstein and Hannover at 9-13 different locations in the crop years 1984-87.

External oatquality: Table 1 shows the main parameters

thousand grain weight (TGW) and hull content (dehulling by hand) for the different varieties. The mean values for the single years confirm the well known fact, that the oat quality is dependent on the different years' growing conditions. So in the years 1984, 1985 and 1987 the oatquality was especially good with high TGW and low hullcontent, whilst 1986 severe dryness caused smaller groat development and higher hullcontent.

The German law for grain market structure demands for oats a minimum TGW of 27 g dm and maximum 26 % hullcontent. In 1986 the TGW demand could not be fulfilled by the varieties: Flämingsregent, Flämingsnowa and Fabian and the hullcontent was exceeded by all varieties with exception of Rollo and Präfekt.

Figure 1 demonstrates that independent of the different growing conditions in the years and the trial locations the individual varieties showed a variety typical quality development.

In table 2 relative figures for TGW and hullcontent from means of the 4 crop years were represented and derived from it so called "quality value numbers". Table 3 shows the derivation system. In addition yield datas are given in table 2.

The best quality varieties - proved over several years - are especially Alfred and to a less degree Panther and Flämingsvita. A remarkable high hullcontent have Flämings Silber, Fabian and Columbus; the same results were obtained 1980-82 (1, 2,3).

There are several new varieties with sufficient TGW (Rollo, Bojar, Präfekt, Lupus) and with low to very low hullcontent (Pilot, Nero). These varieties should have special observations during the next years.

Nutrient content: Protein and oil content of the groat -

dehulled with a laboratory air pressure huller - are obviously variety typical (Table 4). The higher protein values (Panther, Flämings Silber) respective the low contents (Flämingsregent, Lupus, Pilot, Nero) could be determined not only as mean values, but also in every single test year and on the different growing locations. This observation applied in a still higher extent to

the oil content. a good potential for oil production have Lorenz and Columbus, whereas Bojar and Präfekt possess an extreme low one.

Industrial milling oats

External quality: In our current control system we, of course, examine also the quality of oat lots usually handled for the milling industry. Table 5 represents the results for W-German oats grown 1984-87 in Schleswig-Holstein/Niedersachsen, and in addition to that the demanded quality requirements for industrial oats are specified.

Compared with the variety trials the quality level is evidently higher, because these milling oats should have a certain minimum quality (f.i. test weight min. 55 kg/hl). Though the differences in the 4 years are not extremely great, there was a poorer grain quality to observe in 1986 - a year with special dry vegetation period - so the grains had more hulls and a smaller grain size value (GSV).

A quality comparison of industrial oats from different countries used in W-German oatmills demonstrates (Table 6) that - regarding the here requested grain physical properties - W-Germany has a very good position under European oat provenances.

East-German oats have lower TGW and grading. So German oats normally develop^a sufficient kernel content to give a good milling quality, but its use for human consumption products of high quality is often limited because of grey-black appearance and damaged grains affected by bad conditions during harvest (weather) and storage.

French oats are of remarkable small grain size, so that the required standard for TGW and grading could not be met in any case; regarding furthermore the high hull content (26 %) it results in a very low TGTW. In spite of this oat mills sometimes need French oats, which have a good sound appearance, especially if other provenances with good sensorial quality are not available.

West-Australian oats are imported to Germany because of its excellent grain quality and appearance. Though the content in hulls and double oats is high, the TGTW is superior.

The portion of foreign grain, foreign matter and double oats in W- and E-German oats often exceeds the permitted maximum; that is the case too for foreign matter in the other oat provenances.

High quality oats in trade are also produced in Sweden and Finland.

Nutrient content: The great protein and oil content of W-German milling oats show only small variations in the different crop years; however the mineral content in 1984 is higher than in 1987.

Between the different oat provenances remarkable variations could be determined: W-Australian oats are relative poor in protein and especially in minerals (potassium, calcium, phosphorus) contrary to Finnish and German oats, caused by higher fertilization and other invirements in N-Europe.

On the other hand W-Australian and French oats contain much oil in the groat.

Conclusion: Extensive quality investigations with different German oat varieties confirmed again that certain varieties with constant high milling quality characteristics are available and could be recommended to the farmers.

Though German milling oats are of good grain physical quality there is a shortage in oats during the last years because of reduced oat cultivation area. The required imported oats are of different external grain quality and nutrient content.

Generally the market in high quality milling oats is very small worldwide.

Lit.:

1. Ganßmann, W.: Qualitätsdaten von Hafer an Hand von Ernteuntersuchungen der letzten Jahre und Qualitätskriterien für die industrielle Verarbeitung. (Quality datas from oats by last years' crop investigations and quality criterions for the industrial processing). - Getreide, Mehl und Brot 37 (1983) 10, S. 298-302
2. Meyer, D., und H. Zwingelberg: Verarbeitungsqualität neuer Hafersorten (Processing quality of new oat varieties). - Getreide, Mehl und Brot 38 (1984) 8, S.227-230
3. Meyer, D., und H. Zwingelberg: Untersuchungen zur Verwendung von inländischem Hafer in der Schälzüllerei (Investigations for usability of domestic oats in oat milling). - Getreide, Mehl und Brot 35 (1981) 9, S.230-234

Table 1: THOUSAND GRAIN WEIGHT and HULL CONTENT
 variety trials Agric. Board Schleswig-Holstein/Hannover 1984 -87
 n = locations

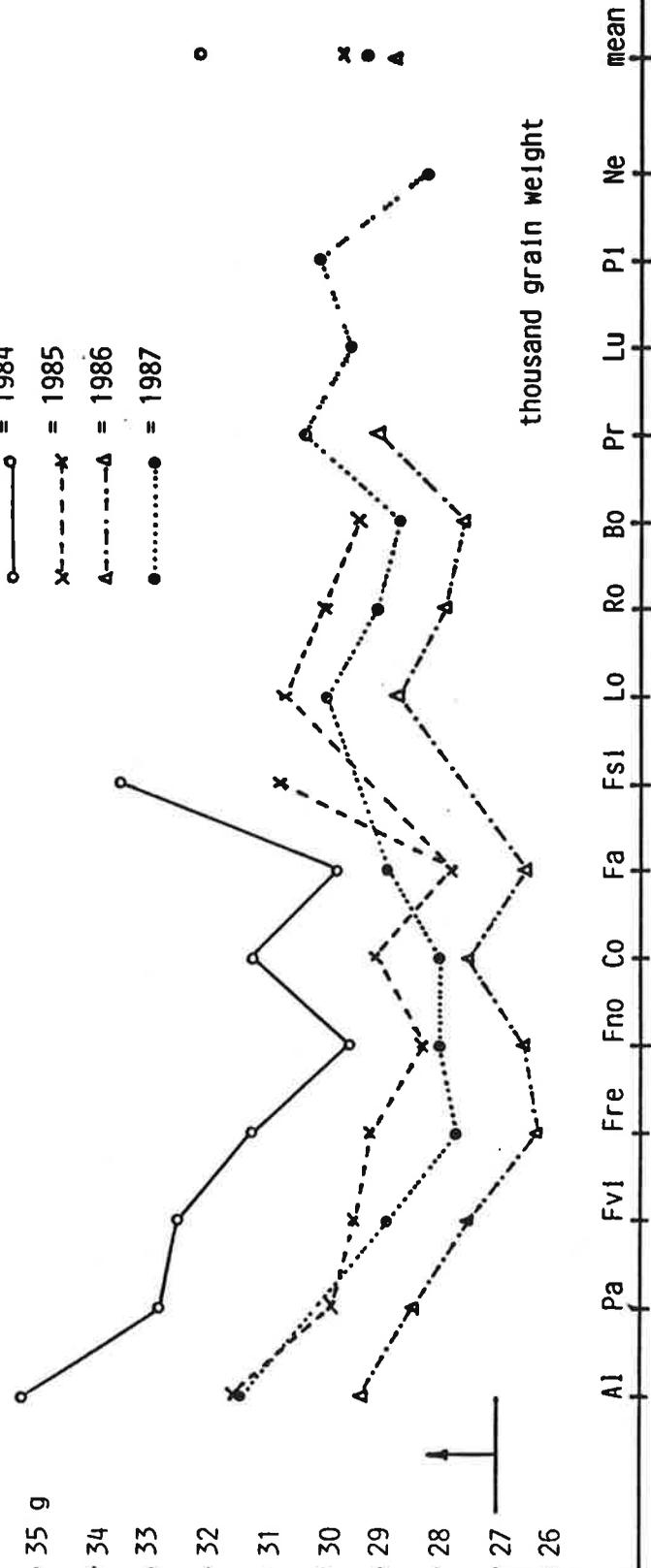
Variety	n	THOUSAND GRAIN WEIGHT (g in dm)					HULL CONTENT (% in dm)				
		1984	1985	1986	1987	1988	1984	1985	1986	1987	1988
ALFRED	45	35,3	31,6	29,4	31,5	24,4	24,6	26,7	25,0		
PANTHER	30	32,9	29,9*	28,5*	-	23,8	24,8	26,1	-		
FLÄMINGSVITA	43	32,6*	29,5	27,5	28,9	24,3	25,6	27,4	25,4		
FLÄMINGSREGENT	45	31,3	29,2	26,3	27,7	24,7	25,2	27,6	25,2		
FLÄMINGSNOVA	23	29,6*	28,3*	26,5*	28,0*	24,2	24,4	26,4	23,7		
COLUMBUS	37	31,3	29,1	27,5	28,0*	26,4	26,9	27,7	27,9		
FABIAN	34	29,8	27,8	26,5*	28,9*	27,5	28,1	29,5	27,0		
FLÄMINGSILBER	14	33,6	30,8*	-	-	28,7	29,5	-	-	157	
LORENZ	36	-	30,7	28,7	30,0	-	26,0	28,9	25,9		
ROLLO	36	-	30,0	27,9	29,1	-	23,7	25,0	24,0		
BOJAR	30	-	29,4*	27,6	28,7	-	24,3	26,7	24,4		
PRAFJEKT	23	-	-	29,1	30,4	-	-	26,0	23,1		
LUPUS	11	-	-	-	29,6	-	-	-	23,8		
PILOT	11	-	-	-	30,1	-	-	-	22,8		
NERO	11	-	-	-	28,2	-	-	-	21,6		
mean		32,2	29,7	27,8	29,3	25,6	25,6	27,1	24,3		
1984 - 87 (n = 429)			29,4					25,6			

* = not on all locations

○ = 1984
 x = 1985
 Δ = 1986
 ● = 1987

thousand grain weight

hull content



Al Pa FvI Fre Fno Co Fa Fsl Lo Ro Bo Pr Lu PI Ne mean

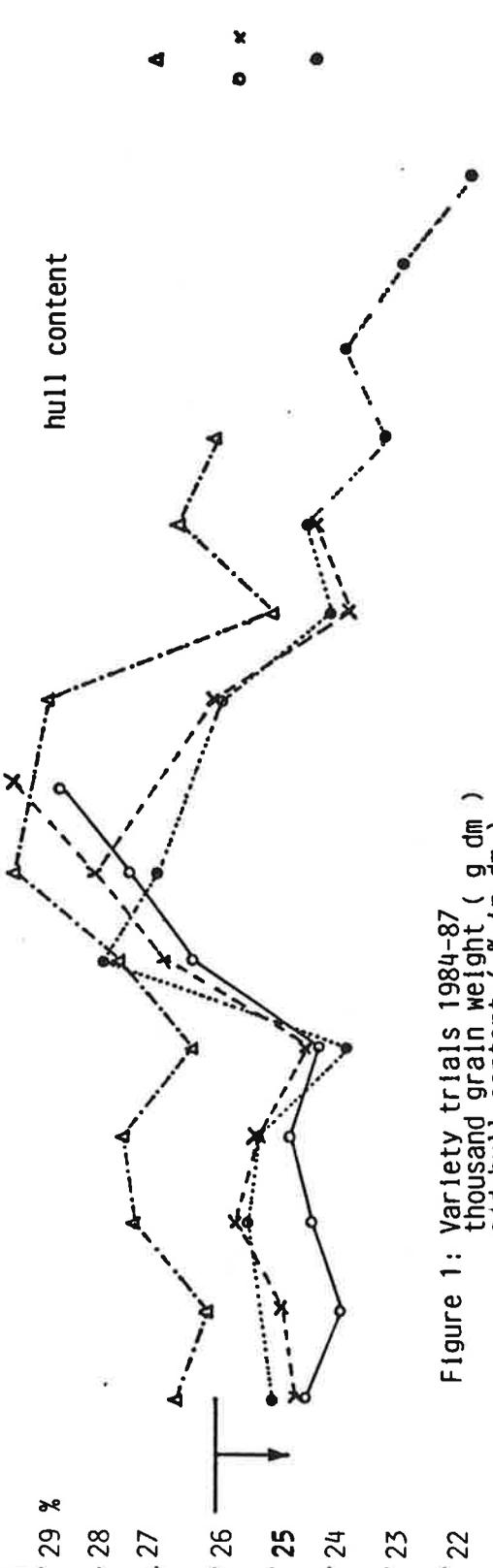


Figure 1: Variety trials 1984-87
 thousand grain weight (g dm)
 and hull content (% in dm)
 (varieties see table 1)

Table 2 : Comparative quality and yield of the different varieties

	Relative figures		Quality value number		Relative grain yield			
	TGW	Hulls	TGW	Hulls	1984	1985	1986	1987
<u>ALFRED</u>	107	98	+ 2	+ 1	102	101	100	99
<u>PANTHER</u>	102	95	0	+ 2	99	98	99	-
<u>FLAMINGSVITA</u>	100	100	0	0	102	104	100	104
<u>FLAMINGSREGENT</u>	96	100	- 1	0	101	103	101	100
<u>FLAMINGSNOVA</u>	95	96	- 2	+ 1	95	94	104	99
<u>COLUMBUS</u>	97	106	- 1	- 2	101	99	95	103
<u>FABIAN</u>	95	109	- 2	- 3	98	94	106	101
<u>FLAMINGSSILBER</u>	104	114	+ 1	- 4	99	97	-	-
<u>LORENZ</u>	103	105	+ 1	- 1	101	102	103	104
<u>ROLLO</u>	100	95	0	+ 2	-	101	101	99
<u>BOJAR</u>	99	98	0	+ 1	-	-	100	97
<u>PRÄFEKT</u>	104	96	+ 1	+ 1	-	-	98	98
<u>LUPUS</u>	101	94	0	+ 1	-	-	-	98
<u>PILOT</u>	103	94	+ 1	+ 2	-	-	-	100
<u>NERO</u>	96	89	- 1	+ 4	-	-	-	100

rel. 100 = average TGW and hull content
for the single years (Table 1)

rel.100 = 60,0 61,7 64,0 59,5 dt/t

Table 3: Determination key for the quality value number

Relative figures	Quality value number TGW	Hulls
87 - 89	- 4	+ 4
90 - 92	- 3	+ 3
93 - 95	- 2	+ 2
96 - 98	- 1	+ 1
99 - 102	0	0
103 - 105	+ 1	- 1
106 - 108	+ 2	- 2
109 - 111	+ 3	- 3
112 - 114	+ 4	- 4

Table 4: Comparison of the protein (N x 6,25) and oilcontent of the different varieties 1984 - 87 (% great dm)

Variety	n	Protein %	Oil %	Protein relative figures	Oil figures
<u>ALFRED</u>	41	14,4	7,0	99	113
<u>PANTHER</u>	21	15,6	7,0	107	113
FLÄMINGSVITA	40	14,3	5,6	98	90
FLÄMINGSREGENT	41	14,2	5,6	97	90
<u>FLÄMINGSNOVA</u>	19	15,1	6,7	103	108
<u>COLUMBUS</u>	33	14,8	7,2	101	116
FABIAN	29	14,9	5,7	102	92
<u>FLÄMINGSSILBER</u>	10	15,5	6,8	106	110
<u>LORENZ</u>	38	14,5	7,9	99	127
ROLLO	36	14,9	5,9	102	95
BOJAR	30	15,2	5,3	104	85
PRÄFEKT	23	15,3	5,1	105	82
LUPUS	11	13,4	5,2	92	84
PILOT	11	13,8	6,3	89	102
NERO	11	15,5	5,3	95	85
mean	n = 394	14,6	6,2	= rel. 100	

Table 5: Oatquality - West-German milling oats

crop year	M %	HL-W kg	TGW g dm	TGTW g dm	Hulls % in dm	Grading			GSV	FG %	FM %	DO %	HO %	TGC %
						a %	b %	c %						
1984 (n=26)	13,9	56,9	31,7 (1)	24,0	24,4 (1)	54	30	12	104	2,5 (6)	0,7 (1)	0,3 (2)	6,6	74,8
1985 (n=47)	14,6	57,1	31,1	23,6	23,6 (1)	54	30	12	104	2,2 (9)	0,8 (13)	0,4 (5)	7,2	75,8
1986 (n=20)	14,0	58,2	30,8 (1)	23,2	24,6 (1)	44	33	16(1)	94	1,8 (3)	0,7 (3)	0,5 (4)	7,8	75,4
1987 (n=16)	14,3	56,5	30,6	23,5	23,3	58	27	11	107	3,5 (9)	0,9 (3)	0,4	9,5	75,5

demands: max. 15,5 min. 55 min. 27 max. 26 a + b + c = min. 90 max. 3 max. 1 max. 0,8

appearance: no grain discoloration, no damaged, dark groats
 smell: sound, not musty and sour

M = Moisture, HL-W = Hectolitre Weight, TGW = Thousand Grain Weight
 TGTW = Thousand Groat Weight, n = test numbers, (n) = demands not obtained
 FG = Foreign Grain, FM = Foreign Material, DO = Double Oats, HO = Hulled Oats

Grading with slit sieve: a = > 2,5 mm, b = > 2,2 mm, c = > 2,0 mm

GSV (Grain Size Value) = a x 1,4 + b x 0,8 + c x 0,4

TGC (Total Groat Content) = CO - (CO x Hulls) + HO; CO (Cleaned Oats) = 100,0 - (FG + FM + HO)

TGW, Hulls and Grading determined in cleaned oats

Table 6: Oatquality - industrial milling oats

Provenance	M %	HL-W kg	TGW g dm	TGTW g dm	Hulls % in dm	Grading a% b% c%	GSV	FG %	FM %	DO %	HO %	TGC %
W-Germany (1984-87) n = 109	14,3	57,2	31,1 (2)	23,6	24,1 (3)	53 30 12	103	2,3 (27)	0,8(20)	0,4 (11)	7,5	75,4
E-Germany (1984-87) n = 174	13,6	59,4	29,3 (9)	22,1	24,4 (9)	37 36 19 (26)	88	1,7 (21)	1,3(63)	0,6 (44)	7,9	75,3
France (1984-87) n = 23	13,3	61,0	22,6 (23)	16,7	26,0 (11)	11 35 32 (23)	56	1,9	2,0(23)	0,3	5,9	72,6
Sweden (1984) n = 12	13,2	62,2	29,3	22,2	24,1	30 43 20	84	2,4 (1)	1,9(12)	0,2	5,9	74,1
Finland (1984) n = 5	12,7	60,5	28,5	22,0	23,0	23 38 28	74	1,5	1,5 (5)	0,2	8,6	76,7
W-Australia (1987) n = 11	9,9	60,4	33,4	24,4	27,0 (8)	14 40 33 (11)	65	1,1	1,7 (11)	1,2 (11)	10,0	73,7
demands	max. 15,5	min. 55	min. 27		max. 26	a + b + c = min.90		max. 3	max. 1	max. 0,8		

(explanations see table 5)

Table 7: Nutrient content of the dehulled milling oats

	Protein (N x 6,25)	Oil	Ash	K	Ca	P
	%	%	mg	mg	mg	mg
	groat dm	groat dm	groat dm	groat dm	groat dm	groat dm
W-Germany						
1984 (n = 20)	14,7	7,0	2,11	453	67	490
1985 (n = 23)	14,4	6,6	2,05	439	71	475
1986 (n = 17)	14,8	6,9	2,07	425	60	467
1987 (n = 16)	14,3	7,0	2,04	418	60	450
W-Germany (1984-87)	14,6	6,8	2,07	435	65	472
n = 76						
E-Germany (1984-87)	14,7	6,4	2,01	415	69	465
n = 114						
France (1984-87)	13,7	8,8	1,93	374	73	442
n = 15						
Sweden (1984)	13,5	6,8	2,00	414	73	457
n = 9						
Finland (1984)	15,5	6,8	2,07	443	65	484
n = 8						
W-Australia (1987)	12,4	9,2	1,52	287	53	333
n = 6						

OATS AS AN ANIMAL FEED

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INTRODUCTION

During the period 1961--65 the annual world oat production was 47.7 M tonnes. According to FAO statistics a similar level of oat production has been reported for the period 1984--87 with a global annual production of 48-49 M tonnes. In North America the annual oat production decreased during the period 1962-64 to 1985--87 from 18.4 M tonnes to 9.2 M tonnes (i.e. 50 %). Also in the Nordic countries (Denmark, Finland, Norway and Sweden) oats have decreased in importance in relation to other cereals. During the period 1961-65 in these countries the annual oat production was 2.98 M tonnes and that of barley 5.51 M tonnes (54 %) against the period of 1983-85 when the production was 3.51 and 10.07 M tonnes (35 %) respectively. However, during this period of time the development, in the different Nordic countries varied, showing an increase in Norway (3.5 times) whereas in Denmark the tonnage of oats decreased to only 18 % of that during 1961--65. During 1986--87 in Norway, Finland and Sweden barley was grown on 40-50 % of the total cereal acreage and oats on 30-35 %, in Denmark corresponding figures were 68 and 2 %, respectively. One reason for these differences in the development between the Nordic countries is probably that the oat yields in the four countries compete with barley and that in Denmark barley is more competitive than oats.

CHEMICAL COMPOSITION

General

Among the cereal grains grown in Middle and Northern Europe oats show the greatest variation in chemical composition (Salo, 1978; Salo & Alaviuhkola, 1980; Thomke, 1961, 1983; Åman, 1987 a,b). Growing and climatic conditions and the genetic background are some of the factors affecting gross composition. This variation influences the feeding properties and the nutritive value of oats. Different chemical and analytical procedures are of importance in estimating the nutritive value as well as in breeding programmes of oats. A main factor influencing the chemical composition of cereal oats is the relative proportion of groats and husks. If not otherwise stated the term oats is subsequently used for the dehulled cereal oats.

As a background for the chemical composition of oats the characteristics of groats and husks are included in Table 1. The content of crude protein (CP, Nx6.25) in the groats is high in relation to that of husks. The value given by Thomke (1960) for husks agrees with the value of 2.9 % reported by Pomeranz et al. (1976). The higher value of 7.0 % CP given by Just et al. (1983) seems to indicate a contamination of the husks by oats since the crude fibre (CF) content in that case seems to be much lower than found in literature. Similarly, there is a great difference in the crude fat (EE) content in the groats as compared with the husks.

Table 1. Chemical composition of cereal oats, oat groats and oat hulls in per cent of dry matter.

	Oat groats		Naked oats	Oat husks		Cereal oats				
	1 ^b	2	3	1	4	1	5	6	7	8
Crude protein CP	15.2	12.2	18.2	7.0	3.0	14.7	12.0	11.6	10.9	12.9
Crude fat EE	7.2	8.8	6.2	3.2	1.5	5.9	6	5.7	5.5	4.5
Crude fibre RF	2.3	2.3	3.9	25.3	32.3	10.0	10		10.6	13.5
NFE	73.2	74.5	69.3	60.5	58.1	66.5	68.8			70.2
Starch									46.2	
Sugars				4.0					1.1	
Ash	2.1	2.4	2.4	6.3	5.1	2.9	3.2	3.0	2.8	
Tannis	1.0			0.9		0.9				
ME ^a	17.1	16.5				13.0	12.7			13.7

^aMetabolizable energy for pigs, MJ kg⁻¹ d.m.

1 ^b	Just et al. (1983)	6	Aman (1987)
2	Thomke (1960)	7	Homb et al. (1987)
3	Quart et al. (1986)	8	Feedstuffs (1987)
4	Thomke (1961)	9	Degussa (1984)

However, the most important difference in the chemical composition between groats and husks is found in the composition of carbohydrates. The content of CF in groats seems to be about 6 % of that in the husks. This difference is still more apparent for starch which could not be expected to be present to any appreciable extent in the husks, but is the predominant nutrient of groats.

Crude protein

The content of CP in oats varies between 8 and 17 %. Under certain circumstances values beyond these limits may be found. Despite the fact that cereals contain relatively limited amounts of CP, they are important sources of essential acids (AA) in animal feeding. In grain based diets for growing pigs and layer chickens more than 40 % of the essential AA are supplied through cereals. Therefore the CP content of oats is of great importance for both ruminants and non-ruminants.

In ruminants the major part of CP is degraded by the rumen microorganisms. However, the rate of break down of the CP should not be too fast in order that it can efficiently be used by the rumen microorganisms. Oat CP is more easily degraded in ruminants than that of barley and maize (Sanne, 1988).

Table 2. Amino acid composition of cereal oats and groats in g per 16g N.

	Oat groats			Cereal oats				
	1 ^a	3	1	1	5	9	7	8
Ala	4.7	5.5	4.9	4.6	4.9		4.8	
Arg	6.8	9.1	6.0	6.4	6.1	6.4	6.7	6.7
Asp	8.0	9.5	7.9	7.8	8.7		8.4	
Cys	2.9	2.4	2.4	2.7	3.0	3.3	3.5	1.7
Glu	21.5	24.3	18.4	21.1	22.2		19.9	
Gly	4.9	5.2	4.9	4.8	5.5		5.5	4.7
His	2.2	2.8	2.0	2.0	2.2	2.0	2.2	2.1
Ile	3.9	4.4	3.6	3.7	4.0	3.6	3.9	4.3
Leu	7.5	8.9	7.0	7.2	7.1	6.9	7.4	7.5
Lys	4.2	4.5	4.1	3.8	4.0	3.4	4.7	3.4
Met	1.8	1.9	1.7	1.7	1.8	1.6	1.8	1.6
Phe	5.0	6.3	4.6	4.8	4.9		5.1	5.2
Pro	5.9	5.8	5.1	5.5			5.9	4.4
Ser	4.7	6.1	4.6	4.4	5.0		6.2	4.4
Thr	3.3	3.8	3.4	3.3	3.6	3.2	3.8	3.5
Trp	1.6	1.1	0.6	1.2	0.9	1.0		1.3
Tyr	3.8	4.5	3.0	3.5	3.5		3.7	4.6
Val	5.4		5.0	4.6	5.1	4.9	5.4	

^aNo. 1-9. see Table 1.

Amino acids

The AA pattern of oat groats, husks and oats is given in Table 2. Only small differences in the AA profile between groats and husks causing similar values for undehulled oats 16⁻¹N. From a nutritional point of view, however, the aminoacids in the husks are of limited value since the CP content of husks is low and also as the CP degestibility is limited.

In the literature the general opinion on the AA pattern of oats with varying CP content is that opposite to wheat, barley and maize, there is only a slight variation in e.g. the Lys content per 16 g N (Pomeranz et al., 1976). The reason seems to be the limited variation in the prolamin content of oats with a varying CP content. In pot experiments with N application over a wide range resulting in CP contents between 10 and 24 %, Stenbjerg et al. (1972) noticed only a slight increase in Glu, His and Arg per 16g N of the oats whereas Lys and other AA were comparatively unaffected. However, Walz (1976) reported that oats fertilized with 22 and 121 kg N ha⁻¹ had CP contents of 9.5 and 11.6 % of d.m., respectively, and corresponding Lys contents of 4.2 and 3.3 g per 16 g N. A decrease in CP quality was noticed by Pomeranz et al. (1976) in groats of oats as a result of the stage of development. The CP content of hulls decreased during the development to about one third of the content of immature hulls, with little changes in the AA pattern, whereas in groats Lys, Thr and Asp decreased and Glu increased.

During germination of oats the content of Lys increases while that of Glu decreases (Dalby & Tsai, 1976. Zarkadas et al. (1982) noticed a somewhat lower content of Lys + Thr + Met in western Canadian (Cv. Sentinel) oats with a CP content of 12.4 % than in eastern Canadian (Cv. Oxford) groats with 14.0 % CP. By screening 289 samples of oat groats with varying genetic background with respect to their AA pattern Robbins et al. (1971) noticed a great variation in CP content (12.4 - 24.4 %) and in the sum of Lys + Thr + Met from 18.2 - 11.1 g per 16 g N. These authors concluded that oats with increasing CP content need not to be accompanied by a decrease in Lys. These authors also pointed out that the variation in Thr seems to be limited indicating that a marked increase in this AA through genetic efforts would be limited.

Thus, under similar environmental conditions the AA pattern per 16 g N seems to be relatively limited, whereas growing conditions, or stages of development and germ plasm might affect the AA pattern of oats.

Crude fat

It is well established that the crude fat (EE) content of cereal maize and oats is much higher than that for other cereals (5 % vs. 2 % of d.m.). Since CF contains more energy than carbohydrates, the content of EE improves the energy value of oats. There seems to exist a great potential for varying the CF content of oats by breeding. Stuke (1959) studying 396 dehulled oat lines noticed a genetic variation between 3.5 and 9.6 % EE. The amount of EE per kernel varied between 0.45 and 2.45 mg. In investigating 6 cultivars Sahastrabudehe (1979) found the variation of total lipids (4.6-11.7 %) to be positively correlated with neutral lipids (3.2-9.3 %), phospholipid level (1.2-1.4 %) and glycolipids (0.26-1.00 %). Triglycerides had less C16 and more C18:1 than glycolipids and phospholipids. The fatty acid pattern of oats is dominated by C18:1 (40 %) and by C18:2 (ca 13 %). Similar results were reported that triglycerides were the most abundant lipid fraction of groats (40 %) scutellum (50 %) and the embryonic axis (58 %).

Carbohydrates

According to Aman (1987 a, b) reporting on Swedish oat analyses, only small amounts of free glucose, fructose, sucrose and fructans occur in oats. There has been shown a variation in starch contents between 39 and 55 % of d.m. The content of total fibre varied between 20 and 40 % of d.m. This author also noticed an average beta-glucan content of 3.2 % (cv. 9.7) and a content of arabinoxylans of 8.0 % with a v.c. of 37 %. This great variation is of interest from a nutritional point of view and could possibly explain differences in the response of poultry to oat feeding. Detailed analyses of fibre constituents were presented by this author, demonstrating cellulose, arabinoxylans, beta-glucans and Klason lignin to be the major components. Most of the fibre components were significantly related to the starch content and thousand kernel weight of oats. Beta-glucans and Klason lignin showed only poor correlations with other fibrous constituents.

The carbohydrate composition of husks has been investigated by Welch et al. (1983, cit. Homb & Matre, 1987). The husk content of oats varied between 23 and 35 %. Following results were obtained (% of husk d.m.): cellulose 32-37, hemicellulose 31-36, lignin 2-10 % and starch 0.4-1.6 %. This latter value for lignin of the husks contradicts the value given for entire oats of 5-13 % of d.m. This seems to be the result of differences in analytical procedures.

Minerals

The variation in content of a number of minerals including trace elements in oats has been investigated by Wetzel et al. (1977). For most mineral constituents the variation was limited, but for Cu the variation differed between growing locations. There were also indications for a suboptimal content of Cu (<5 ppm) and Mn (<20 ppm) from a nutritional point of view. Naked oats have been reported to contain 0.4 % P and a total phytic acid content of 1.1 %, Maurice et al. (1988).

DIGESTIBILITY OF NUTRIENTS

Inter species differences

It is a well established fact that differences exist between animal species in their ability to digest nutrients and feedstuffs of varying chemical composition. Between ruminants and non-ruminants there exist only limited differences in their capacity to digest for example maize. Ruminants, pigs and poultry digest the organic matter of maize at 89, 89 and 87 %, respectively. However for roughages these differences are much more pronounced, as can be demonstrated for the organic matter of alfalfa, which is digested at 73,54 and 41 %, respectively. The explanation is, as well known, anatomical differences between species which enable the ruminants via the rumen microbes to break down complex carbohydrate structures such as cellulose and to make use of the degradation products, whereas non-ruminants this ability or it is very limited. For oat with husks contains high proportions of complex carbohydrate structures, this ability of ruminants make them less sensitive to than non-ruminants feeding poor quality oat than the non-ruminants. Furthermore, pigs are anatomically equipped with a somewhat more developed digestive tract than poultry, which makes the latter animal species more susceptible to increasing fibre level. This is demonstrated by following the equations according to Thomke (1961) for the digestibility of organic matter, y (%) as dependent on the CF content of oats, x (% of d.m.).

Ruminants	$y = 96 - 1.8 x$
Pigs	$y = 96 - 2.3 x$
Poultry	$y = 93 - 2.6 x$

Ruminants

With increasing levels of CF in oats the nutrient digestibility for ruminants is decreasing. Also demonstrated for pig (Table 3) the digestibility of crude protein, crude fat and carbohydrates decreased by feeding lower quality of oats, which also affects the energy value of oats. The organic matter digestibility of oat husks for ruminants has been reported to be 36 (DGL, 1961, Lantzsch et al., 1968) against groats of 96 %. (DGL, 1961). Based on literature studies, Thomke (1983) reported a decrease in the energy value of oats by approximately 2 % per percentage increase in CF content on a d.m. basis. Differences in CP digestibility of different oat consignments were noticed in experiments on lambs by Wehner et al. (1981). The cv. Dal had the highest CP content of digestible CP.

Pigs

Reviews on the use of oats for pigs have earlier been published and reference to them have been made, recently by Homb & Matre (1987). These authors stressed the importance of giving information on the fibre contents of oats used in a particular investigation since this affects the digestibility of the nutrients. In agreement with what already has been pointed out for the dependence of the organic matter digestibility of oats on their CF content other nutrients are more or less affected as demonstrated by Table 3.

Table 3. Nutrient digestibility (y) of oats for pigs in relation to the crude fibre content of oats in per cent of d.m. (x), (Thomke, 1961).

Crude protein	$y = 85 - 0.96 x$
Crude fat	$y = 88 - 0.518 x$
N-free extractives	$y = 99 - 1.85 x \frac{a}{a}$
Crude carbohydrate	$y = 99 - 2.54 x \frac{a}{a}$
ME, MJ kg ⁻¹ d.m.	$y = 17.46 - 0.49 x \frac{a}{a}$

a P < 0.001

This table demonstrates clearly that the carbohydrate fraction is more affected than CP and EE, mainly because part of the carbohydrates of oats are localized as constituents of the husks.

The energy value of feedstuffs is greatly reflected by the digestibility. In Table 4 the energy value of oats in relationship to that of barley according to different authors has been summarized. These values published from Central and Northern Europe indicate that the energy value of oats with a CF content of 10-11 % of d.m. is about 90 % of that found for barley.

Table 4. Energy value of oats in relation to barley according to different authors (after Homb & Matre, 1987).

	Crude fibre content % of d.m.		Rel. energy value
	Oats	Barley	Oat:Barley
Kirchgessner (1970)	11,8	5,3	89
Beckor (1971)	11,2	5,2	89
Just et al. (1983)	10,0	5,2	89
Eriksson et al. (1976)	10,0	5,0	90
Sundstöl et al. (1986)	11,3	5,7	88
Homb & Matre (1987)	11,4	5,8	92

In a literature study Thomke (1983) found that the relative energy value of oats for pigs decreases by about 3.5 % for each percentage unit increase in CF content on a d.m. basis. This value agrees fairly well with that calculated from the data of Salo & Alaviuhkola (1980) of 3 %.

In metabolic experiments on sows Mroz et al. (1986) noticed ad. m. digestibility of 31 % and a ME value of 6.0 per kg, which corresponds to a value of approximately half of that for oats. These authors also found a reduction in blood plasma cholesterol content of gestating sows fed oat husk. Similar results were reported by Zoiopoulos et al. (1983) who did not find any lowering effect on CP digestibility by oat husks inclusion in a sow diet. In comparing the availability of phosphorus in oats, wheat middlings and wheat bran on piglets Stober et al. (1980) arrived at values of 23, 35, and 34, respectively. However, with growing pigs Lantzsch et al. (1968) arrived at a digestibility of the organic matter of husks of only 20 %.

Poultry

As pointed out earlier poultry respond somewhat more to increasing CF contents in oats than pigs. There is no reason here to go into further details, instead reference is made to e.g. Thomke (1961). However, the occurrence of colloidal fibrous constituents such as beta-glucans and arabinoxylans in oat may have certain implications on the digestion processes as has been demonstrated by e.g. Hesselman (1983) for barley.

PROCESSING

The physical structure of oat groats differs from barley and wheat by being softer and more plastic. Therefore it is important to decide on the level of grinding before feeding. When comparing unground barley, wheat and oats when feed to steers Toland (1976) found 48, 40 and 7 %, respectively, of the whole grains in the faeces. Although the beneficial effect of rolling oats is small, significant improvements may be gained from rolling wheat and barley. Similarly, Morgan & Campling (1978) concluded that the benefits from rolling oats are small and should preferably not be undertaken when feeding oats to adult cattle. However, the need of rolling should also be considered from the intake capacity point of view which justifies rolling.

There is no reason to roll oats when feeding sheep, For horses it does not seem to be necessary to roll oats in order to achieve proper digestibility (Günther, 1984).

According to the literature review by Homb & Matre (1987), the need to reduce particle size depends on the level of inclusion of oats, if ad libitum feeding is applied and if the compounded feed is pelleted. If there is a need to improve palatability because of an insufficient disintegration of the husks, this can be overcome either by further disintegration or pelleting. From a digestibility point of view it does not seem necessary to use fine screens in the mill.

The effect of different processing methods of rye, barley, oats and maize on in vitro digestibility were investigated by Buckley & Devlin (1983). The results suggested that with the exception of maize there is little benefit from processing cereals.

FEEDING OF OATS

Cattle

Oats are regarded as a valuable and suitable concentrate source for cattle. The physical conditions in the rumen are favoured by oat feeding. According to textbook literature oats are palatable to ruminants. Danish, Norwegian

and Scottish experiments with oats to dairy cattle in comparison with barley or barley + oats have demonstrated similar results with respect to milk yield and butter fat content (Breirem, 1987). According to a separate contribution at this conference by Sanne (1988), however, an improvement in milk yield and spreadability of butter fat was noted for oat versus barley feeding. This author suggests the EE content of oats is a main factor involved. This could imply that oat feeding should be chosen instead of barley in occasions a deficit of dietary EE can be expected. A plus effect on milk production by feeding high protein oats rather than normal oats was noticed by Schingoethe et al. (1982). There are no reports which indicate that oats should not be useful in beef cattle or sheep feeding.

Pigs

Pig production in many countries is preferably based on cereals including oats. The usefulness of oats for pigs depends on the quality, i.e. the husk or fibre content of the oats. The lowest grades of oats should be avoided since ruminants make better use of the husks than pigs are and poultry.

In comprehensive Norwegian investigation, Homb & Matre (1987) have evaluated oats in experiments with growing pigs. The performance results indicated that oats with a CF content of 11.5 % (d.m.) had 90 % of the energy value of barley (Homb et al., 1988). In comparing oats with barley, the same performance results were achieved. However, differences in performance occurred which could be explained by differences not expected in advance in the grade of oats. On ad libitum feeding of diets including high levels of oats (50 and 100 % of the cereal part) retardation on the growth rate was noticed especially the first six weeks in comparison with barley (Homb & Matre, 1987).

Backfat of oat fed pigs showed significantly higher proportions of C18:2 and lower of C16, C18 and C18:1. There was also a tendency towards increased rancidity of the backfat determined by oxidation test, especially after long-time freeze storage of the carcass samples (Homb & Matre, 1987). However the evaluating on of the fresh fat by a taste-panel could not demonstrate any significant differences between oat and barley feeding. By including 0, 5, 10, 15 and 20 % oats in diets for ad libitum fed piglets Nicholls & Aherne (1984) did not find any significant differences between treatments for feed intake, growth rate or final weight, which suggests that limited amount of oats may be used in ad libitum feeding of piglets. A limitation in performance results occurred when the diets contained more than 30 % oats (Wahlström & Libal, 1979).

Horses

Oats is a well established cereal for horses in Europe and many other countries. Levels of up to 10 kg per day may be fed to horses in heavy work. The most common way is to feed oats unrolled. The improvement in nutritive value by rolling does not justify the processing cost. However, for older horses with defective teeth, rolling is recommended. The feeding of oats should be combined with a limited amount of hay or straw to avoid behavioural abnormalities (Günther, 1984).

Poultry

In two broiler chicken experiments with barley, oats and dehulled oats as the sole cereals in pelleted diets (32.5 and 65 % of the diet) the effect of beta-glucanase supplementation was investigated (Elwinger & Säterby

1987). Birds fed dehulled oats showed superior performance results in comparison with unhulled oats or barley (Table 5). In one of the experiments the oats gave a small but significantly lower frequency of sticky droppings than the dehulled. Oats and barley diets differences in litter bed condition were observed.

Beta-glucanase treatment improved performance (Table 5), but the effects differed between the experiments. In the experiment with 65 % oats the effect of enzyme inclusion was more pronounced for dehulled oats and barley than for unhulled oats. In the experiment with 32.5 % oats the effect of enzyme supplementation did not differ between grain types. The general outcome

of these experiments was that beta-glucanase supplementation increased feed intake during the first 3 weeks on an average by 2 %. For the period 3 to 5 weeks the enzyme supplementation effect was very limited or nil. Pelleting the diets did not destroy enzyme activity.

Table 5. Broiler chicken experiment with baley, oats and dehulled oats in diets unsupplemented (-) and supplemented (+) with enzymes means of 2 experiments. (Elwinger & Säterby, 1987).

	Barley		Oats				P-value ¹ Effect of Grain Enzyme	
	-	+	Undehulled		Dehulled			
	-	+	-	+	-	+		
Mortality	5.0	5.3	4.5	5.0	4.6	5.0	0.28	0.96
Live weight, g								
21 d.	692	797	705	719	706	738	0.09	0.001
35 d.	1470	1485	1466	1475	1487	1515	0.68	0.06
Feed intake, g								
21 d.	996	1008	1028	1034	990	968	0.04	0.08
35 d.	2569	2551	2604	2593	2512	2486	0.03	0.02
Feed conv. ratio								
21 d.	1.53	1.52	1.54	1.52	1.53	1.42	0.03	0.04
35 d.	1.80	1.77	1.83	1.81	1.74	1.69	0.003	0.42
MJ, ME kg ⁻¹ w.g.								
35 d.	21.9	21.5	21.5	21.2	21.9	21.4	0.99	0.430
Sticky droppings, %								
7 d.	16	6	16	11	18	7	0.50	0.001
Litter condition								
points ^a	4.1	3.8	3.6	3.4	5.2	4.3	0.001	0.21

^a 1 - 10; 1 good condition ; 10 poor condition

In broiler chicken experiment naked oats were evaluated at different levels (Maurice et al., 1985). At 69 % inclusion in the weight gain. Bone strength evaluated at 3 weeks declined with increasing level of naked oats in the diets. It was suggested that the relatively high phytic acid content of the oat - soybean meal diet influenced the phosphorus metabolism. The authors concluded that 40 % naked oats may be included in broiler chicken diets without any adverse effects. Oats may also contribute to the supply of essential polyunsaturated fatty acids.

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OATS FOR DAIRY CATTLE

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Oats and barley make up about 70% of the total concentrates to ruminants in Sweden. Barley is the main feed grain with a production of 2,3 million tonne per year (1987). The oat production is about 1,7 million tonne per year. Of the total harvest of feed grain in Sweden, about 30% is used by ruminants.

Oats is a widely used cereal for dairy cattle in Sweden. Milk producers claim that milk production and the content of fat in milk increase when oats are used as an ingredient in the concentrate instead of barley.

Chemical constituents

Differences in chemical constituents between oats and barley may have an influence on the feeding value for dairy cattle (table 1)

Fat

Oats has a higher content of crude fat. That fat may to some extent be bound in the endosperm, which may have an important influence on the feeding value. The oat fat is highly unsaturated.

Protein

The crude protein content (N x 6,25) of oats and barley may be the same or in average higher in oats (+1-2% units). The contents of globulins are higher and the prolamines and glutelins lower in oats than in barley. This makes the proteins in oats more soluble. The degradability of the oat protein in rumen will be higher, making the utilization of the proteins differ between the two grains. The amino acids availability in the intestine (AAT) is higher for barley, but the protein balance in the rumen (PBV) lower, which indicate that the nitrogen content is high in relation to the content of energy from carbohydrates.

The level of acid detergent fiber nitrogen is low in both oats and barley indicating no drying with too hot air.

Table 1 Comparative chemical analysis of protein, oats and barley.

Samples	Oats 15	Barley 39
Crude protein % of dm	13,2	12,1
Digestible (table)	80	76
% of cp		
buffer soluble	35,7 (26-48)	26,3 (19-36)
pepsin soluble	92,6 (89-95)	88,8 (84-95)
ADF-N		
% of total N	3,2	3,4
Crude protein % of dm	14,9	14,9
Rumen degradable, %	85	80
g/kg dm		
AAT	76	94
PBV	+1	-29
% of crude protein		
albumin	1	13
globulin	78	12
glutelin	5	23
prolamin	16	52

Carbohydrates

The amount of crude fiber is higher in oats than in barley while the amount of nonstructural carbohydrates or nitrogen free extract is mainly starch. About 10%-units difference in average starch content between oats and barley we have found in our analysis, but the difference within cereal is about 20%-units (table 2).

Table 2 Comparative chemical analysis of carbohydrates, oats and barley.

	Oats	Barley
% of dm		
NFE	67	76
Crude fiber	11	5
Starch	46	58
Inredos	2	3
ADF	12	6
NDF	31	24

Even if the relation between amylos and amylopectin in starch from oats and barley do not differ, the difference in the structure of the starch granules may be of importance. The fact that fat in oats to some extent is bound in the endosperm may have an important influence on the feeding value.

Feeding trials

Lantmännen in Sweden has a research farm with dairy cattle. There we are regularly making feeding experiments with dairy cows from 3 weeks before calving and up to 16 weeks after calving. The breed is Swedish Red and White Cattle with an average weight of 550 kg. In the trials we are using a basic feed of 5 kg gras hay and 3 kg dm of grassilage. The cows are fed concentrate in relation to milkproduction. The energy of the concentrates are based on calculations from chemical analyses.

Table 3 Trials with oats and barley/Viken, dairy cattle

Trial no	1	2	3	4
Milk, kg				
Oats	25,0	23,0	23,7	23,9
Barley	20,0	19,6	23,8	24,0
Fat, %				
Oats	4,4	4,3	4,3	4,2
Barley	<u>4,7</u>	<u>4,5</u>	4,3	<u>4,3</u>
Protein, %				
Oats	3,3	3,3	3,3	3,1
Barley	<u>3,4</u>	<u>3,5</u>	<u>3,4</u>	<u>3,3</u>
4% milk, kg				
Oats	26,5	23,9	24,6	24,3
Barley	22,1	21,2	<u>24,8</u>	<u>24,6</u>

In four trials (table 3) we have compared oats and barley in the rations. The milk production has been higher after feeding oats but the level of fat and protein in the milk higher after feeding barley.

The trials indicate, that the different levels of fat in the seeds will have a decisive influence on the effect on milk production. Not yet we have shown the possibility to replace the fat given with oats with other sources of fat.

The oatfat is very unsaturated and may be bound in the seed to other ingredients, which will decrease the release of fat in the rumen.

Milkquality

Beside the amount of fat in the produced milk, the quality of the fat is important for the economy in milkproduction. At Lantmännens research farm with milking cows we have compared the amount of milk fatty acids after feeding barley and oats. This has a positive effect on the spreadability of the butterfat and the health of the human consumer.

The jodine number of the milk fat was 32 after feeding oats and 27 after feeding barley.

Table 4 The milkfat composition after feeding oats and barley, average values

	Milk fatty acids, %		
	Saturated	Unsaturated	
		Single	Poly
Barley	78	20	2
Oats	71	26	3

OATS FOR GRAZING

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INTRODUCTION

Oats are considered an important forage crop for pasture for temporary grazing in some regions of the world. The utilization of winter oats for both grazing and grain production has been more common than spring oats for many years in most of the oat growing countries. At times half or more than half of the total oat hectareage in southern United States, Australia, New Zealand and South Africa is grazed entirely or grazed and then left for grain production (Milne and Wright, 1969; Brown *et al.*, 1976; Pass *et al.*, 1977; McDaniel *et al.*, 1977; Fitzsimons, 1974 and 1984; Barr, 1985). Brinkman (pers.comm.), Floss *et al.* (1982) and Floss (1985) indicated that some of the oats that are grown in Brazil and Chile and most of the oats that are grown in Argentina are grazed. The common practice is to graze cattle on oats during the vegetative period, usually for 2 or 3 weeks, and then to remove the livestock and allow the oats to grow to maturity for a grain harvest. Brinkman (pers.comm.) further states that some farmers will turn their cattle into the oats and graze them for the rest of the season, thereby foregoing a grain harvest. Argentina has the largest oat hectareage in South America and at least 80 % of Argentina's oats are grazed for at least a week or two by beef cattle and sheep and then grown to maturity for grain yield.

VARIETIES

Clipping and grazing trials have included varieties and other advanced selections bred for grain production, and there has been little breeding for forage production *per se*. Shands and Chapman (1961) advocated that resistance to crown rust and Victoria blight, ability to grow during cold weather, and intermediate or prostrate plant types are some of the important characteristics of oats grown for winter pastures. Shands (1981) further advocated that the improved genotypes that have high forage yield, grazing adaptation (regrowth), high grazing yield (animal gains), followed by acceptable grain yields would be more suitable for production in developing countries.

Some of the varieties developed as dual purpose (forage-cum-grain) include Cooba, Coolabah, Blackbutt, Echidna, Dolphin, Swan, West, Avon and Balbon from Australia; Amuri from New Zealand; Coker 76-16, Cimarron, Chilocco, Nora, Ora, TAM and X-lines from USA; INIAB-69 and Santa Catalina-67 from Ecuador; and UPF-1, UPF-2, UPF-3, UPF-4, and UPF-5 from Brazil (Mengersen, 1967; Milne & Wright, 1969; Fitzsimmons, 1974; Barnett, 1977; Paz, 1978; Pass *et al.*, 1978; Barr, 1985; Brinkman & Shands, 1985; and Floss, 1985). Varieties such as Gema from Mexico; Akiyutaka, Zenshin and Moiwa from Japan; and UPO-94, OS-129 and OS-132 from India have been bred prominently as forage type (Jime'nex-Gonzalez and Navarro-Franco, 1978; Kumagai and Tabata, 1982; Mishra *et al.*, 1982; and Jhorar *et al.*, 1986).

For many years diploid oats (*Avena strigosa*) have been grown extensively for grazing, particularly in Brazil, Uruguay, and

Argentina (Brinkman and Shands, 1985). According to Brinkman (pers.comm.) attempts are being made to develop hexaploid oats in Brazil that are good grazing types by measuring grain yield and test weight produced by oat regrowth. Preta Comum is used as diploid check. Suregrain, probably the most popular cultivar in Argentina, has long been regarded as a good grazing oat. The main objectives of the grazing research in Argentina is to develop oats that have good grain quality when regrown after grazing (Brinkman, pers. comm.).

CULTURAL PRACTICES

As with all crops, efficient cultural practices are important in the economical production of the oat crop. Recommendations are that oats for pasture should be sown 3 to 4 weeks earlier than for grain production alone. Crowder (1954) found that stands were better and forage yields higher from September seeding than from August seeding. However, Burton *et al.* (1952) observed October 1 to be the optimum seeding date. In Brazil the optimum seeding dates for oats vary from late March to the first half of April (Vilela *et al.*, 1971) and under Indian conditions October 28 seeding produced more forage than when sown on October 8 or in November (Rai *et al.*, 1976).

Rate of seeding for forage production in oats have been recommended differently depending on soil condition and climate. For example, 40-60 kg/ha in Columbia (Echeveni, *et al.*, 1966), 75-150 kg/ha in India (Rai *et al.*, 1976), and 150-250 kg/ha in Saudi Arabia (Younie, 1976). In the United States 110-180 kg/ha of oats per hectare are recommended for forage seeding (Crowder, 1953; Chapman, 1956). It has been observed (Crowder *et al.*, 1953) that heavier rate and cross-drilling or broadcast reduced the penetration of cattle hooves and resulted in greater total root development than light seeding and single-drilling.

Generally, oats for forage receive more liberal fertilizer applications, especially of nitrogen, than for grain production. Burton *et al.* (1952); Crowder *et al.* (1953), Cook *et al.* (1951), Hoveland (1955), Bokde (1965), Sinha (1968), Sandhu *et al.*, (1976) and others observed that nitrogen produced a greater response in oats for pasture than did other fertilizer elements. It is also observed that for early grazing, the heavier rate of fertilization is preferable.

CLIPPING/GRAZING MANAGEMENT

Results from clipping (simulated grazing) indicate that when oats clipped at a height of 6 to 9 cm produced more than those clipped at lower levels (Crowder *et al.*, 1953; Thurman and Grisson, 1954). However, Kishor *et al.* (1986) reported that 5 cm stubble height produced more tillers and regrowth as against 10 and 15 cm. It has been observed that clipping oats bi-weekly or monthly produced more forage than weekly intervals (Chapman, 1956; Wallace, 1956). Thakur and Shands (1954) reported that 1, 3 and 5 clippings reduced root volume by 15, 50 and 70 per cent, respectively.

Clipping injury to small grain plants is closely associated with floral development and stem elongation. It is reported (Gardner

and Rogers, 1956; Gardner and Wiggans, 1957) that clipping is not seriously detrimental as long as the plant remained vegetative. Kishor et al. (1986) suggested that first clipping should not be delayed beyond 60 days after seeding under Indian conditions.

From extensive clipping management trials in Uruguay, Millot and Rebuffo (Shands, H.L., pers.comm.) reported that the 'byzantina' types (considered the best grazing oats) showed the best regrowth and were much less affected by delay in flowering. Furthermore crown rust infections were lower on clipped plots. Most varieties produced more grain in unclipped plots, but 'byzantina' types had increased yields in clipped plots. For 'byzantina' types they emphasized that three times clipping or grazing is required to avoid severe lodging. Groat percentages generally were decreased by clipping, however, groat percentages of the 'byzantina' types were considerably improved by clipping.

Results have indicated that oats were more valuable for dual usage than for grain alone. Oat grazing when terminated by February 15 to March 1 would reduce grain yield 13 to 25 per cent or little more, but grain yields may be reduced to 75 per cent or more when clipping was extended another month (Burton et al., 1952, Morey et al., 1953; Crowder, 1954; Chapman, 1956; Morris and Gardner, 1958). Zillinsky and McMohan (1974) observed that when oat was clipped 3 times, there was no grain yield but it produced 5 t/ha of dry matter and 1.5 t/ha forage protein. However, when it was clipped once and twice it produced 4 and 3.5 t/ha of grain and 2.5 and 4 t/ha dry matter, respectively. Under South African condition Kilpatrick and Pakendorf (1982) indicated that seed yield of 2-cuts averaged 11 per cent of the non-cut plots. Also, regrowth following one cut was better than 2-cuts.

Gardner and Wiggans (1960) reported that the average forage yield from one clipping was highest at the 7-leaf stage than 2 - and 5 - leaf stages while reverse was true for grain yield. Clipping after 5-leaf stage removed flower primordia and reduced test weight. It is observed (Chapman, 1955) that varieties with upright growth habit were more susceptible to overgrazing than those with intermediate or prostrate habit. Grazing in the northern part of the winter area is less harmful to grain yields than in the South. Sprague (1954) found that due to grazing grain production was increased by 13 (fall grazing) to 19 (spring grazing) per cent, delayed internode elongation, and caused 0 (spring grazing) to 5 (fall grazing) per cent lodging. Straw yields were reduced by spring grazing but were unaffected by fall grazing.

In a grazing experiment with oats and triticale Floyd and Zillinsky (1978) observed that oats produced more forage and had better regrowth than triticale and identified strains with ability to recover fairly rapidly after clipping and hence good high protein forage types but poor grain potential. According to Dann et al. (1983) when wheat or oats were grazed by sheep and/or cattle in Australia, the grain yield decreased by 25 to 79 per cent. It was observed that wheat was generally inferior to oats for grazing and grain production. In another study Ralph (1983/1984) reported

that oats and barley were superior to wheat and rye for grazing. Grain yield reduction was estimated to be 20 per cent and provided highest grain production when grazed in August.

The results from clipping indicate that close grazing would result in poor root system and reduced top growth. Rotational grazing will therefore give greater returns by maintaining 5 to 6 cm growth and will avoid overgrazing (Burton *et al.*, 1952). Morey *et al.* (1953) indicated that oats should be 9 to 12 cm tall and have a well-developed root system before being grazed by livestock.

ANIMAL PRODUCTIVITY

The quantity and digestibility of herbage ingested are major factors affecting animal productivity. Oats produce an abundance of excellent forage at a time when other succulent, high protein feed is scarce. Digestibility of oat forage dry matter is above 75 per cent (Hawkin and Autrey, 1955; Bhagwan Das, 1982).

Burton *et al.* (1952) reported that steers made 12-year average gains of 102 kg per hectare from grazing Red Rustproof oats. Annual gains ranged from 60 to 218 kg per hectare with an average grazing period of 89 days. Southwell and Parham (1955) indicated that well fertilized winter grazing oats were economical for fattening market steers. They observed 308 to 463 kg of live-weight gain per hectare when grazed for 100 to 140 days.

Grazing of beef cattle is very common in South America and many of the livestock growers fatten their cattle to market weight by grazing them on oats and other grasses such as fescue. The quality of the beef in South America, especially Argentina and Chile, is excellent in terms of flavor and texture (Brinkman, pers.comm.). Carrillo *et al.* (1969) in Argentina observed that in a trial lasting 89 days during winter-spring, the Aberdeen Angus steers when grazed on oats cv. Bulk 152 gained 0.767 kg/animal/day. The liveweight gains per hectare of 250.6 kg was obtained in another trial lasting 45 days during summer.

Utley *et al.* (1977) reported that average daily liveweight gain of steers on ryegrass or oat pasture was similar, whether sod sown or seedbed sown. Ralph (1983/1984) observed that oats and barley were superior to wheat and rye for animal liveweight gain after grazing. Grazing in August produced highest animal production. McCullough (1955) reported that heifers grazing Arlington oats made average daily gains of 0.94 kg, as compared with 0.81 on rye and 0.80 on fescue grass.

Oat pasture increased milk production on an average by 1.98 to 2.72 kg daily as compared with no such pastures (Copeland, 1943). Marshall (1957) reported that oat had an average carrying capacity of 2.75 lactating cows per hectare and obtained 5.4 kg daily of TDN from oat pasture sufficient for body maintenance. Fernando and Carter (1970) found that nitrogen at the rate of 178 kg per hectare caused a significant loss in liveweight of lactating cows but did not influence the yield and quality of milk. When compared with the lowest rate of nitrogen (35.6 kg/ha), dry matter intake was markedly reduced at the two higher

nitrogen rates (89 and 178 kg/ha) and cows spent 47 minutes less time per day grazing oats given the highest rate of nitrogen.

Pigs on oat pasture required less concentrate per unit gain and saved protein supplement than those in dry lot (Baker, 1949; Southwell and McCormick, 1949). Croker and Suiter (1977) reported that the stocking rate of 5 months old weaner sheep was 40 weaners per hectare when grazed on oats cv. Swan sown at the 50 kg/ha as compared to peas cv. Derimat (67 kg/ha) under sown to oats cv. Swan (11 kg/ha). Liveweight gain was, however, greater in the mixture than the pure oat crop.

BREEDING FOR FORAGE PRODUCTION

There has been very little breeding for forage production per se in oats. Knowledge of fundamental problems are associated with the evaluation of experimental lines, grazing, growth habit, plot size and environment.

Sufficient genetic variation for forage attributes exist in oats (Dhumale and Mishra, 1979; Singh et al., 1981). Mishra (unpub. data) observed that there existed wide genetic variability for regrowth in oats germplasm. Characters such as leaf area, leaf number, tiller number, culm height and thickness, and days to heading have been identified as the most important for increased forage production (Mehra et al., 1971; Solanki et al., 1973; Nair and Gupta, 1976; Dhumale and Mishra, 1979).

High number of tillers per plant has been considered a major plant trait for increased forage production. Roberto Ritter in 1970 (H.L. Shands, pers. comm.) showed that for crosses X 2410 and X 2411 the earlier F_3 lines had higher number of tillers per plant. The lines having plants with many tillers were shorter and better yielders. Transgressive segregation for high tiller number has been observed by Dwivedi et al. (1983) in F_2 populations of diverse crosses. Intra- and inter-specific crosses, combining ability analyses, bi- and multi-parental combinations and other mating types have indicated that a tremendous forage yield potential and other forage attributes exist in oats and can be exploited to breed better forage/grazing types (Solanki et al., 1974; Jatasra et al., 1982; Mishra et al., 1982a & c; Manga and Sidhu, 1984, Dwivedi et al., 1984, and Kishor et al., 1986).

Introgression of genes from A. sterilis, A. fatua, A. magna and A. strigosa may be helpful in obtaining disease resistant lines with increased herbage productivity, better regrowth, greater vegetative growth rate and drought tolerance (Mishra et al., 1982b, Choube et al., 1985). Harsh selection procedures should be adopted to screen breeding materials for winterhardiness and grazing tolerance. The most important characters of forage/grazing type variety should be prostrate growth habit having large leaf area and leaf number with high tillering, vegetative primordia, fast regeneration capacity, deep root system and relatively late maturity to tolerate frequent cutting/grazing.

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OATS FOR SILAGE

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1. INTRODUCTION

Harvesting oats prior to ripening by ensiling the swathed plant is a common practice in oat growing areas of the world where dairying is prevalent and ensiling equipment is available. When oats are ensiled, the objective is to produce a high yield of oatlage that has suitable quality for the ruminant livestock which consume it. Recommendations for ensiling oats in the northern US include wilting swathed plants to 60-65% moisture, chopping so that stem pieces are as short as possible, and packing the silage in the silo. Fine cutting and packing remove some of the air contained in the hollow stems, which provides better conditions for fermentation.

2. FACTORS INFLUENCING TIME OF HARVEST

It is well established that oats are higher in forage quality prior to heading than after heading, and that forage yield increases until the plant reaches physiological maturity (5, 8). This presents a dilemma of sorts, as the oat grower must decide when to ensile his oats--early for higher quality, or later for higher yield. The decision that the oat grower makes usually is influenced by intended use, total feed needs, and quantity and quality of feed that the grower has in storage. Oat growers who intend to feed oatlage to livestock with high energy needs, such as high producing dairy cows or fattening lambs, are likely to ensile their oats at early heading or before. Growers who intend to feed oatlage to livestock that does not necessarily have high energy needs, such as dry cows, breeding stock, etc, may decide to delay ensiling oats until after heading to achieve higher yields. In addition, livestock growers who supplement oatlage with grain as an additional source of energy may decide to delay harvesting oatlage until after heading.

Another important consideration that affects time of harvest is the legume underseeding. Farmers who use oats as a companion or nurse crop to establish a legume such as alfalfa or red clover may emphasize early harvest of oats to facilitate establishment of the underseeded legume. In southern Wisconsin, farmers who ensile oats at heading or before (early to late June) will usually harvest a cutting from underseeded alfalfa by the end of August if moisture conditions are adequate during the summer. Another harvest of alfalfa can be made in mid October after a killing frost has occurred if additional forage is needed during the establishment year. However, harvesting this late in the season is risky because forage yields usually aren't high and a legume that has been harvested just prior to freeze-up is more likely to sustain winter damage than a stand that has good snow-catching ability.

3. FORAGE QUALITY CHARACTERISTICS

Forage quality has been defined as the ability of a forage to supply livestock with needed energy and nutrients. When livestock rations consist primarily of forage, forage quality is acknowledged to be the major factor restricting performance if energy requirements of the livestock are high. High quality forage should be low in two fibrous constituents, acid detergent fiber (ADF) and neutral detergent fiber (NDF), because fiber reduces digestibility and intake of the forage, and limits efficiency of nutrient utilization.

Three major categories of forage quality evaluation are dry matter digestibility, dry matter intake, and metabolic efficiency. Metabolic efficiency refers to the efficiency with which feed is consumed, digested, and converted into animal products. Dry matter digestibility (DMD), often referred to as digestible dry matter (DDM), is frequently used to estimate the energy value of forage. DDM is an estimate of the percentage of a forage that is digestible and is determined from (predicted by) ADF concentration. ADF is the percentage of highly indigestible plant material in a forage. It consists primarily of cellulose and lignin, and has low *in vivo* (inside the animal) digestibility. A low ADF percentage is desirable because it results in high digestibility. As ADF decreases, the amount of forage an animal can consume and digest increases (Figure 1).

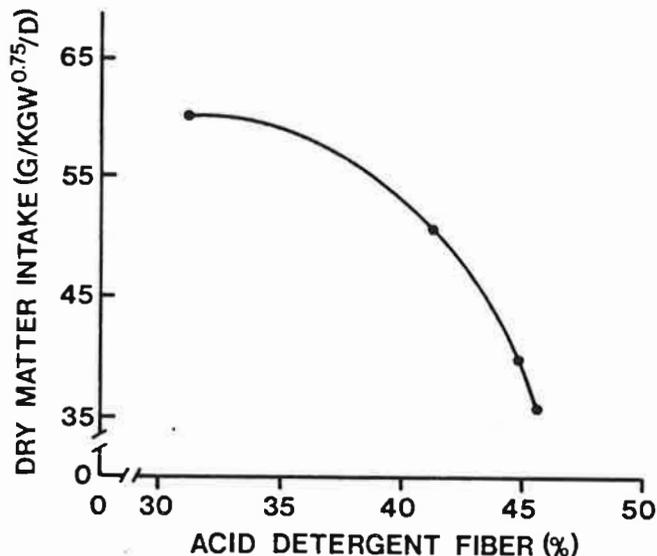


Fig. 1. Relationship between dry matter intake and ADF concentration of oat forage (Burgess et al.).

Dry matter intake (DMI) represents the amount of forage that animal will consume, and is determined from (predicted by) NDF. NDF consists primarily of the cell wall fraction of forage, and is composed of hemicellulose, cellulose, and lignin. NDF includes ADF and is inversely related to dry matter intake. A low NDF is desirable because an animal can consume more forage if NDF is low.

Although crude protein (CP) percentage has little value in predicting energy availability, CP is important because it does indicate the capacity of a feed to meet an animal's protein needs. Crude protein is a mixture of true protein and non-protein nitrogen, and also includes insoluble crude protein. In general, high CP is desirable (Figure 2). When dairy farmers harvest alfalfa in the pre-bloom stage, their objective is to produce a high quality forage that has 19% or higher CP, 31% or lower ADF, and 40% or lower NDF.

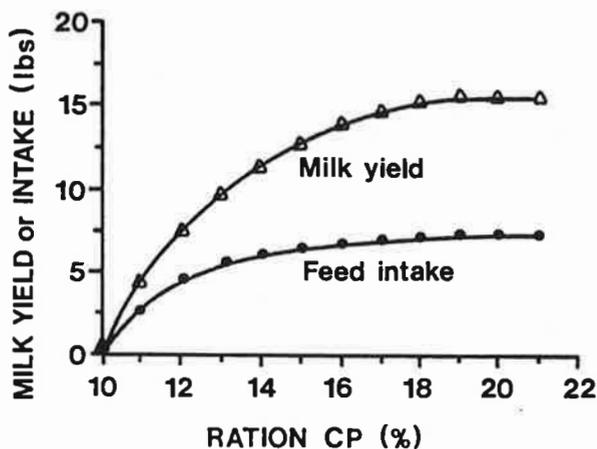


Fig. 2. Change in milk yield and feed intake with increasing level of crude protein (Roffler et al.).

4. SUMMARY OF OAT FORAGE RESEARCH AT WISCONSIN

Although reports on forage yield of oats are relatively common in the literature, forage quality of oats has not been evaluated extensively. Minimal breeding effort has been directed towards improving oat forage yield and quality. Consequently, the small grains project at the University of Wisconsin has recently evaluated forage yield and quality of a number of oat cultivars and selections. Our research has indicated that when a single harvest is made in spring oats, short, early types usually have lower forage yield and higher forage quality than tall, late oats, which confirms what is indicated in the literature (1, 4). However, we have found notable exceptions to this trend (Table 1), and have concluded that testing oat cultivars and selections for forage yield and quality is a worthwhile effort in areas where oats are commonly ensiled. The five selections listed in Table 1 are considered to be among the best of 64 entries that were evaluated at Arlington, Wisconsin in 1987 and 1988. These selections have more potential as forage oats than most of the cultivars that are currently grown in the north central region of the United States. SN404 will be released in 1989 and will be marketed strictly as a forage oat, for it has been average or below in grain yield in three years of statewide testing. Selection 85TL308 is especially promising, as it is high in both forage yield and forage quality. While 85TL308 has not been tested as extensively as SN404, we will proceed towards probable release if it continues to perform well.

Table 1. Forage and milk production characteristics of 15 oat cultivars and five selections harvested at early heading at Arlington, WI in 1987-88.

Variety	Harvest date	Ht at harvest date	Forage yield	CP	CP yield	ADF	NDF	Milk ^{1/} prod /day
	June	in	lb/a	%	lb/a	%	%	lb
Webster	4.7	21.5	2797	14.4	404	26.9	46.7	3022
Hamilton	5.5	22.2	2769	14.1	390	27.8	48.7	2791
Starter	5.5	23.0	2865	14.0	396	29.0	51.7	2610
Don	5.8	21.8	2573	13.9	354	27.8	51.3	2455
Ogle	8.7	25.3	3723	12.8	464	31.0	53.1	3092
Hazel	9.0	25.7	3925	13.0	497	29.6	51.8	3510
Proat	10.0	25.8	3753	13.6	498	28.8	50.5	3554
Centennial	10.2	25.7	3625	11.8	419	30.4	54.4	2954
Trucker	10.3	28.3	4076	12.9	521	30.4	53.0	3461
Riel	10.5	26.3	3887	12.6	481	27.8	49.2	3792
Sandy	11.8	28.8	4180	12.2	498	29.9	51.8	3712
Valley	12.3	25.0	3950	12.6	484	28.3	52.0	3655
Porter	12.7	25.3	3961	12.6	486	28.9	51.6	3633
Lodi	13.2	30.0	4073	12.6	500	29.4	52.9	3571
Dal	13.8	27.8	4099	12.6	511	30.4	53.4	3440
85TL147-1	11.0	25.3	4074	12.1	488	28.1	50.1	3964
84SAT46-1	12.8	27.3	4449	12.7	554	27.2	49.6	4463
85TL308	13.7	29.0	4658	13.4	614	27.5	49.8	4629
QR146-2	14.3	26.2	3981	11.8	462	27.6	48.8	4035
SN404	14.8	30.8	4297	12.4	508	29.2	51.1	3962

^{1/} Milk production figures are for a 1350 lb cow producing 65 lb of milk per day with a milk fat test of 3.8%. Milk production was calculated from an equation developed by Dr. W. T. Howard, Department of Dairy Science, University of Wisconsin-Madison. Forage characteristics integrated in the equation include forage yield, ADF, and NDF.

To improve the quality of oats that are ensiled, dairy farmers in Wisconsin and surrounding states have recently re-instituted the practice of mixing field peas with oats and harvesting the oat-pea mixture when the oats are in the late boot to early heading stage. Oat-pea mixtures were common in several northern dairy areas of the continental US prior to the introduction of winterhardy alfalfa cultivars in the 1950's, and they have been the most popular annual forage in Alaska for many years (2, 6). Our research with Porter oats and Trapper field peas has shown that both forage yield and forage quality of oat-pea mixtures increase as pea seeding rate increases (Table 2). Seeding peas with oats tends to increase forage quality more consistently and extensively than forage yield.

Table 2. Forage traits in an oat-pea seeding rate study at Arlington, Wisconsin, 1986-1988.

Seeding rate in seeds per square foot	Oat-pea results (harvested in June)							Alfalfa yield in August of establishment year ^{2/}	Total 1st year forage yield ^{3/}	1st cut alfalfa yield during year after establishment ^{4/}
	Forage yield	CP	CP yield	ADF	NDF	Lodg ^{1/}				
Porter	Trapper	lb/a	%	lb/a	%	%	0-9	lb/a	lb/a	lb/a
0	20	3309	21.1	698	30.3	38.0	7.0	1240	4549	5370
10	0	2829	14.5	410	30.5	55.0	0	1802	4631	5692
10	4	2987	16.4	490	30.5	50.1	0.9	1646	4633	5750
10	8	3339	18.1	604	30.2	47.6	2.0	1674	5013	5425
10	12	3545	18.2	645	31.2	47.0	5.6	1532	5077	5662
10	16	3557	18.9	672	29.9	43.3	6.5	1484	5041	5474
15	0	3362	13.4	450	32.5	58.3	0	1704	5066	5512
15	4	3603	15.6	562	31.1	52.5	0.9	1785	5388	5546
15	8	3640	16.7	608	30.9	50.6	2.0	1598	5238	5851
15	12	3848	17.6	677	31.1	47.6	4.4	1553	5401	5610
15	16	4020	17.8	716	31.4	46.8	5.0	1411	5431	5278
20	0	3601	13.0	468	31.8	57.3	0	1673	5274	5649
20	4	3647	15.7	572	31.3	53.6	0.5	1719	5366	5737
20	8	3768	16.1	607	32.1	52.7	2.0	1544	5312	5685
20	12	3878	17.0	659	31.4	49.9	3.8	1425	5303	5485
20	16	3790	18.4	697	30.2	46.7	3.8	1315	5105	5844
25	0	3683	12.6	464	32.4	59.4	0	1715	5398	5500
25	4	3817	14.9	569	31.6	54.6	1.0	1601	5418	5500
25	8	4021	15.7	634	32.8	53.1	1.2	1485	5506	5836
25	12	3968	16.6	659	31.6	50.8	1.8	1456	5424	5617
25	16	3882	16.8	652	31.5	50.0	3.4	1281	5163	4948

¹ Lodging scale: 0=erect 9=flat. Lodging was measured in 1986 and 1987. There was no lodging in 1988 due to drought.

² Alfalfa was harvested in mid to late August each year. Fall regrowth was not harvested in October in any year.

³ Total first year forage yield = forage yield from oat or oat-pea mixture harvested in June plus alfalfa yield harvested in August.

⁴ Means are for two years.

The results in Table 2 also indicate that seeding oat-pea mixtures at a rate of 10 to 15 oat seeds/ft² (30 to 50 lb/a) and eight pea seeds/ft² (100 lb/a of Trapper peas) should result in high yields of high quality forage with minimal effects on alfalfa establishment and yield. At these oat and pea seeding rates, crude proteins of 17 to 18% and NDF's of 50% or lower are attainable. Higher oat seeding rates may increase forage yield, but NDF's are likely to increase.

5. GENERAL CONCLUSIONS

Oats that are swathed and ensiled can provide a forage that is a valuable component of the total forage program used by a farmer. Stage of harvest is influenced by factors such as type, maturity, and energy needs of livestock being fed, and the amount of forage and other feedstuffs that a farmer has at his disposal. Ensiling at early heading or before emphasizes forage quality, while ensiling later emphasizes forage yield. Forage yield and quality evaluations on a number of oat genotypes has shown that substantial differences in forage quality exist that are not necessarily associated with height and maturity. Tall, late genotypes that are similar in height and forage yield can differ substantially in forage quality. Our results to date indicate that forage quality differences are repeatable over years. Seeding peas with oats should improve forage yield and quality if the pea seeding rate is at least four seeds per square foot.

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OATS FOR HUMAN FOOD: PROTEIN AND OIL

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A. Protein

Oat (*Avena sativa* L.) groats contain the highest levels of nutritionally balanced protein, and produce the highest protein yields per hectare amongst the cereal grains. Contemporary North American spring-sown cultivars frequently produce groat protein levels in excess of 21%, yet oat researchers believe a further increase of 4 to 5 percentage points is a reasonably attainable breeding objective. Recent research indicates that this proposed elevation in protein percentage in the kernel can be achieved while maintaining, or increasing, grain yield. Increased protein levels in the oat crop would: a) enhance its feed value, b) enhance its standing as a traditional breakfast food, and c) increase its potential for use in the specialty food market (e.g., as a protein additive in foods and beverages) Oat protein concentrate has the advantages of a bland taste, suitable solubilities, and the potential for adequate production capacity (35).

Youngs (57) found oat kernel protein concentrated in the groat. Over 90% of the total protein was contained in the bran and starchy endosperm. Elevated protein percentage was associated with increased protein concentration in the bran and endosperm, increased bran weight and thickness, and a decrease in endosperm weight. As separation of the bran and endosperm does not routinely occur during the milling process, this increase in bran thickness should not be detrimental. The normal end products of oat milling for human consumption are the rolled, rolled and steel cut, or finely ground groat. When oat flour is the desired end product, however, increased bran thickness will decrease flour yield.

Nutritional Value of Oat Protein.

1. Chemical Analysis. The nutritional value of oat protein is equal to, or superior to, protein of other cereal grains except rice (*Oryza sativa* L.) and rye (*Secale cereale* L.). The mean levels of nine essential amino acids in 289 cultivated genotypes surveyed by Robbins *et al.* (43) compared favorably with the FAO-WHO recommendations (11) (Table 1). Lysine, threonine, and possibly methionine are limiting essential amino acids in cultivated oat groats. In the related hexaploid species, Rines *et al.* (42), working with *A. fatua* and Briggie *et al.* (3), working with *A. sterilis*, observed mean groat protein levels of 5.5 to 8.8% greater than those observed in the cultivated species. But mean lysine and threonine varied only slightly from the cultivated species, and genetic variation for methionine was low.

Oats are at variance with other cereal grains in that protein quality does not decrease with increases in groat protein percentage. This results from the predominance of the globulin fraction in oat storage protein (Table 2) (40,44,45). The critical lysine, threonine, and methionine levels in the globulin fraction compare favorably with levels in whole oatmeal (10), while the low lysine and threonine prolamin fraction constitutes an unusually small percentage (10 to 15%) of the storage protein for a cereal grain. In other cereal grains, increases in protein levels are often accompanied by

Table 1. Means and ranges for crude protein and essential amino acids of 289 oat samples (with FAO-WHO suggested levels)

	Mean	Range	Suggested level
	----- % -----		
Protein	17.1	12.4-24.4	--
Lysine	4.2	3.2-5.2	5.5 (76%)
Methionine	2.5	1.0-3.3	} 3.5
Cystine	1.6	0.6-2.6	
Threonine	3.3	3.0-3.5	4.0 (83%)
Histidine	2.2	1.2-3.1	--
Leucine	7.4	4.8-7.8	7.0
Isoleucine	3.9	3.4-4.1	4.0
Valine	5.3	4.9-5.7	5.0
Phenylalanine	5.3	4.9-5.7	6.0

Source: FAO-WHO (11) and Robbins *et al.* (43).

Table 2. Osborne protein fractions as a percentage of total protein

Fraction	Percent of protein	Lysine content
Albumins	10	High
Globulins	70-80	Mod.-High
Prolamins	10-15	Low
Glutellins	<10	Mod.-High

Source: Draper (10), Peterson and Smith (40), and Robert *et al.* (44,45).

disproportionate increases in the prolamin fraction (16); this further reduces the levels of already limiting essential amino acids such as lysine. In oats, however, Frey (13) found that the prolamin fraction remained a constant proportion of total protein as protein levels varied. He noted (14) that lysine, leucine and methionine increased at a greater rate than did protein percentage itself. Peterson (39) concluded that increased protein levels were primarily related to increases in the globulin fraction. The amino acid balance was not altered by the environmentally induced changes in protein because the globulin fraction increased at a greater rate than the other fractions. Prolamin and albumin fractions were relatively stable across environments. An encouraging low, negative correlation (-0.18) between protein and lysine was observed by Robbins *et al.* (43); but larger, negative coefficients were recorded for protein level with threonine (-0.47) and with methionine (-0.39), which indicated that breeders may need to monitor changes in some amino acids when

increasing protein levels. Hischke et al. (23) reported that an 18.5% increase in protein was associated with only a 5.5% decrease in lysine.

2. Biological evaluations. Biological evaluations through feeding tests confirm the data from chemical analysis concerning the nutritive value of oat protein. Howe et al. (24) demonstrated the superior protein efficiency ratio (PER) (1.84) of oats over seven cereal grains fed to weanling rats. Oats supplemented with 0.2% lysine and threonine had a PER (2.50) equal to casein. No differences in PER (mean 2.30) were observed among seven oat cultivars with protein ranging between 18.1 and 22.2% by Hischke et al. (23), while Goulet et al. (21) estimated PER values of 2.15 and 2.31 for two oat cultivars with 22.8 and 15.5% protein, respectively. The process of protein concentrate extraction does not decrease protein nutritive value; McCluskey et al. (35) reported a PER of 1.9 for a high protein cultivar, and 1.8 for the protein concentrate extracted from it.

The similar digestibilities for both high protein and normal protein oats fed to swine (1) indicated that high protein oats should require less supplemental lysine and sulfur amino acids. Wahlstrom and Libal (54,55) did not reduce daily gains or feed to gain ratio when they included high protein oats up to 50 and 60% of the grain in diets of weaned and growing-finishing pigs, respectively. Utilization of high protein oats with 0.66% lysine resulted in up to a 65% reduction in supplemental soybean meal. Genetic increases in protein content have been shown not to reduce protein quality in chicken and rat diets (34). High protein oat cultivars produced more essential amino acids than lower protein cultivars, and supported higher growth rates in diets without lysine supplementation.

Breeding for Increased Protein.

For almost two decades oat breeders have been directing most of their efforts to the wild *A. sterilis* species as a source of genes with which to further increase protein percent and protein yield in the cultivated species. While very significant increases in protein content have been realized in North American spring oat cultivars utilizing cultivated germplasm only, the interest in the wild species results from the widely held belief that the potential for increased genetic variability resulting from interspecific hybridization will increase the rate of genetic gain. Nevertheless, a few studies have highlighted the potential of other species in the genus, notably, *A. fatua* (32,41) and *A. magna* (50).

Studies on the inheritance and gene action governing oat protein predate the interest in utilization of interspecific hybridization. For brevity, the following summarizes results across studies dealing with all species. Groat protein is polygenically inherited; the numbers of genes or chromosome segments involved have been estimated as between one, a 'few', to 25 (7,18,20,27,47). Additive gene action with partial dominance for low protein is frequently reported (7,18,20,26,38,47). Reciprocal effects, although not unknown (46), do not seem to be of major importance. There is convincing evidence that genes in some interspecific crosses act in a complementary fashion to produce high protein transgressive segregates (7,8,31,32). Mean heritability for groat protein percentage is a moderate 45% (Table 3), indicating that progress from selection for this trait is expected. Nine of the 12 estimates are 39% or greater.

Table 3. Heritability of protein percentage

Study	Method	Heritability %
Frey <i>et al.</i> (1954)	Comp. Var ($F_{2:3}$)	15
Frey <i>et al.</i> (1955)	Comp. Var $F_{2:3}$)	89
Campbell & Frey (1972)	Comp. Var ($F_{2:4}$)	41
	Regression ($F_{2:3}$ - $F_{2:4}$)	30
Ohm & Patterson (1973a)	Regression (F_1 - F_2)	51
Ohm & Patterson (1973b)	Regression (F_1 - F_2)	76
Sraon <i>et al.</i> (1975)	Comp. Var ($F_{2:3}$)	41
Frey (1975)	Regression (F_2 - F_3 and F_6 - F_7)	43
Takeda & Frey (1979)	Comp. Var ($F_{2:3}$)	39
Reich & Brinkman (1984)	Regression (F_2 - F_3)	19
Cox & Frey (1985)	Comp. Var ($F_{2:3}$ - $F_{2:4}$)	54
Takeda & Frey (1985)	Comp. Var (F_2 -derived lines)	39
Mean		45

An overall negative association between grain yield and groat protein percentage is found in oats, consistent with the other cereal grains. But this negative association appears to be germplasm-dependent. In addition, a significant negative correlation between the two traits for a whole population does not infer that individual deviant lines are not observed; studies consistently report the occurrence at low frequencies of high protein transgressive segregates with overall agronomic acceptability. Neither should the conclusion be drawn that populations containing deviants from this negative association result only from interspecific matings; Wych and Stuthman (56) showed that breeding populations of cultivated oats in Minnesota, between 1923 and 1980, produced cultivars that increased grain yield by 0.18 q/ha per year, with no associated reduction in groat protein percentage. Total protein yield increased, reflecting an increase in grain yield and in nitrogen harvest index (NHI). However, Takeda and Frey (48) and Kuenzel and Frey (31) have shown that in certain populations containing high protein genes from both *A. sativa* and *A. sterilis*, selection for protein yield need not be based solely on genetic variation for grain yield, but may be based on a simultaneous exploitation of genetic variation for both grain yield and grain protein percentage.

Finally, a combination of recommendations from several authors suggests that the following procedures should be pursued in a program designed to increase protein percentage, grain yield and protein yield in oats: hybridization of high protein *A. sativa* and *A. sterilis* germplasm should be followed by backcrossing to the *A. sativa* parent for two to three generations. Progeny evaluation should be followed by the intermating of high protein and agronomically desirable segregates to concentrate high protein alleles in an agronomically acceptable germplasm pool (26,33,47). $F_{2:3}$ or $S_{0.1}$ lines from this population should be evaluated for protein percentage in micro plots with few replicates. The top 50% of lines should be selected and tested for yield in larger plots and over several environments (49).

B. Oil

Mean lipid content in oats is higher than those reported for other cereal grains. In parallel with protein distribution in the grain, most of the total lipid is found in the bran and starchy endosperm, although the highest concentration occurs in the embryo (60). Approximately 80% of the lipid in the groat is free lipids (ether extracted). Triglycerides are the most abundant component in all groat fractions, and large amounts of free fatty acids do not naturally exist in mature oat groats. When stored at normal temperatures and at a moisture content of less than 10%, undamaged oat groats undergo little change in lipid composition (58). To prolong shelf-life, denaturation of lipase located on the surface of the caryopsis (e.g., by steam treatment) is customary in the production of rolled oats.

Groat oil content of cultivated oats grown in the U.S. has been reported to range from 3.8 to 9.8% (5), and in Great Britain from 4.0 to 11.0% (25). Thus, oats have never been utilized as an oilseed crop. The initial interest in oil content stemmed from a desire to increase the energy value of oats as a livestock feed. Subsequently, Youngs et al. (60) indicated that it might also be important in increasing food caloric production. Frey and Hammond (17) estimated that oat cultivars with 17.0% groat oil, combined with present levels of protein and grain yield, would compete with soybeans as an oilseed crop in Iowa for the production of culinary oil.

Several studies have examined the genetic variation amongst oat species for groat oil content. The data presented by Brown and Craddock (4) on over 4000 entries in the world oat collection are the most comprehensive and are representative of the data presented by other researchers. Oil content varied between 3.1 and 11.6% with a mean of 7.0%. A near-normal frequency distribution was observed with 90% of the entries falling between 5 and 9%. Five entries had greater than 11.0%. In contrast to groat protein percentage, breeding efforts to increase groat oil content utilizing cultivated *A. sativa* germplasm exclusively were limited, but studies of the inheritance of groat oil content involved crosses among *A. sativa* genotypes and *A. sativa* with both *A. sterilis* and *A. fatua* (2,6,19,32,51). A synopsis of results on the inheritance of oil content in both intra- and interspecific crosses indicates the following: oil content is polygenically inherited, additive gene effects are predominant, no reciprocal effects, little genotype x environment interaction, transgressive segregation is common, and heritability is high (>70%).

The major fatty acids of oats are palmitic (16:0), stearic (18:0), oleic (18:1), linoleic (18:2), and linolenic (18:3) (Table 4). Palmitic, oleic, and linoleic together constitute over 95% of the fatty acids measured. Oleic and linoleic acids are almost equal in quantity, resulting in a balance of stability and nutritive value. Variation among genotypes is common for all the fatty acids and, in general, saturated fats comprise about 20-25% and unsaturated fats 75-80% of total lipids. Fatty acid composition is relatively stable across environments; but, if large temperature differences discriminate between environments, the relative contributions of saturated to unsaturated fatty acids can vary within the same genotypes.

Increased lipid content is correlated with an increase in oleic acid and decrease in palmitic, linoleic and linolenic acid (Table 5). These changes are in part related to the relative changes in triglyceride and phospholipid classes (9).

Table 4. Relative fatty acid composition of oats

Fatty acid	Mean %	Mean (mol. %)	Range
Palmitic (16:0)	18.9	19.6	13.0-28.0
Stearic (18:0)	1.6	1.4	0.5-4.0
Oleic (18:1)	36.4	38.7	18.7-53.0
Linoleic (18:2)	40.5	38.9	26.0-53.0
Linolenic (18:3)	1.9	1.5	0.5-5.0

Source: de la Roche *et al.* (9), Hammond (22) and Youngs and Puskulcu (59).

Table 5. Correlation between the major fatty acids and total lipid content

Fatty acid	Frey and Hammond (1975)	Youngs and Puskulcu (1976)	de la Roche <i>et al.</i> (1977)	Forsberg <i>et al.</i> (1974)
Palmitic	-0.08	-0.76**	-0.89**	-0.42
Stearic	0.03	--	--	0.36
Oleic	0.37	0.91**	0.98**	0.66**
Linoleic	-0.38**	-0.85**	-0.98**	-0.40
Linolenic	-0.36**	--	--	-0.11

Studies on the inheritance of fatty acids (29,30,52,53) indicated that both simple and polygenic inheritance is involved in the expression of palmitic, oleic and linoleic acids; two to three genetic factors have been implicated in the inheritance of oleic and linoleic acid, and it has been postulated that a single gene, multiple allelic control of oleic and linoleic acids may be involved. Additive gene action is most important, but partial dominance and epistasis is sometimes observed. Reciprocal effects are not important. Heritabilities are moderate to large. Correlations between all fatty acids tend to be negative with the exception of palmitic and linolenic, and linoleic and linolenic.

Quality in a culinary oil is determined by the relative contents of the various fatty acids. Saturated acids, such as palmitic, contribute to oil stability, while the unsaturated oleic, linoleic, and linolenic contribute to the physical properties necessary for culinary oil. It is noteworthy that the polyunsaturated linolenic acid, which is a major contributor to flavor instability, is lower in oat oil than in soybean oil.

Thro *et al.* (53) concluded that oat genotypes could be selected for: a) groat oil high in saturated (palmitic) acid, b) groat oil high in polyunsaturated (e.g., linoleic acid), or c) groat oil composition similar to existing genotypes. They emphasized the unique characteristics of oat oil such as the occurrence in near equal amounts of both of oleic and linoleic acid and the high palmitic acid content. They cautioned that selection for increased total

oil should be accompanied by positive selection for palmitic and linoleic acids if it is desired to conserve the fatty acid composition of oats, because increase in total lipid is highly positively correlated with oleic acid.

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BIOMEDICAL CONSIDERATIONS OF OAT DIETARY FIBER AND BETA-GLUCANS

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INTRODUCTION

The nutritive value of oats is well documented. Oat products consumed by humans are generally from the entire groat and thus are essentially considered to be whole-grain products. In the normal milling of oats, only the fibrous hull and adhering portions of the oat grain are removed. The bran, the aleurone layers, endosperm, and the germ remain in the fraction consumed as food. The outer cellular layers of the groat are especially rich in protein, fiber, vitamins, and minerals. Therefore, the milling, separation and isolation of oats yields a product high in nutritive value and dietary fiber (Peterson et al, 1975; Gould et al, 1980).

In addition to the general nutritive value, oats has recently received increased attention from the nutrition and medical communities because of its dietary fiber content and associated role in reducing cholesterol levels--a recognized risk factor for coronary heart disease, its affect on sugar levels associated with insulin needs and diabetes, as well as its impact on colon cancer and related disorders. Many of the metabolic and physiological effects of oat products have been attributed to the soluble dietary fiber and particularly the beta-glucan content of oats. This review provides an overview of the physiological effects and potential health implications of oat fiber consumption as well as a brief discussion of the structure and physical properties of oat beta-glucans.

I. STRUCTURE AND PHYSICAL PROPERTIES OF BETA-GLUCANS

Histochemical studies have shown beta-glucans to be located throughout the oat groat (Fulcher, 1986; Wood et al, 1986). However, beta-glucan levels of typical commercial varieties of oats are more concentrated in the subaleurone/outer endosperm areas of the groat (Henry, 1987). The oat husk contains virtually no soluble fiber and is comprised primarily (99%) of insoluble polymers containing cellulose and considerable amounts of xylans and lignin (Frolick and Nyman, 1988).

The dietary fiber and beta-glucan content of commercial oatmeal and oat bran are outlined in Tables 1a and 1b. The soluble dietary fiber component is primarily comprised of beta-glucans. Beta-glucans are high molecular weight polymers of beta-1, 3 and beta-1, 4 linked D-glucopyranosyl units. The ratio between the number of beta 1, 3 linkages to beta 1, 4 linkages is 1 to 3.2 (Hyldon and O'Mahony, 1979). The resulting irregular configuration makes these molecules partially water soluble. Extraction and purification of the beta-glucan fraction of oats have yielded concentrated forms of oat gum (Wood, 1986). Physical factors such as flour particle size, temperature, pH, and ionic strength have been reported to influence beta-glucan yields and solubility (Wood et al, 1978).

Analysis of 35 commercial oat cultivars indicate a range of 3.1 to 5.9% in total beta-glucan content (Table 2) (Webster, impl. data). This variation is largely due to genetic and environmental differences among the different cultivars. The mean is 4.2%. Variation in beta-glucan content suggests there may be dose related physiological effects. Compared to other cereals, oats and barley have relatively high contents of beta-glucans. One estimate of the beta-glucan content of barley indicates a range of 3.0 to 6.9% (Aman and Graham, 1987).

TABLE 1a*
Total Dietary Fiber in Oatmeal and Oat Bran

	<u>Total Dietary Fiber % Original Dry Weight</u>
Oatmeal	12.1 ± 0.2
Oat Bran	18.6 ± 0.5

TABLE 1b*
**Beta-Glucan Content of Soluble and Insoluble Fractions of Dietary Fiber
 In Oatmeal and Oat Bran**

	<u>% Total Fiber</u>	<u>% Beta-Glucan</u>
Oatmeal		
Soluble	40.5	74
Insoluble	59.5	8
Oat Bran		
Soluble	38.7	74
Insoluble	61.3	19

* Adapted from Shinnick et al, 1988.

TABLE 2

Beta-Glucan Content of Oat Cultivars

<u>Cultivar</u>	<u>% Beta-Glucan</u>
Kelly	4.3
Nodaway	4.8
Webster	3.8
Ogle	4.5
Proat	4.6
Otee	5.8
Porter	4.9
Noble	4.3
Dal	4.9
Multiline E-77	4.1
Preston	4.7
Larry	5.9
Lyon	4.0
Lang	4.5
Woodstock	4.6
Oxford	4.3
Ogle T-39	4.2
Ogle T-35	4.0
Kamouraska 1	4.2
Kamouraska 2	4.5
A - 1 Argentina	3.7
Tulancingo	4.5
Paramo	3.9
Tibor #1	3.7
Tibor #2	3.6
Rodney	3.4
Garry	3.6
Coker - 820	3.5
Coker - 227	4.2
Coker - 84	4.2
Donald T.4	3.6
Manic 1	4.0
Manic 2	3.5
Wild Oats	3.1
CR - A Grade	4.0
Old Fashioned Retail	4.4

The effect of viscosity development and solubilization of the beta-glucan due to cooking of rolled oats was investigated (Yiu et al, 1987). Comparison of a rapid cooking method and a gradual cooking method indicate the latter induced more structural disruption of cell walls and an increased release of beta-glucans. Both cooking methods improved the digestibility of the rolled oats, however, increased solubilization of the beta-glucans by gradual cooking may further modify their physiological effects. Gum viscosity in general, has been implicated in mediating several physiological effects such as gastric emptying, intestinal absorption, blood lipid concentrations and postprandial glucose levels (Jenkins et al, 1978; Ink and Hurt, 1987). The effect of cooking on physiological function needs to be further investigated as gradual cooking and rapid cooking methods are both commonly used procedures in preparing oatmeal for consumption.

It has long been believed that soluble dietary fibers in general pass relatively unchanged through the small intestine into the colon where it is fermented (Cummings and Branch, 1986). In the case of soluble oat fiber, this premise had not been demonstrated in humans until recently. Digestion and absorption studies in seven ileostomy patients support the view that human digestive enzymes do not break down the nonstarch polysaccharides (NSP) of oats as the beta-glucans in oats were almost completely recovered after these patients were fed test meals of 100 grams of oats (Englyst and Cummings 1985).

II. HYPOCHOLESTEROLEMIC EFFECTS

(i) **Animal Studies**

As early as 1963 De Groot et al reported that rolled oats incorporated into the diet of rats decreased their serum cholesterol. The hypocholesterolemic effects of oats was greater than that found for all of the other grains tested. Fisher and Griminger (1967) reported that plasma cholesterol levels were significantly reduced in chicks fed whole oats, oat hulls or oat groats. Oat starch and oat oil did not affect cholesterol status. The results of these studies remained unexplained until the health implications of dietary fiber became a significant area of research.

A patent was issued to Hylton and O'Mahony in 1979 for demonstrating in rats the hypocholesterolemic effects of oat or barley gum in rats. The active cholesterol lowering properties of oat bran was shown to be related to its water soluble gum content. Similar findings were reported by Chen and Anderson (1979). They showed that serum total cholesterol concentrations could be lowered when rats were fed diets supplemented with either 36.5% oat bran, 10% pectin or 10% guar gum. Liver cholesterol concentrations were also reduced. A repeat experiment was conducted with 36.5% oat bran, 10% oat gum or 10% pectin. The oat gum (Chen et al, 1981) yielded more pronounced reductions. Total serum cholesterol concentrations were 40% lower in the oat gum and pectin groups and 24% lower in rats fed oat bran. Increases in HDL-concentrations was highest in the oat gum fed group. The oat gum and pectin groups had significantly lower liver cholesterol concentrations than the oat bran groups.

Other evidence linking the beta-glucan fraction of oat bran to its hypocholesterolemic effect is the demonstration that high beta-glucan containing barley is also effective in lowering serum cholesterol. Prentice et al (1982) showed both oats and barley were effective in reducing plasma and liver cholesterol levels in rats. Fadel et al (1987) recently demonstrated chicks fed a high viscosity barley had lowered serum cholesterol and LDL-cholesterol levels. Addition of beta-glucanase, a beta-glucan degrading enzyme reversed this effect.

(ii) Human Studies

The cholesterol lowering properties of rolled oats observed with laboratory fed rats, prompted DeGroot and his coworkers (1963) to conduct similar studies in hypercholesterolemic men. They were able to reduce serum cholesterol levels by (11%) in these men when they ate 140 g of rolled oats as bread each day for three weeks.

Subsequent studies over the past two decades have repeatedly demonstrated the lipid lowering effects of oat consumption in humans (Table 3). The degree to which serum cholesterol is lowered may be influenced by a host of variables such as the initial cholesterol status of subjects, the total fat and cholesterol content of the diet, and the amount and nature of the oat product (i.e. oatmeal versus rolled oats versus oat bran, versus oat fiber) that is incorporated into the diet. Generally greater decreases in serum cholesterol are achieved by subjects that have an elevated serum cholesterol level.

Studies in which relatively low daily doses of oat fiber were consumed (e.g. 43 g oatmeal, 0.6 g/kg BW oat bran) by individuals with normal to low serum cholesterol levels consuming self-selected or high cholesterol diets have resulted in lesser changes in serum cholesterol (Gromley et al, 1978; Kretsch et al, 1979). The decrease in cholesterol is shown to correlate well ($r = .867$) with the oat bran dose. (Gold and Davidson, 1988). Gold and Davidson (1988) approximate this relationship to be: percentage decrease in cholesterol = $0.156 \times (\text{gram oat bran/day}) + 1.0$.

Decreased total serum cholesterol and more specifically LDL-cholesterol concentrations have been associated with a lower risk of coronary heart disease (CHD). Higher HDL-cholesterol concentrations are associated with a reduction in the risk of CHD. Most clinical studies with oat products have demonstrated lowered LDL-cholesterol levels and increased or no change in HDL-cholesterol levels. Kirby and co-workers (1981) demonstrated a significant decrease in serum cholesterol (13%) and LDL-cholesterol (14%) after hypercholesterolemic subjects consumed 100 grams of oat bran for two weeks in a hospitalized setting. To determine whether these results were applicable in a free living situation, eight men were followed for a period of 24 to 99 weeks (Anderson et al 1984b). These men were instructed to consume a low cholesterol diet that included oat bran and beans in their daily diets. After 99 weeks, serum cholesterol had maintained a 22% reduction, LDL-cholesterol a 29% reduction, and HDL-cholesterol an increase of 9%.

The hypocholesterolemic effects of fat modified diets have been well documented. The ability of oat products to enhance the blood lipid lowering effects of a low fat diet has been studied by several investigators. Turnbull and Leeds (1987) observed an 8% drop in the serum cholesterol levels of 17 hypercholesterolemic individuals consuming a diet containing no more than 35% calories from fat, for a period of one month. Subjects were then randomized to one of two treatment groups for another month, in which they were instructed to continue eating the low fat diet supplemented with either 150 g of rolled oats or 137 g of wheat. Oat supplementation further reduced serum cholesterol levels by 5%, whereas wheat supplementation did not produce further significant reductions below that which resulted from the fat-modified diet alone.

Van Horn et al (1986) demonstrated similar added effects of oatmeal or oat bran on cholesterol levels of free-living normolipidemic individuals consuming the type of low fat/low cholesterol diet advocated by the American Heart Association (AHA).

TABLE 3

HUMAN STUDIES INVOLVING OAT FIBER INTAKE

<u>Reference</u>	<u>Subjects</u> (Chol. Status)	<u>Test</u> <u>Duration</u>	<u>Diet</u>	<u>Fiber Source</u> <u>Amount/Dav</u>	<u>Results</u>
1 deGroot et al (1963) <u>Lancet</u> 2, 303	21 males 30-50 yrs. (High-normal)	3 week	Self-selected	140 g rolled oats in bread	Serum cholesterol decreased significantly (11%) when rolled oats were added to the diet.
2) Luyken et al. (1978) <u>Voeding</u> , 26, 229.	76 males 19 women 20-16 yr. (High-normal)	4 or 8 wk	Self-selected	50 g oatmeal in bread	The use of oatmeal bread for 8 wks was accompanied by a significant drop in the cholesterol level of about 6%.
3) Cormley, et al. (1978) <u>Ir. J. Fd.</u> <u>Sci. Technol.</u> 2, 85.	58 males 10 females 30-50 yr. (Normal)	6 wk	Self-selected	43 g oatmeal	Serum cholesterol and HDL-cholesterol levels were not reduced compared to cornflakes.
4) Kretsch et al. (1979) <u>Am. J. Clin.</u> <u>Nutr.</u> 32, 1492.	6 males 23-40 yr. Normal	15 days	Controlled	oat bran or toasted oat bran (0.6 g/kg BW)	No significant differences in serum cholesterol and triglyceride levels were found.
5) Gould et al. (1980) In: "Cereals for Food and Beverages." G.E. Inglett & L. Munck, Ed. Academic Press, NY p. 447	12 males 2 women 32-53 yr. (Normal)	4 wk	Self-selected	1½ oz. Instant (oats)	No significant change in the mean serum levels was observed, though a significant depression was found in four subjects over age 40.
6) Kirby et al. (1981) <u>Am. J. Clin. Nutr.</u> 34, 2061.	8 males 35-62 yr (high)	10 days	Controlled	100 g oat bran as cereals & muffins	Significant decreases in serum total cholesterol (13%) and LDL-cholesterol (14%) were found. HDL-cholesterol remained unchanged.
7) Judd & Truswell (1981) <u>Am. J. Clin.</u> <u>Nutr.</u> 34, 2061	6 males 4 women 27-37 yr (Normal)	3 wk	Controlled	125 g rolled oats	Mean reduction of 3% was not significant; although 7 of 10 subjects showed reduction in plasma total cholesterol.
8) Anderson et al. (1984a) <u>Am. J.</u> <u>Nutr.</u> 34, 2061.	20 males 34-66 yr. (High)	3 wk	Controlled	100 g oat bran or dried beans	Both fiber sources decreased serum cholesterol levels (19%) and LDL-cholesterol (23%) significantly over the test period.
9) Anderson et al (1984b) <u>J. Can.</u> <u>Diet. Assn.</u> 45:140-149	20 males 34-66 yr. (High)	24-99 wks	Fat Modified	41 g oat bran and 145 g beans	After 24 wks serum cholesterol was decreased by 26% and LDL-cholesterol by 24%. After 99 wks serum cholesterol was decreased by 22%, LDL-cholesterol by 29%, and HDL-cholesterol increased by 9%.
10) Van Horn et al. (1986) <u>J. Am. Diet.</u> <u>Assoc.</u> 86:6, 759-64	208 incl controls 30-65 yrs. (Normal)	12 wks.	Fat Modified	35-39 g oatmeal or oat bran	Total cholesterol dropped 8% with fat modified diet and oatmeal product; 5% with fat modified diet alone.
11) Turnoull & Leeds (1987) <u>Am. J. Clin.</u> <u>Nutr.</u> & <u>Gastroenterology</u> , Vol. 2	9 men 8 women (high)	12 wks	Fat Modified	rolled oats 150 g	Total cholesterol dropped 13% with fat modified diet and oats; 8% with fat modified diet alone.
12) Gold et al (1988) <u>Western J. Medicine</u> 148:99-307	72 incl. controls (Normal to low)	4 wks	Self-selected	34 g oat bran	Total Cholesterol dropped 5.3%, LDL-cholesterol 8.7%, and no change in HDL-cholesterol.
13) Van Horn et al (1988) <u>J. Pre-</u> <u>ventive Med.</u> 17:3	236 incl. controls (Normal)	12 wks	Fat Modified	56 g oatmeal	Total cholesterol dropped 8.3% with fat modified diet plus oats; 6.6% with fat modified diet alone. Subgroup with >198 mg/dl baseline dropped 10% with fat modified diet plus oats, 6.6% with fat modified diet.

After six weeks of dietary fat modification, total serum cholesterol levels dropped 5-6%. The inclusion of 35-39 g of oat products per day for another six weeks resulted in a further 3% drop in cholesterol levels. Van Horn et al (1988) confirmed the reproductibility of their findings with a similar study of 236 healthy volunteers with normal cholesterol status. Supplementation with about 2 oz./day of oatmeal to the AHA diet resulted in a total serum cholesterol decrease of 8.3%, whereas the AHA diet alone had resulted in a decrease of 6.6%. A subgroup of individuals in this cohort with initial cholesterol levels ≥ 198 mg/dl experienced a 10% decrease in total serum cholesterol with oat supplementation and 6.6% decrease with the AHA diet alone.

Reductions in serum cholesterol levels by the ingestion of oat bran or oat fiber have been reported among young normocholesterolemic individuals even while consuming the usual Western diet (i.e. 40% calories from fat). Gold and Davison (1988) observed a drop in total serum cholesterol of 5.3%, a drop in LDL-cholesterol of 8.7%, and no change in HDL-cholesterol when a group of young, healthy medical students ingested 34 g of oat bran daily in the form of oat bran muffins for four weeks. More concentrated formulations of oat fiber have demonstrated even further reductions in total serum cholesterol among young individuals with normal to low cholesterol status. Vorster et al (1986) observed a reduction of 15-20% in total cholesterol values of young physiology students when daily dietary fiber intake was increased from 22 g to 32 g. Dietary fiber intake was increased by the consumption of 15 fiber tablets that supplied 9.75 g of oat fiber. Body weight changes during the three week experimental period were insignificant.

Evidence that oat fiber may be a useful dietary adjunct in treating hypercholesterolemia is increasing. The public health significance of dietary induced reductions in serum cholesterol can be quantified since recent data indicate that every 1% fall in the level of serum cholesterol leads to as much as 2% fall in the incidence of first major coronary events (LRCP, 1984). The advantages of using oat products include its low cost of intervention and availability (Kinosian et al, 1988).

(iii) Beta-Glucan Concentration and Processing

Diets containing 10% oat gum beta-glucan content in rats was shown to be more effective in lowering serum cholesterol than diets containing 35% oat bran (Chen et al, 1981). The effects of processing and soluble fiber intake on the hypocholesterolemic properties of oat fiber was assessed by Shinnick et al (1988). Rats were fed high cholesterol diets containing 2-6% dietary fiber as cellulose, oatmeal, oat bran, high fiber oat flour or one of flour processed high fiber oat flours for three weeks. The soluble beta-glucan content of oatmeal and oat bran was 28-30% of the total dietary fiber and 29-43% of the total dietary fiber in high fiber oat flours.

All of the diets containing oat fiber products demonstrated a 30-35% decrease in plasma cholesterol concentration with no alteration in food intake or growth. As little as 4% dietary fiber derived from processed oat flour significantly reduced serum cholesterol concentrations. Processing increased the soluble fiber fraction and the amount of total beta-glucans in the high fiber oat flour, as well as demonstrated a trend towards producing a greater hypocholesterolemic effect.

The increased benefits of processed oat fiber was also reflected in lipoprotein changes. Ney et al (1988) reported the lipoprotein profile of rats fed these same diets containing 1% cholesterol and 0.2% cholic acid and 6% dietary fiber from oat bran, high-fiber oat flour, or a processed oat fiber product for 20 days. All oat fibers reduced total lipoprotein cholesterol by 25-45%, VLDL and LDL cholesterol by 40-60% and increased

HDL cholesterol by 25-40%. The processed oat fiber product which contained a higher proportion of soluble fiber reduced lipoprotein cholesterol levels significantly more than oat bran or high oat flour. Lipoprotein cholesterol concentrations in animals fed the processed oat product were no different from controls not fed the high cholesterol diet. Alteration in the lipoprotein fraction has been suggested to represent the most significant factor in reducing the risk of atherosclerosis. All of the oat products tested demonstrated this effect, but the enhanced effect of processed oat fiber seems to confirm the hypothesis that soluble fiber is the component of oat fiber responsible for the hypocholesterolemic properties observed in experimental animals and man. Processing of oats may decrease the dose of oat fiber needed to produce significant cholesterol lowering effects in man. This finding may be of significance in the dietary management of free-living hypercholesterolemic individuals.

Beta-glucans isolated from oats, barley, wheat and sorghum incorporated independently into 7% of pan white breads, produced similar serum-liver-and HDL-cholesterol effects in rats (Klopfenstein and Hosney, 1987). Feed efficiencies of the wheat and barley glucan breads were not different from that of the control bread, whereas efficiencies of 7% and 13% oat-glucan breads were lower than that of the control. Therefore, beta-glucans from different cereals apparently have different physiological affects in relation to nutrient absorption interference.

(iv) Mechanism of Action

The biochemical or physiological basis for oat fiber induced changes in cholesterol metabolism is not clearly understood. A variety of mechanisms have been proposed for the hypocholesterolemic effects--i.e. acceleration of cholesterol catabolism or inhibition of cholesterol biosynthesis.

It is speculated that plant fibers increase bile acid and neutral sterol excretion by binding these sterols and preventing their reabsorption (Anderson and Chen, 1986). Neutral sterols include cholesterol and coprostanol--the bacterial metabolite of cholesterol. Reduction in bile acid reabsorption is thought to cause the liver to divert cholesterol from lipoprotein synthesis. Subsequently, less cholesterol-rich lipoproteins are available for secretion into the circulation, resulting in lowered serum cholesterol levels. Interruption of the enterohepatic circulation of bile acids stimulates liver hepatocytes to synthesize primary bile acids such as cholic and chenodexychoic acids. Illman and Topping (1985) report increased excretion of cholate in rats fed oat bran. Population studies of individuals who consume high fiber diets have also indicated a higher ratio of primary to secondary bile acids in their feces.

Both animal (Fisher and Griminger, 1967; Illman and Topping, 1985) and human (Kretsch et al 1979; Kirby et al, 1981; Anderson et al 1984; Judd and Truswell, 1981) studies have reported an increase in bile acid excretion after oat bran ingestion. In relation to fecal cholesterol excretion, there are some inconsistencies. Fisher and Gruminger (1967) did not observe neutral sterol changes in the feces of chicks, whereas Illman and Topping (1985) observed in rats a 480% increase in neutral sterols consisting primarily of coprostanol. It is thought when dietary fiber binds bile acids, they interfere with cholesterol miscelle formation and absorption (Anderson and Chen 1986). Decreased cholesterol absorption may further contribute to the hypocholesterolemic effect of these fibers.

A second theory proposed is based on the observation that oat fiber is extensively degraded and fermented by colonic bacteria, with the generation of the short-chain fatty acids (SCFA) acetate, proprionate and butyrate (Storer et al, 1983). These short

chain fatty acids are believed to be rapidly absorbed from the lumen of the colon (Cummings, 1983). Propionate has been shown to significantly inhibit cholesterol synthesis in isolated rat hepatocytes (Anderson and Bridges, 1981) and in rats fed propionate supplemented diets (Chen et al, 1984). Illman and Topping (1985) examined inhibition of cholesterol synthesis via propionate formed through colonic fermentation in rats fed oat bran. The concentration of propionate in the hepatic portal vein although increased by oat bran ingestion, was less than 2% of that observed to inhibit cholesterol synthesis *in vitro*. Thus the actual impact on cholesterol homeostasis remains speculative.

Another possible influence of oat consumption on serum cholesterol levels is the presence of a compound in oats with Vitamin E activity identified as alpha-tocotrienol. Qureshi and coworkers (1986) isolated this compound in barley and showed it suppresses hepatic HMG-COA reductase activity, the first rate-limiting enzyme in the synthesis of cholesterol. Of the cereal grains, oats and barley contain the highest concentrations of the tocotrienols. The alpha-tocotrienol content of oats is apparently similar to that of barley and presumably functions as a cholesterol biosynthesis inhibitor. However, the precise role these compounds may have relative to the beta-glucan cholesterol lowering properties of oats is unclear.

III. OTHER HEALTH IMPACTS

(i) Glycemic Effect

Much of the interest in the use of water soluble dietary fiber in the management of diabetes was stimulated by the work of Jenkins et al (1978, 1981) which demonstrated that incorporating purified fibers (i.e. guar gum, pectin) into meals could lower the glycemic index of a food. The glycemic index is defined as the blood glucose response following the consumption of a 50 g carbohydrate portion of a food expressed as a percent of the response after a standard 50 g starch portion of white bread taken by the same individual (Jenkins et al, 1981; Wolever and Jenkins, 1986).

Oat bran or oatmeal supplementation studies with normal or diabetic subjects have also been conducted. One of the first studies that measured the glucose response after ingestion of an oat product (porridge), reported the glycemic index to be 49 compared with 75 after wheatabix consumption, and 80 after corn flakes consumption (Jenkins et al, 1981). Comparison of plasma glucose and insulin responses among healthy volunteers after eating whole groats, rolled oats and oatmeal were similar (Heaton et al, 1988). This was in contrast to wheat and maize consumption, where peak plasma insulin response increased stepwise in the following manner: Whole grains < cracked grains < coarse flour < fine flour. Smaller glucose and insulin responses were evoked from oat based meals than from wheat or maize based meals. Milled wheat and maize resulted in significantly faster digestion *in vitro* and enhanced absorption and insulin response *in vivo* than its coarsely milled equivalent. The structural integrity of oats was less important in mediating postprandial glycemia. The viscous properties of the oat beta-glucans has been cited as the factor responsible for this observation. It is suggested that this component imparts a viscous microclimate in the intestinal lumen that impedes the rate of glucose diffusion and absorption.

Preliminary studies utilizing high beta-glucan oat gum confirm that beta-glucan is the active component which inhibits postprandial rise in glucose and insulin (Braaten et al, 1988a, 1988b). An oat gum preparation containing 80% beta-glucans or guar gum was fed to seven healthy volunteers in conjunction with a glucose test load. After 30 minutes, peak blood glucose was significantly less in the presence of oat gum (6.6 ± 0.4 mM/L) or guar gum (6.5 ± 0.5 mM/L) than in the presence of glucose alone (8.4 ± 0.5 mM/L). Peak insulin levels at 40 minutes, paralleled these findings.

Extension of this investigation was carried out on Type II non-insulin dependent diabetics using preparations of oat bran and oat gum containing 15% and 80% beta-glucan respectively (Braaten et al, 1988b). Three different meals were given to the subjects: Cream of wheat, cream of wheat supplemented with oat gum or oat bran supplying approximately 8 g of soluble fiber. After 30 minutes, blood glucose levels were 50% and 40% for the oat gum and an oat bran supplemented product respectively. Peak glucose response was delayed 40 minutes with oat gum and oat bran supplementation compared to the control. The insulin response corresponded to the glucose response. These results clearly implicate a promising therapeutic role for oat beta-glucan in diabetes management. Future work is needed to elucidate appropriate doses and long term effects of oat beta-glucan supplementation. One of the major drawbacks of aggressive supplementation with guar gum has been its low tolerance (e.g. nausea and vomiting) in a significant percentage of subjects. To date, much of the research with oat bran and oat gum has indicated these are relatively well tolerated by most subjects.

The current mechanism of action proposed for the hypoglycemic response observed with the consumption of viscous fibers incorporates some of the concepts included in Burkitt's original fiber hypothesis. Jenkins et al (1986a) proposes that the consumption of fiber dilutes the nutrients in the lumen of the bowel and subsequently releases nutrients in a more energy dilute form from the stomach and along the length of the small intestine. In contrast, energy dense foods would be rapidly absorbed high up in the small intestine followed by a rapid rise in blood glucose with possibly an undershoot due to excessive insulin release. Changes in the rate of gastric emptying or nutrient delivery to the small intestine; alterations in intestinal motility with possible increases in thickness of the unstirred water layer; and overall impedance in the diffusion of nutrients may all be soluble fiber effects which contribute to a flattening of postprandial glycemia. Prolongation of the rate of absorption of carbohydrates may result in more effective uptake by peripheral tissues, a phenomenon that is of specific significance in the treatment of diabetes.

(ii) Effects related To Cancer Risk

On the basis of epidemiological data, Burkitt (1974) proposed that high fiber diets may provide a protective role against colon cancer. This premise is based on the potential of dietary fiber to (1) increase fecal bulk and decrease the concentrations of interluminal carcinogens and (2) reduce transit time and decrease bacterial conversion of potential carcinogens.

Increase in fecal bulk and reduced transit time may be of less significance for soluble fibers than for insoluble fibers. Wheat bran for example provides an average increase in fecal weight in humans of 5.7 ± 0.5 g per each gram fed in comparison to oat bran or rolled oats which provides an average increase of 3.9 ± 1.5 g per each gram fed (Pilch, 1987). The increased fecal bulk observed with some fibers may be due to increases in bacterial cell mass promoted by the fermentable substrates in the colon (Cummings, 1983). Transit time has also been observed to be decreased with wheat bran, whereas pectin and other soluble fibers have limited or no effect (Pilch, 1987).

It has been suggested a source of the carcinogens responsible for colorectal cancer are compounds derived from the bacterial action on bile acids or cholesterol (Thorton, 1981). It is proposed that a high colonic pH promotes carcinogen formulation from these compounds (Thorton, 1981). Hence, colonic acidification through soluble fiber

fermentation and SCFA production, may protect against the development of colon tumors. Low colonic pH also inhibits the activity of some of the enzymes responsible for carcinogen formation, such as 7-alpha-dehydroxylase (Cummings, 1983). Reduced activity of this fecal microbial enzyme results in decreased conversion of primary bile acids such as deoxycholic acid to secondary bile acids (Hill, 1986). Hill and his colleagues (1975) have shown correlations between the incidence of colon cancer and total fecal bile acid concentration, proportion of fecal bacterial possessing 7-alpha-dehydroxylase activity, and fecal concentration of deoxycholic acid. Colorectal patients have also been shown to have significantly more 7-alpha-dehydroxylase activity per 100 g of dry feces than normal controls (Mastromarino, 1976). Another mechanism through which SCFA from fermentable dietary fiber may exert an anti-tumorigenic effect is in the release of the volatile fatty acid butyrate. This SCFA has been shown to inhibit the growth of *in vitro* human colorectal adenocarcinoma cell lines (Kim et al, 1982; Kruh, 1982; Cummings, 1983). The precise mechanism of action is not well known.

Epidemiological studies of populations consuming high fiber diets have suggested a protective effect of a high fiber diet (Bingham, 1986). Distinction between soluble and insoluble fiber intake have not been made in these evaluations. However, a recent study showed the population (Parikkala) with the lowest incidence of cancer also had very high intakes of nonstarch polysaccharides (NSP) (Englyst et al, 1982). The majority, 1/2-3/4% of total NSP intake was derived from cereals, of which 1/4-1/2% was from beta-glucan containing cereals, rye, oats, and barley.

An additional consideration in the relationship of dietary fiber and colon cancer is the report of intestinal cell proliferation and promotion of neoplasia in rats fed various sources of soluble fiber. Studies in which rats fed the various fiber sources injected weekly with a known colon carcinogen, dimethylhydrazine (DMH), had significantly greater incidence of malignant tumors when eating diets containing 20% oat bran, 10% pectin or guar gum (Jacobs and Lupton, 1986). In the same laboratory when rats were fed diets supplemented with the same fibers at similar doses without DMH, no tumors were prevalent but expanded cell proliferative zones in the gastric (Lupton and Jacobs, 1987) and small intestine (Jacobs, 1983) mucosa were observed. Expanded cell proliferative zones are thought to precede neoplasia.

Interpretation of these studies have been difficult in light of current theories and human epidemiological evidence; methodological concerns also make extrapolation to humans difficult. The amount of soluble fiber incorporated into the rodent diet is subject to question--such as the incorporation of oat bran at 20% of the diet. A high dose such as this would not be applicable for long term use in humans. The suitability of the rat model in assessing human colon cancer is also questionable. While histopathology, immunologic parameters and cellular kinetics in the rodent and human are strikingly similar, several other factors are distinctly different between the two species in the development of colon cancer. Colon tumor formation in rats follow a proximal distribution such as the cecum and ascending colon, which contrasts with the distal pattern observed in man (Jenkins et al, 1986b). The metabolic activity of the rat cecum may play a role in increasing tumor development in the adjacent proximal colon; in contrast the human cecum is a small metabolically inactive junction between the ileum and the colon. Intestinal cancers in animals are always multiple, which is uncommon in humans (Nigro and Bull, 1986); also rats do not develop spontaneous tumors as humans do. Induction of tumors in rodents is dependent on the type and dose of the carcinogen, the mode of administration, the background diet, sex, and species used (Jenkins et al, 1986; Kritchevsky, 1986). Furthermore, all animals that develop cancer will die regardless of any treatment thus far attempted (Nigro and Bull, 1986). Indeed the evidence suggests that the cancer challenge in the animal model is far stronger than it is in humans (Nigro and Bull, 1986).

The role dietary fibers and specifically soluble fibers such as oat beta-glucans, play (if any) in the etiology of colon cancer is still to be determined. Given the complexity of the tumor development process and the heterogeneity of man's diet, it is unlikely an answer will be readily forthcoming. Cancer research in relation to diet is still in its infancy; hence, any judgements at the present time regarding the effects of specific fiber on the development or the inhibition of cancer is premature. The National Cancer Institute endorses a high fiber intake as one component of cancer prevention and advocates the consumption of dietary fiber from a variety of food sources to achieve this end.

(iii) Vitamin and Mineral Bioavailability

There is some concern that the consumption of high fiber diets may lead to reduced bioavailability of vitamins and minerals. A recent review of research examining the effect of dietary fiber on mineral bioavailability indicate conflicting results (Pilch, 1987). Most of these studies examined the effect of insoluble dietary fibers. Results of human balance studies suggest that insoluble fibers such as wheat fiber may have a more deleterious effect on mineral balance than soluble fibers (Pilch, 1987). Diets containing 25 g dietary fiber (primarily soluble) from fruits and vegetables did not affect mineral balance unless oxalic acid in spinach was included (Ink, 1988). Studies utilizing purified soluble fibers such as locust bean gum, karaya, and pectin have reported minor or no effects on mineral balance (Pilch, 1987).

A recent balance study evaluating calcium bioavailability confirmed this trend. Ninety grams of oat bran was supplemented in the diets of healthy males confined to a metabolic ward (Spencer et al, 1987). The oat bran, eaten as muffins, had no effect on the absorption of calcium in the majority of patients and consistently decreased urinary calcium.

The effects of dietary fiber on vitamin bioavailability have not been extensively studied. The few studies that have studied the effects of soluble fibers (i.e. pectin, guar gum) have been conflicting. Kasper et al (1979), Phillips and Brien (1970) found pectin had no effects on Vitamin A accumulation. On the other hand, Schaus et al (1985) observed decreased Vitamin E bioavailability with 6 and 8%, but not 3% pectin supplementation.

Any potential adverse effect of a moderate increase in dietary fiber that includes soluble fiber, may be minimized when consumed as part of a balanced diet. The likelihood of an intestinal and metabolic adaptation to altered vitamin and mineral bioavailability will likely permit moderate increases of dietary fiber without posing a problem. The expert panel on dietary fiber (Federation of American Societies for Experimental Biology) in their report to the Food and Drug Administration recommend the consumption of a wide variety of whole grain products, fruits, and vegetables, leading to a dietary fiber intake of 20-35 grams/day for the healthy, adult population (Pilch, 1987).

IV. CONCLUSION

Approximately 40% of the total dietary fiber in oats is soluble and 74% of the soluble fraction is comprised of beta-glucans. The total beta-glucan content of oats is dependent on genetic and environmental factors. Research is needed to identify cultivars which have been optimized for yield and nutritional benefits. Processing may enrich the beta-glucan content of oat products, especially in the case of lower containing beta-glucan cultivars.

Oat dietary fiber and beta-glucans have been implicated in many of the physiological effects of oats. The data presented in this review support the position that oats as part of a total dietary plan to modify serum cholesterol, demonstrates a moderate but independent serum cholesterol lowering effect. Oat products may also play a role in mediating the rise in blood glucose following meal ingestion. Enriched oat beta-glucan products obtained through processing have the potential of enhancing both the hypocholesterolemic and hypoglycemic effects observed.

Increased consumption of oats are in tune with the dietary recommendations of U.S. federal agencies such as USDA, Health and Human Services, and health organizations such as the American Heart Association, the American Diabetes Association, and the National Cancer Institute, which advocate an increase in the intake of dietary fiber and complex carbohydrates. Given these findings, there appears to be a sound foundation for advocating increased consumption and increased agricultural interest in this commodity.

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DIETARY FIBRES IN OATS

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Introduction

The production of oats is important in Sweden with a total annual harvest of about 1.5 million tons. The main part is used for animal production, and human consumption reaches only about 2.5 kg per person and year. From a nutritional point of view oats are very interesting, with high quality protein, oils and dietary fibre compared to other cereals. The biomedical effects of fibre in oats, like for instance hypocholesterolemic properties, were reviewed at this meeting by Hurt et al.

Non-starch polysaccharides and lignin in the cell walls form dietary fibre in oats. The content and structure of the non-starch polysaccharides vary both between different oat varieties and within different parts of the grain, leading to a wide divergence in physiological and technological properties. In this paper the content, variation and structure of non-starch polysaccharides in oats and oat fractions will be presented.

Dietary fibre components

In oats, as in other cereals, cellulose, xylans and mixed-linked β -glucans are dominating cell-wall polysaccharides (Fincher & Stone, 1986). Cellulose is composed of 4-linked β -D-glucopyranosyl residues, xylans of a main chain of 4-linked β -D-xylopyranosyl residues with side chains which may contain arabinose and/or glucuronic acid residues, and mixed-linked β -glucans of 3- and 4-linked β -D-glucopyranosyl residues in a ratio of about 1:3. Xylans may also contain non-carbohydrate constituents like ester-linked ferulic acid and acetyl groups. Low amounts of glycoproteins have also been identified.

The phenolic polymer lignin is the main non-carbohydrate component in the cell-walls of hull and bran fractions.

Analysis of dietary fibre components

Several methods are available for analysis of dietary fibre (Spiller, 1986). In the procedures used in our laboratory (Theander & Åman, 1981; Theander & Westerlund, 1986), soluble and insoluble fibres can be determined separately after isolation following enzymatic starch removal and precipitation of soluble fibre with 80 % ethanol. A detailed characterization of the neutral fibre-polysaccharide constituents in the fibre fractions is then obtained by acid hydrolysis and GLC-analysis of released sugars as alditol acetates on a capillary column. The acid-insoluble residue, Klason lignin, is determined gravimetrically whereas the content of uronic acid residues in the fibre fractions is determined separately by a decarboxylation method.

Total mixed-linked (1->3), (1->4)- β -D-glucans (mixed-linked β -glucans) and insoluble mixed-linked β -glucans can be determined enzymatically (Åman & Graham, 1987) after extraction of soluble fraction with water for 2 h at 38°C. The method involves complete removal of starch, hydrolysis of mixed-linked β -glucans to glucose with a technical β -glucanase preparation, and analysis of glucose formed by a glucose oxidase method.

Soluble mixed-linked β -glucans can be calculated as the difference between the total and insoluble β -glucans. Since arabinoxylans, cellulose and mixed-linked β -glucans are dominating fibre polysaccharides in oats, the content of these components can be estimated from the dietary fibre and mixed-linked β -glucan analyses as follows. Arabinoxylans are calculated as the sum of arabinose, xylose and uronic acid residues and cellulose by subtracting the content of mixed-linked β -glucans from the glucose residues (Åman, 1987).

Content and composition of dietary fibre in whole oats

Whole oats with widely different starch and thousand kernel weight

Table I. Content of different fibre constituents (% of DM) of oats (n=16) with different starch content

	Mean value	Range of values	Coefficient of variation (%)
Starch	47.3	38.8-54.7	10.5
Dietary fibre:	29.6	19.8-38.7	17.2
Arabinose residues	1.5	1.1-2.0	20.6
Xylose residues	5.4	2.4-10.6	45.8
Mannose residues	0.3	0.2-0.4	15.9
Galactose residues	0.7	0.6-0.9	14.2
Glucose residues	12.2	9.6-15.7	15.2
Uronic acid residues	1.1	0.7-1.9	28.7
Klason lignin	8.4	5.4-12.8	28.8
β-Glucans	3.2	2.7-3.6	9.7
Arabinoxylans ^a	8.0	4.1-14.5	37.3
Cellulose ^b	9.1	6.0-12.9	20.9
Crude fibre	9.1	5.8-13.3	19.7
Thousand kernel weight	35.5	24.9-40.1	11.3

^aThe sum of xylose, arabinose and uronic acid residues of non-starch polysaccharides

^bGlucose residues of non-starch polysaccharides minus mixed-linked β-glucans.

values were analysed for dietary fibre constituents (Åman, 1987). On average these oats contained 30 % dietary fibre (Table I). The main polysaccharide residues were glucose, xylose, arabinose and uronic acids, together with small amounts of mannose and galactose. The average content of mixed-linked β-glucans was 3.2 %, arabinoxylans 8.0 %, cellulose 9.1 % and Klason lignin 8.4 %. The content of crude fibre was only 9.1 % which corresponds to the cellulose value. The coefficient of variation was highest for xylose residues and arabinoxylans and lowest for mixed-linked β-glucans.

Content and solubility of mixed-linked β-glucans

Swedish oats (n = 121) contained on average 3.2 % total (0.6 % insoluble and 2.5 % soluble) mixed-linked β-glucans (Åman & Graham, 1987). Histogram of the frequency of classes of total mixed-linked β-glucans and β-glucan solubility are presented in Fig. 1. On average the solubility was 80 % with a range from 65-90 %. The mixed-linked

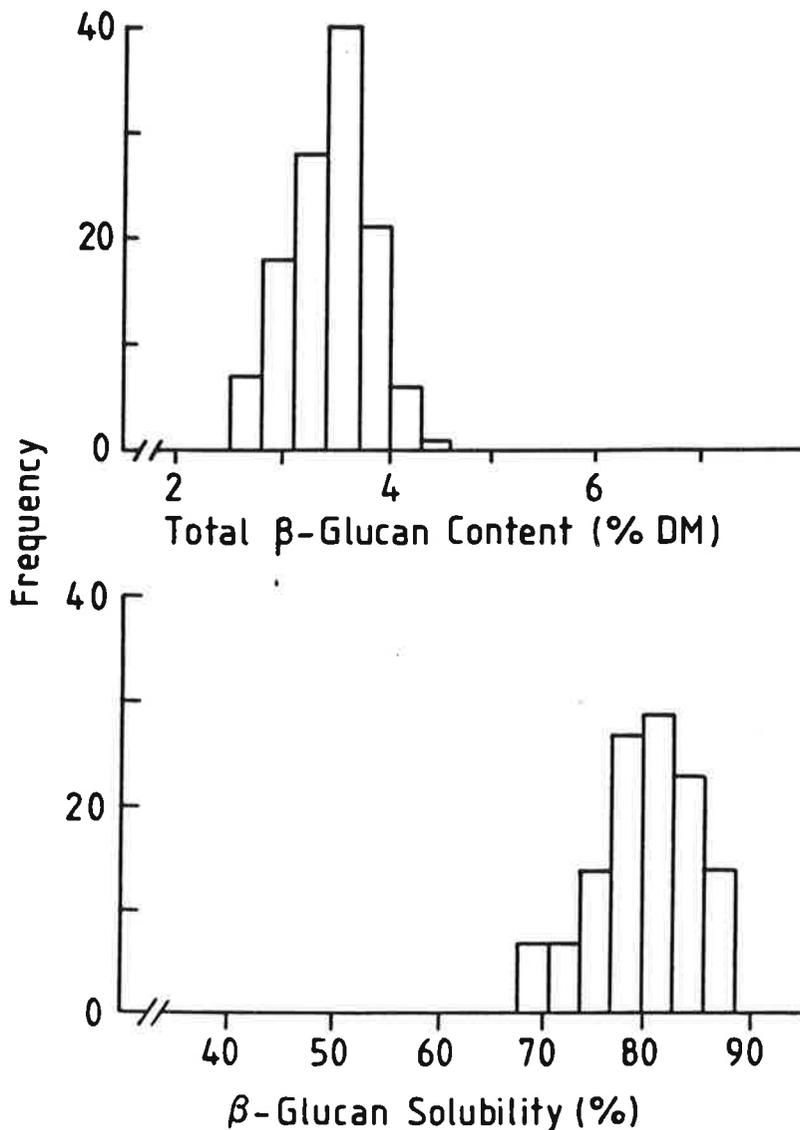


Figure 1. Histograms of the frequency of classes of oats ($n=121$) with different content of total mixed-linked β -glucans and mixed-linked β -glucan solubility.

β -glucans in oats are known to be present predominantly in the sub-aleurone and endosperm cell walls of oats.

Content of dietary fibre in oat fractions

The content of fibre components were analyzed in whole oats, dehulled oats and oat hulls (Pettersson *et al.*, 1987). In whole oats mixed-linked β -glucans (glucose residues) dominated in the soluble dietary fibre fraction while arabinoxylans (arabinose, xylose and uronic acid

Table II. Content of dietary fibre components in oat fractions (% DM)

	Whole oats	Dehulled oats	Oat hulls
<u>Soluble dietary fibres:</u>	3.5	4.6	0.8
Glucose residues	3.1	4.1	0.4
<u>Insoluble dietary fibres:</u>	24.0	6.1	71.4
Arabinose residues	1.4	0.8	2.7
Xylose residues	5.5	0.9	18.9
Glucose residues	8.4	2.2	24.7
Uronic acid residues	1.1	0.3	2.1
Klason lignin	7.0	1.4	22.0
<u>β-Glucans</u>			
Soluble	2.8	3.1	0.3
Insoluble	0.9	1.9	0.2

residues), cellulose (glucose residues) and Klason lignin were predominant in the insoluble dietary fibre fraction (Table II). Mixed-linked β-glucans constituted 33 % of the glucose residues in the dietary fibres and about 75 % of these β-glucans were soluble in water at 38°C. The oat hulls contained predominantly insoluble fibre components with arabinoxylans, cellulose and Klason lignin as main constituents. As a consequence soluble dietary fibre as well as soluble and insoluble mixed-linked β-glucans were enriched in the dehulled oats.

Dehulled oats were steamed, flaked and fractionated by milling (unpublished results). Three fractions, bran (25 %), outer endosperm (28 %) and inner endosperm (44 %) were obtained with dietary fibre contents of 20, 5 and 5 % respectively (Table III). Both insoluble and soluble dietary fibre contents were highest in the bran fractions. Glucose residues were dominating in all soluble dietary fibre fractions due to the presence of mixed-linked β-glucans. The insoluble dietary fibres in all three fractions contained significant amounts of β-glucan, cellulose, arabinoxylan and Klason lignin.

Table III. Content of dietary fibre components in dehulled oat fractions (% DM)

	Bran	Outer endosperm	Inner endosperm
<u>Soluble dietary fibres:</u>	7.2	1.9	2.9
Glucose residues	5.9	1.6	2.1
<u>Insoluble dietary fibres:</u>	11.3	2.9	2.6
Arabinose residues	1.7	0.3	0.3
Xylose residues	2.5	0.4	0.4
Glucose residues	3.7	1.2	1.1
Klason lignin	2.7	0.7	0.6
<u>β-Glucans</u>			
Soluble	3.6	0.8	0.8
Insoluble	3.8	1.1	1.2

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OAT BREEDING FOR HUMAN FOOD IN HUNGARY

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Oats are not considered in Hungary as a plant for human food. There are no traditions of its human consumption and how to prepare human food of it. No exact milling technology has been developed. Mills can process almost exclusively wheat products even nowadays.

At present nobody doubts the excellent inner value and the versatile nutritive and therapeutic effect of oats but to change nourishment traditions seems to be a very difficult task. The agricultural authorities did a lot in the past years and they do even today to promote healthy nourishment. But unfortunately, no considerable investment can be realized under the declining economic conditions in this field either. We must be satisfied with the less expensive but very modern technological equipments, by which enjoyable final products suiting the food industrial standard can be produced.

As it is well-known, the most important moment of the whole manufacturing is the de-husking of covered oats, whose expenses and energy demand amount to 25-30% of the total expenses modestly estimated. At the same time, the first class final product yield is not more than 50%. The other 50% can be used only as fodder mainly for ruminants. Our principal purpose was in the 1970's when we started to breed naked oats to reduce the expenses of manufacturing.

As basic material for breeding and as crossing partner, the local naked variety "Tápláni csupasz", which is a previously registered and still grown variety, and some other naked oats from the gene-bank were used. The latter ones had weak agronomical parameters but their protein content was ca. 20% and that was why we used them in our crossing program. At last in 1985 we succeeded in developing a new variety, "GK-Zalán", very

suitable for human food, whose patent has been applied for according to the UPOV-standard.

"GK-Zalán" proved to be the most suitable naked oats variety under our Middle-European dry climate up to now: it gives top yield among the foreign and domestic naked oats (its hull-less yield is almost 70% of the covered oat varieties); its agronomic traits (standability, disease resistance, etc.) are practically as good as those of the normal varieties. At present this variety is being multiplied and a small-scale laboratory test is carried out with it in the cooperation of the Cereal Research Institute and the Milling Industrial Research Institute to elaborate an appropriate food industrial technology. The Milling Industrial Enterprise builds a rolling factory equipped with machines imported partly from the GDR and partly from western countries. The yield of "Tápláni csupasz" and "GK-Zalán" in 1988 will be processed in that factory.

The final product capacity of the rolling factory will be 3,000 t/year according to preliminary estimations and marketing research, based mainly on the raw material provided by our institute. Flakes, groats and other food industrial products from other cereals will be made there, too. We hope that the domestic demand for oat products will increase by starting this rolling factory and many imported products can be substituted. Moreover, we reckon, that a considerable quantity of naked oats as raw material, semi-finished and finished goods can be exported.

Not only the production of oat flakes is aimed at. Groats and oatmeal can serve as raw material for child food, confectionary- and baking industry, and households. The antioxidant effect of oatmeal is widely utilized all over the world. It is very important, however, for oatmeal to be fine-grained in order to provide the adequate contact with the constituents to which it is added. Hydrothermal treatment (inactivation) is highly recommended for oatmeal in order to stop rancidity and increase

of acidity degree.

It is very difficult to extrude oats owing to its high oil content. We tried out numerous extruders with domestic and foreign origin suitable mainly for maize extrusion. Our experience is that a lot of technological alterations ought to be carried out in order to get a good quality and economically producible extruded product. Our plan is that the so called big-leaved and instant flakes, and extrudates from the mixture of oats and other cereals should be manufactured in the rolling factory starting this year.

The debate has not ceased up to now: Are covered or naked oats the ideal raw material for milling industry? Domestic economic calculations cannot be detailed in the present lecture. The final result can be summed up as follows: Naked oats yield less than covered oats. The difference is approximately equal to the weight of lemma. The price of naked oats is higher, but it need not be de-husked, so the food industrial finished products can be produced from it by 15-20% cheaper than from covered oats. Regarding our naked oats breeding work, the intensification of yielding potential and reducing of the danger of kernel loss at harvest should be aimed at in the future. As regards "covered oats", more attention should be devoted to the selection of varieties and lines with higher groat volume (less "lemma percent"). The latter objective is of great importance because it is not all the same to start the food industrial manufacturing from a normal oat with 70% groat volume (e.g. Leanda) or from one with 75% groat volume (e.g. Szegedi korai, a Hungarian variety). Higher yield in the field must be realized in caryopsis volume.

The excellent therapeutic effect of oats was emphasized by several authors on the "Second International Oats Conference" and since then, too. Nowadays it is well-known, that oat fibre content has unique physiological properties besides its balanced protein and fatty acid composition and valuable microelements. Tests with animals and humans proved that oat diet

reduces the serum cholesterol levels in the blood of patients with hypercholesterinaemia and levels out the blood sugar levels in diabetics, and reduces their insulin demand.*

Oats have been used as natural medicine in the popular therapeutic practice in Hungary for a long time. People observed the diuretic and blood pressure reducing effect of the tea cooked from oat-grain. In the past few years this popular observation was controlled by us with the collaboration of medicals. In most cases, the blood pressure reducing effect of oat-grain tea could be proved if it was applied regularly, what is more, it had no deliterious side effects.often caused by medicines. An important observation was made by us: medicines reduce blood pressure powerfully or drastically depending of the applied quantity, but oat-grain tea treatment adjusts it to the level suitable for the given patient's organism. Lemma is supposed to contain effective material, too, as naked oats have no similar effect. In veterinary therapeutics, oat-grain tea is used to cure diarrhoea and dysentery.

From this year on the Hungarian Ministry of Health allows to sell plants under the name "medicinal product" without a long therapeutic procedure, which were not registered as "medicinal plants" previously. Our intention is to introduce oat-grain following appropriate cleaning as blood pressure reducing and levelling medicinal product in Hungary.

As a final conclusion it can be stated that it is most probable that oats, this valuable grain crop will soon have its deserved place among the foodstuffs of Hungarian people.

* By the way, Hungary has a front position in the world statistics considering the number of deaths owing to heart and vascular diseases, unfortunately.

COMMENTS ABOUT HUMAN FOOD

There was an interesting discussion regarding oats for human food. Most speakers praised the different components of oats and the different ways to use them. The question remained, however, how to handle all those components. Milton McDaniel gave a relieving solution by citing an unknown poet.

METHUSELAH

*Methuselah ate what he found on his plate,
 And never, as people do now,
 Did he note the amount of the calorie count;
 He ate is because it was chow.
 He wasn't disturbed as at dinner he sat,
 Devouring a rost or a pie,
 To think it was lacking in granular fat
 Or a couple of vitamins shy.
 He cheerfully chewed each species of food,
 Unmindful of troubles or fears
 Lest his health might be hurt
 By some fancy dessert;
 And he lived over nine hundred years.*

UNKNOWN

LABORATORY EQUIPMENT

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Laboratories conducting physiological, biochemical or cytological research on oats will be equipped with many instruments common to similar laboratories investigating other plant species. This paper concerns laboratory equipment that is of special interest to the scientist who wishes to evaluate populations of breeding lines for kernel morphology, certain quality characteristics, such as grain protein, oil or moisture and to identify genotypic-specific characteristics, such as seed protein or isozyme electrophoretic banding patterns.

Near-Infrared Reflectance Analyzers.

Near-infrared reflectance (NIR) offers the capability to analyze many samples quickly, once an instrument is calibrated, saving considerably on time and costs of wet laboratory methods. It can be very useful in breeding programs where many lines need to be analyzed for protein, oil, or other components.

The principle of near-infrared (NIR) reflectance analysis is based on the Beer-Lambert Law, which indicates that the transmittance of light of a particular wavelength through an absorbing substance is proportional to its concentration:

$$\log (I_0/I) = \log (1/T) = kcl = A$$

where I_0 and I are the intensity of light incident to and emerging from the sample, T is the transmittance ($T=I/I_0$), k is the molecular extinction coefficient, c is the concentration of the absorbing molecules, l is the path length, and A is the absorbance or optical density. In NIR, reflectance (R) is analogous to transmittance, thus the equation can be expressed:

$$A = \log (1/R)$$

Because the samples consist of a complex mixture of components absorbing light at many wavelengths, is sometimes necessary to measure light at more than one wavelength to develop a suitable calibration equation relating reflectance to concentration of a particular component.

A typical instrument contains a light source, focusing lens, filters to select appropriate wavelengths, sample tray, detectors, and the electronics to amplify and process the signals received by the detectors (Fig. 1). Some instruments use a tilting filter wheel with three to seven filters, providing a range of wavelengths from each filter as the angle changes with respect to the incident light. Others use a filter wheel containing a number of discrete filters that pass sequentially through the light path. Research instruments use a grating monochromator to achieve the complete spectrum of NIR light.

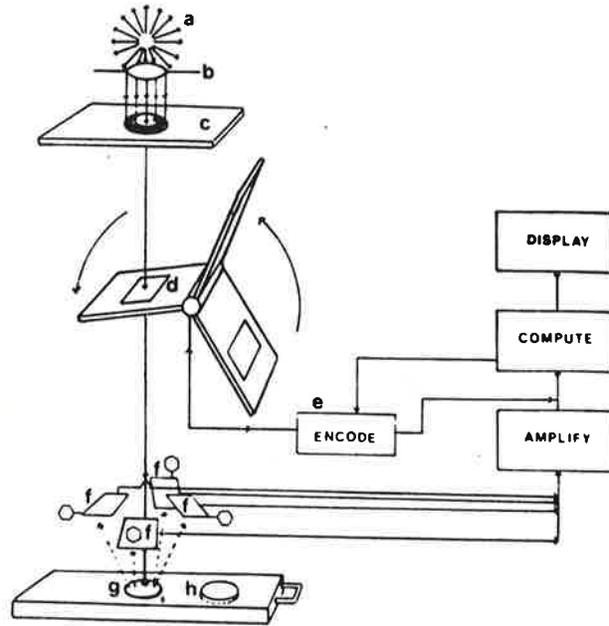


Fig. 1. Basic near-infrared analytical system. a, light source; b, collimating lens; c, slit system; d, tilting filter system; e, encoder; f, detectors; g, ceramic standard; h, sample (4).

The reflected spectra from agricultural samples are complex, and include components from water, oil, starch, cellulose, protein and other minor constituents (Fig. 2). Some instruments use $\log(1/R)$ data directly, whereas others compute the first or second derivative which are more sensitive to subtle changes in slope of the spectra. The primary reasons for using derivatives are to separate overlapping absorption bands and to remove baseline shifts.

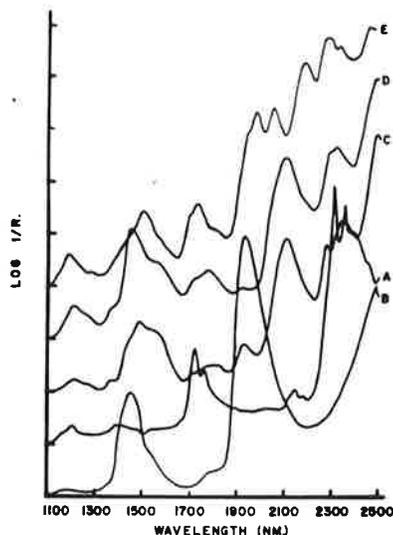


Fig. 2. Near-infrared reflectance spectra of grain constituents (4). A, water; B, oil; C, starch; D, cellulose; E, wheat protein.

Calibration is the regression modeling procedure that identifies the minimum subset of wavelengths that best explains the chemical property across a population of similar samples showing multivariate changes in composition. Although wavelength band assignments can be based on chemical structures, in practice the process is empirical because of imprecision and overlapping absorbances among the various components of the samples.

The calibration process involves measuring the log (1/R) values from a set of wavelengths and relating them to the concentration of the component as determined by a standard reference method. This is done by multiple linear regression, and typically 40-50 samples covering the entire range of sample variability are required. The calibration constants are then validated with a separate set of samples whose component concentrations have also been determined by the reference method. Errors appear from three sources: sampling, the reference method, and the NIR instrument. At best, NIR can only achieve the precision of the reference method.

Although the first commercial NIR analyzers were introduced 17 years ago, there have been few reports in the literature on their use in the analysis of oats. Hymowitz et al (1) in 1974 used a NIR analyzer manufactured by the Dickey-john Corporation to measure protein and oil in oat groat samples with a wide range of protein and oil, but held within a narrow range of moisture. After calibration with 69 samples, the equations were validated with 30 additional samples. The correlation coefficients for protein and oil were 0.945 and 0.978, respectively, with a mean difference between NIR and reference values of about 0.3. These results were considered good enough to use the technique to evaluate breeders' samples. Williams (2) also analyzed oats for protein, oil and moisture using two early generation instruments, and concluded that accuracy was sufficient for routine analysis.

In our laboratory, we have been using a Pacific Scientific (Neotec) GQA 41 to analyze breeders' oat groat samples for protein and moisture for many years. Because we receive sample batches from diverse environments over a period of months each year, we have found it necessary to use a closed calibration method. This involves grinding and analyzing an entire sample batch, and storing the reflectance values in a computer. A computer program was written to select from these samples a subset of about 40, chosen to include a uniform distribution of samples over the entire range of values recorded for each of the four wavelengths monitored by our instrument. These samples are then analyzed for protein by a modification of the Kjeldahl procedure, and the data are used to compute the calibration constants. The equation is then used to compute the protein values for the entire batch of samples, and the data are returned to the breeders on an as is and a dry basis. We normally analyze from 10,000 to 20,000 samples each year for university and USDA oat breeders in the United States. Because certain breeding programs are also interested in oil concentration, we are developing calibration constants for oil as well.

Until recently, ground samples are required for analysis. However, recent developments have allowed the measurement of protein and moisture in whole kernels of wheat and barley. This has been reported by use of a transmission instrument (NIT) using shorter wavelengths (900-1050 nm) (3, 4) and also for barley by use of a scanning instrument in the reflectance mode at 1100-2500 nm (5). With whole grain analysis, larger samples are required, 150-250 g for NIT and 70-80 g for NIR, which may preclude the usefulness of these instruments for early generation breeding lines. However, there are certain advantages.

Testing is nondestructive, original moisture can be measured and sample preparation is minimal. For the NIT instrument, precision was comparable to that of standard analyses, and accuracy was satisfactory for segregating wheat into subclasses. Moisture testing was equivalent to that achieved with moisture meters. With the NIR instrument, excellent agreement with reference moisture values was obtained, but the agreement with total nitrogen was satisfactory only within varieties of barley. To my knowledge, whole grain analysis of oats has not been reported.

Nuclear Magnetic Resonance Spectrometers

Broad-band nuclear magnetic resonance (NMR) spectrometers have been applied to the analysis of oil in a number of species (6) including oats (7). The NMR technique measures the hydrogen associated with liquid oils, independent of hydrogen associated with the surrounding matrix of starch, protein and other components. Liquid-associated hydrogen exhibits narrow, intense signals, which can be separated instrumentally from the weak and broad hydrogen signals associated with solids. However, it is necessary to dry the samples to less than 4.5% moisture to eliminate the contribution of hydrogen in liquid water (7). Measurements are made on whole seeds, and for oats, three or four groats are sufficient (7), although larger samples may be more representative.

The instrument itself consists of three major components: a magnet unit housing the permanent magnet and associated coils, the console containing the control panels, recorder and electronic circuitry, and the integrator. A weighed sample is placed in the cell in the sample cavity of the magnet, and the instrument sweeps through the resonance condition, storing the data on energy absorbed in the integrator. At the end of the cycle, the total energy absorption is displayed and is directly proportional to the amount of liquid hydrogen or oil.

NMR has been used to analyze samples of oat groats from the progeny of crosses in a study of the inheritance of groat oil (8). Samples of 3.5 to 5.0 g were used. Additive gene action was found to be most important, and considerable gain has been achieved in breeding for high oil.

Electrophoretic Apparatus

Proteins found in the grain or other tissues can be separated and visualized by electrophoresis. A common use for this technique is to identify unknown cultivars by comparing the banding pattern with that of known standard samples. Protein banding patterns appear to be genetically determined, with minimal environmental influence except under extreme circumstances, such as sulfur deprivation. The apparatus and techniques are relatively simple. A power supply is needed capable of delivering either constant current or constant voltage. A cell consisting of two parallel glass plates separated by spacers holds the gel mixture during its polymerization. The polymerized gel is inserted between two buffer reservoirs containing electrodes connected to the power supply. The samples are applied in wells at the top of the gel, and current flowing through the gel causes the proteins to migrate and separation is achieved. Polyacrylamide gels have largely replaced starch gels that were used earlier. Separations may be of proteins complexed with sodium dodecyl sulfate at pH 8.6, or in an acidic gel at pH 3.1. In the former case, the proteins separate primarily on the basis of their size, and in the latter, by size and charge. Alternatively, isoelectric focusing in a pH gradient of mixed ampholytes will separate proteins with different net charges. The separated

proteins are visualized by staining, usually with Coomassie Blue or silver nitrate.

Oat species and cultivars have been differentiated by electrophoresis of their avenins in an acidic gel system (9, 10). Although some cultivars have unique patterns, others fall into groups with identical patterns. Recently, Altosaar and coworkers suggested that the efficiency and reproducibility of the technique could be improved by employing precast, ultrathin-layer polyacrylamide gradient gels (PhastGel, LKB-Pharmacia) (11). In our laboratory, using procedures similar to Lookhart (9, 10), we have examined 38 cultivars and cataloged them by pattern (Fig. 3). We have preliminary data demonstrating the presence of biotypes for several cultivars.

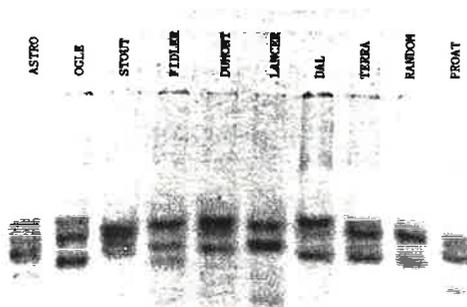


Fig. 3. Electrophoregram of oat avenins separated on acidic polyacrylamide gels.

The unequivocal identification of cultivars is becoming important because of plant variety protection in the United States and elsewhere. These techniques have also become useful in the seed trade in general, especially for the sale of certified seed, where varietal identity and purity are crucial. We have assisted several public seed vendors in cases where growers were suspected of misrepresenting the variety or had mixtures resulting from the failure to thoroughly clean harvesting equipment between varieties.

Digital Image Analysis

Computer-based imaging systems can be used to measure spatial characteristics of oat kernels. At the level of gross morphology, size and shape can be determined. These data can be related to milling quality, seed purity, within sample variation, and varietal characterization. Image analysis can also be done at the light and electron microscope levels, to determine tissue, cellular and subcellular characteristics. Potential applications include ratios of bran, germ and endosperm, protein distribution, cell wall thickness and hull percentage. Biochemical components, such as lipase and esterases, for which histochemical staining techniques are available can potentially be quantified.

The equipment consists of a microcomputer system which is connected to an array processor. Video signals from a TV camera are converted into digital data and stored in the computer's memory. The images can be obtained from a macro stand, where seeds are viewed with back lighting, or from a light or electron microscope. Sample parameters such as length, width, area and perimeter are measured from the stored data.

Kernels from the primary, secondary and tertiary florets of six oat cultivars were differentiated on the basis of kernel length and shape (12). The size of the primary and secondary kernels was similar for all six cultivars, but kernel shape differed among them. Since image analysis measures the characteristics of each individual kernel in the sample, variation within populations is easily described. Symons and Fulcher (12) pointed out that populations from the same environment could be fingerprinted by their size-shape characteristics.

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FIELD MACHINERY IN CROP RESEARCH

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Mechanization has been occurring in agricultural research for as long as people have been interested in agriculture. As people have tired of manual labour they have found easier ways of doing things. Since the 1950's there has been a rapid expansion in the mechanization that has occurred not only in agriculture but more particularly in agricultural research. As the Western world emerged from the period of the world wars with increasing affluence, a climate emerged which freed people to develop and test new ideas. In varying degrees around the world, agricultural research moved away from the sickle and hand threshing to more mechanized systems. This was made possible in no small way by the replacement of the horse with the internal combustion engine.

Since the 1950s we have seen the development of quite sophisticated experimental equipment. Combined with this and no doubt inter-dependent upon it, has been the development of computers to the point where they are now accessible to virtually all research programmes.

The development of experimental equipment specifically designed for the job, has allowed a transition from research workers struggling to use commercial equipment necessitating large plots, through to the present day opportunities of much more concise compact trials. This in turn has had a significant effect on both the quantity and quality of research.

No doubt the two most significant developments in the area of field machinery for crop research have been the development of the cone seeder and the small self propelled experimental plot harvester.

The cone seeder originally developed in Norway, has been through a number of design stages as people, confronted with limitations, have come up with ways to solve the problems. The most recent form of the cone seeder, incorporating the cone and an endless belt, have resulted in a trouble free seeding system, able to be operated at high sowing rates and in adverse conditions. In our experience it is not difficult to obtain sowing rates of 1,500 plots per hour or more (5 m x 5 row plot).

The self propelled experimental plot harvester, now available from a number of manufacturers, has made it possible to handle large numbers of plots in research. This has been one factor in enabling breeding programmes for example to move from the very labour intensive systems such as pedigree breeding, towards the less labour intensive systems such as bulk breeding.

It is interesting to observe that in my country, Australia, where large scale breeding programmes are generally a recent phenomenon and cheap labour has not been available, virtually no breeding programmes use the pedigree type methods but operate on variations of bulk methods which maximise the value of mechanisation. This is in contrast with much of the rest of the world.

On-going development of plot harvesters over the last 20 years or so has resulted now in units which are both efficient in operation and economical for labour. There is no doubt that the increased competition between manufacturers in this area has been one of the major factors responsible for the rapidly improving quality of the machines available on the market.

Equally as significant as the cone seeder and plot harvester for their impact on the efficiency of agricultural research programmes has been the impact of computer technology. The power of computers to handle the sheer volume of book-keeping and data handling generated by increases in sizes of programmes, has been absolutely essential for breeders and other research workers to take advantage of the opportunities available through mechanization. It is not possible to take advantage of mechanization without access to computing facilities.

Closely allied to the explosion in computing power has been the expansion of a whole range of electronic equipment to go with it. This has allowed the collection of data never possible before. The opportunity to monitor environmental parameters continuously, gives us at least a glimmer of hope of being able to systematize it in a way that will be useful to both researchers and farmers. The field note book can be replaced totally by an electronic system. Portable hand-held computers are available with seemingly unlimited memory. This not only allows the collection of large quantities of data, but also the ability to call up and display previously collected information on each plot, thereby fully duplicating and extending the previous field book situation.

Of course the improved ability to collect data has meant that there has been a need for more efficient ways of storing and accessing this data. This has been made possible with an increasing range of database options and techniques for analysing and summarizing such data. New approaches in data analysis to minimize the effects of experimental error, such as nearest neighbour designs, have the potential to greatly improve the efficiency with which data can be analysed in most situations.

The availability of electronic control through micro-processors has enabled the development of automation in both seeding and harvesting equipment. Most people would now be familiar with the opportunities of direct recording of plot weights, and even moistures on the plot harvester. In our own situation, we have developed a microprocessor for our seeders to control the feeding of seed magazines and to monitor the operation for errors or misfeeds. Plot length is automatically measured through a metering system which is readily calibrated on site. This has given us a high degree of flexibility in both how we sow plots and how we use our labour force, resulting in improvements in operational efficiency. The system has both reduced the number of seeding errors and sped up our seeding operation.

One area of electronics which is going to have a major contribution in the future is an area commonly referred to as "Robotics". This will greatly improve the efficiency of experimental research. We have taken this to the first stage, by developing an automated seed packaging system which takes account of the randomizations and design of the trials and allocates seed directly into magazines. The machine is currently undergoing preliminary testing. The prototype unit has a capacity to handle up to 7200 plots in any one packaging run. It has proved to be very space efficient occupying an area of 4 m x 3 m x 2 m.

Such automation will give us the opportunity to reorganize our labour force so that we can send staff on leave during the period between seeding and harvest and have them available to collect more useful data during the growing season. Not only is more accurate packaging of seed possible but it will also enable us to be more flexible in accommodating variations in seed size, germination rate and rate of seeding; things we have tended to ignore in the past because it is too complex for manual packaging.

It has become very obvious to us through our involvement in this project that there is considerable scope for automating many of the routine, monotonous, time consuming operations particularly associated with research programmes. For example there are many operations for evaluating quality in a breeding programme that can be readily automated such as, hectolitre weight, grain colour, grain plumpness, and grain weight. There are other measurements which involve routine grinding of samples. All of these repetitious operations can be automated, freeing staff to do more useful work.

For plant breeders particularly, electronic technology may provide opportunities for selection of numerous physiological traits which in the past have been avoided because they have been far too time consuming to be practical. For example, remote sensing may provide opportunity to measure such things as crop density and ground cover which would enable rapid early generation quantitative screening for physiological characters such as early growth, early vigour, leaf area index etc. which plant breeders traditionally have avoided because of the difficulty in measuring them. Infra-red thermometry is another area that is being explored although, at least in our environment, it would appear that such a technique is nowhere near as promising as first thought.

The power of computing available to plant breeding programmes now also means that much more effective use of modelling is possible. This combined with the opportunity to collect physiological data using electronic equipment opens up a new field for early generation screening in breeding programmes. It is an area that deserves considerable investment of research over the next few years. It is just possible that the work of physiologists over the last 50 years may at last 'be of use to the plant breeder'.

Finally with the tremendous scope for automation in agricultural research, it is useful to lay down some guidelines. It is important for research workers to identify the limiting factors in their particular programmes that are affecting their efficiency. Common sense clearly suggests that the best way to gain improvements in efficiency is to eliminate the most limiting factors.

For example in the breeding programme within my own organization, limiting factors in the early days used to be the number of plots that we could plant. As we improved the efficiency of our seeding operations, the limiting factor then became the harvesting. As we upgraded the efficiency of our harvesters and converted them gradually from three to two to one person operations our limiting factor moved back to seeding. Now with our present seeders, the limiting factor has rapidly become the amount of work that our staff can handle between harvest and seeding and this has been the reason for developing the automated seed packaging system. It would be nice to have automatic weighing systems for each of our plot harvesters but at this stage that is nowhere near our major limiting factor, and is not envisaged to be so for some time in the future. We probably will not see automatic weighing on our plot harvesters for some years to come. It is certain that once we have the automatic packaging system operational, the limiting factor in our breeding programme will not be in the field but the quality laboratory and in fact already is.

The other principal I wish to emphasize in relation to automation is the need to consider the integration of other disciplines with your own particular research programme. Again I use our own experience as an example. Because the quality work has been carried out by a separate group to the breeding staff, we as breeders have tended to concentrate on those limiting factors associated with our particular operations, and have ignored the problems that

were being created in the quality laboratory by the rapid escalation in numbers of samples that we were generating, with our improvements in efficiency in the field. In hindsight, we should have been putting more attention on automating the laboratory, because that has not only become a limiting factor in our programmes, but the rationalization that has occurred over the years to accommodate the shortcomings in the laboratory has meant that we now are not adequately testing our material for quality. That is a mistake which we plan to address in the near future and we currently have two automation projects on the planning board for automating a lot of the routine, repetitious quality screening work.

In summary, I strongly commend the value of investing in automation in agricultural research programmes. Our own experience has shown that we have made major advances in improvements in operations by involving ourselves in an ongoing automation programme. For example in my own breeding programme in the last 15 years we have increased our capacity from 700 plots per person per year to over 10,000 plots per person per year. That has allowed us to run programmes of a size large enough (50-60,000 plots per year) to allow good progress in our environment.

Developing automation, particularly with electronics, is expensive. You need, therefore, to carefully consider your requirements and invest in areas which are going to give the greatest benefit. It is preferable for such development to be applicable to more than one breeding programme so that the development cost can be spread over a larger number of users. Once a prototype has been developed reproduction is a far cheaper exercise.

I have one final word of warning. Automation is an area that can be extremely frustrating because advances in technology are such that in many cases the unit you develop will be using obsolete components by the time you have it working, and this needs to be accommodated in your planning and development process. It requires an awareness of what is on the market and the flexibility to develop equipment which can accommodate new developments as they become available. I cannot emphasize too strongly the value of involving competent electronic specialists in such projects. The difficulty often is finding such people who are prepared to struggle through the development with you. In that regard we have been most fortunate.

Some people have an inherent fear of automation; they fear redundancy. Our experience is one of always having more work than our resources, however good, can service. I certainly do not fear redundancy but rather look forward to a better quality of research and with it a better quality of life through automation.

PRESENTATION OF SVALÖF EQUIPMENT

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During the years Svalöf AB (former The Swedish Seed Association) has been working with plant breeding, equipment adapted to the different activities has been developed within the company, as is the case in most research institutes. The modifications or inventions often stay within the institutes without being spread to or known by others. Now Svalöf AB is offering other organisations to benefit by some of the equipment developed at the company.

At the Swedish University of Agricultural Sciences a lot of equipment is developed for special purposes and commonly used in the field tests in Sweden. However, none or very little marketing of this equipment abroad has been made. Through Svalöf AB it will be possible also for others to use some of this outfit.

Equipment available at the moment is:

AT SPRUMO

This test sprayer was developed at the Swedish University of Agricultural Sciences (SLU) to combine high precision with good working environment. The sprayer is self-propelled or adapted to a 3-point linkage of a tractor. The driver is protected from the spray by a transparent screen and sits in front of and at a long distance from the boom. The filling of pesticides and cleaning of internal parts of the sprayer is done with great security for the operator. Batch tanks for different plot sizes are available.

SV SEEDTREATER

In plantbreeding only small quantities of seed is often available. To be able to treat this seed-lots with liquid dressing avoiding mixing, an apparatus was developed at the Swedish Seed Association. Health considerations require that treated seeds are handled as little as possible by man. The Seedtreater eliminates all handling of exposed seeds. The principle of the apparatus is that the dressing is sprayed onto the seed as it flows down a transparent sloping tube. The seed is immediately collected in the bag intended for sowing.

GTH BIRDSCARER

This equipment for scaring birds by means of alarm calls was developed at SLU. It is composed of a tape-recorder with auto-reverse, controlling unit with timer, loading circuit with lead accumulator and loudspeakers. By means of a light sensitive eye it is only in operation during day-time. Alarm-calls from rook, jackdaw and hooded crow are available on tape. It is also possible to use locally recorded calls from birds or other animals.

SV BANDGRADER

This equipment is developed at Svalöf AB to separate none round parts from round ones, for example half peas from round ones or sclerotia from Brassica seeds. The working principle is a moving rubber cloth which is sloping in a right angle direction to the moving one.

EARTH BORERS

Borers for manually taking none destructive soil samples. Different borers for diameters from 22 to 30 mm and maximal depth of 1 m are available.

EVAPORIMETER

Apparatus for measuring the evaporation. A plexiglass container equipped with a micrometer measures the amount of water evaporating. Converting formulas for calculating the evaporation from the soil (with or without crop) are used.

SV LABEL APPLICATOR

Tool for putting wooden labels in the field from a standing position. Available in two sizes.

The administration of the equipment selling is located at the Svalöf branch station in Uppsala, Sweden.

THE USE OF MICROCOMPUTERS IN PLANT BREEDING
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Microcomputers can enhance variety development programs in many ways. Microcomputers can be used to handle the large amounts of data required to have a successful program. Handling information quickly and efficiently is crucial in variety development programs.

MSTAT, a software package started by Dr. Oivind Nissen at the University of Norway and modified by Michigan State University, has over 60 programs including two plant breeding programs. MSTAT represents a software breakthrough that captures the low-cost power and speed of microcomputers to help agricultural scientists manage their research program. MSTAT is easy to use, while providing quick and easy access to sophisticated research design and analysis procedures. It can have a dramatic impact on the speed and efficiency of plant breeding programs. The current MSTAT version has programs written in C and BASIC (compiled). It requires an IBM compatible computer with 256K and a version of Microsoft BASIC (BASIC, BASICA, MBASIC, etc.). The cost is \$100 for non-profit organizations/individuals.

The BR series plant breeding program developed by Ringlund, Nissen and Heen, will manage information concerning parentage, generation, row number and selection criteria. It will print field books and labels based on a file where you must indicate the number of plots to be planted from previous row numbers.

The AC series plant breeding program developed by Freed, Nissen and Tohme, is based on a master accession file which includes an accession number, name, pedigree and 32 one digit descriptors. It is more complex than the BR series. You can enter selection criteria (disease, insect, height, quality rating, etc.) for each plot which will then be carried forward in the subsequent generations. Then when you select between lines in later generations, you will have the information from previous years available for identifying the superior lines. The AC series has incorporated aspects of the mainframe programs developed by Dr. Everson and Dr. Adams of MSU.

In addition to the two plant breeding programs, MSTAT has over 60 programs which will (1) generate randomized block designs with one to five factors (zero to four splits) and incomplete lattice designs; (2) print field books, labels and maps; (3) analyze data with one- and two-way ANOVA, factorial, lattice, hierarchical or non-orthogonal designs; (4) calculate correlation, regression, multiple regression, basic statistics, LSD, Duncan's, Tukey's and Student Newman Keul's and (5) transform and select data.

USE OF COMPUTERS AND COMPUTER PROGRAMS.
FOR GERMPLASM COLLECTIONS.

S.Blixt

Nordic Gene Bank, Alnarp

Use of electronic data processing, hardware and software, in the genetic resources preservation work, including then germplasm collections, has become a standard and routine procedure. This does not mean, however, that one standard and routine procedure for the field of genetic resources preservation is widely in use or even available. It is very much a developing field of work.

What is meant by germplasm collection? In most peoples minds this might be connected most closely with an Ex Situ seed collection. However, this is only one of the main components in genetic resources conservation, the other being the In Situ conservation. For the cereals in the Nordic region the Ex Situ collection is the most important, since the Nordic countries harbor no indigenous primary gene pools of cultivated Avena, Triticum, Hordeum or Secale. We do have some cereal indigenous primary gene pools, though most people have forgotten them by now, for instance in the genera Elymus and Glyceria.

However, for the most important Nordic crops, the pasture and meadow plants, In Situ conservation is most important, since these species, such as Festuca, Poa, Dactylis, Trifolium, are indigenous and widely distributed in the area. The same is valid for some fruits and berries. Computerized information is particularly important here, since the In Situ conservation requires, e.g., a certain amount of control of changes in the environment. The software to be used in this area is developing, partly perhaps available, from the fields of botany and geography but may need modification to suit completely genetic resources work. One reason for this is that botanists usually work with taxonomic levels from species and higher, the main interest for the genetic resources is from species level down to the genotype. Since it is my intention to say also a few words on the situation in Europe with regard to Avena, I can go no deeper in these matters here, but will restrict the presentation to use of computers mainly in Ex Situ germplasm seed collections.

It is usually helpful in clarifying the issue to consider the use of computers in germplasm collections, and probably also more in general, on two levels, which we can call the R&R- and the A-level, derived from Registering & Retrieval and Analysis, respectively. Most genebanks holding germplasm collections have computer facilities capable of working at the R&R-level, i.e. data can be registered, sorted, searched and printed. This is included in most software packages for database management, for instance dBase, Integrated 7 and many others. Also the package BIRS, used at the Nordic Gene Bank, works presently at this level. BIRS, however, is under further development by the Nordic Biometry Project and a number of

further utility programs may be expected. In this kind of processing, the computer is first of all a tool saving time and facilitating overview. Characteristic for the kind of software used is that it will gladly work with any kind of data, i.e. these programs are for general use.

When a database for a germplasm collection is approaching 50000 accessions, each with about 30 descriptors, as for instance the Central European Barley Database, already this simple processing aid becomes very important. For the curators of germplasm collections it actually goes a long way. There is, however, much more potential in the computer particularly for the users of germplasm collections, i.e. breeders, researchers and others. This comes when utility programmes are designed to hold an amount of specific information, or knowledge, of biological nature which allows them to recognize and analyse biologically meaningful interactions and thus produce new information from the data registered. We are not talking about statistical processing, as for instance by SAS or MSTAT, which is still general packages with no build-in biological knowledge. I am thinking of the types of expert programmes that are available for instance in medicine and biochemistry and is under development in systematics. Unfortunately, germplasm is, at least not yet, the kind of business that attracts the big money from state or private enterprise and consequently the attention of big software-houses and therefore no standard packages are, to my knowledge, available presently. The few programs that have been produced are typical home-mades, i.e. programs made by geneticists and botanists for their own use.

What can be done in the existing databases of the germplasm collections today? Obviously this depends not only on the computers and software available but first and foremost on the quality and quantity of the registered data. And here the span is very large. Many genebanks have rather scanty information, in many cases mainly passport information, i.e. name of cultivars, originator/breeder, or collector, country, and not much more. When biological data are included, these are often in form of characters, more or less well defined, often genetically very broad, often given as scales, very difficult to work with and almost useless at the A-level.

On the opposite extreme, some collections exist where one can find each accession provided with information on up to 500 single genes, including disease resistance, flowering, maturity, height, and a number of other agronomically important characters. This, of course, is a crucial point for efficient utilization of genetic resources in Ex Situ collections. Such user categories as breeders and researchers are actually looking in the collections mainly for genes or gene combinations since genes is what can be combined and selected for in breeding programmes and are most often worked with in research. As long as this type of information is largely lacking, computers and computer programmes developed beyond the R&R-level are unfortunately of limited utility - because the lack of data to work with. In addition, the use of computers and computer programmes in plant breeding seem still in its infancy, dealing mainly with practical procedures such as field plans and labels, or statistics of trials. If packages dealing with selection based on specific genetic information exist, I am not aware of it.

Still, pooling the world genetic resources of any crops, as is now in the process, much can be done also with few data. Perhaps the most well-known example comes from finding disease resistance by using geographic passport information to find collections from areas where a certain disease have been prevalent for a long time and to screen such accessions for resistance.

One program at the Nordic Gene Bank, PEDIGREE, using specific databases, might be of interest to many breeders and therefore worthwhile specific mentioning. Databases may be constructed with the descriptors:

- Cultivar name
- Cultivar name, synonym
- Breeders identity code
- Genetic origin
- Parent A
- Parent B
- Breeding technique
- Year of release
- Breeding company, name
- Breeding company, country
- Crop name
- Reference

Providing the database have been filled with relevant data, which is always the big problem, the program will, for instance, run out the pedigrees, in different ways, for any given entry. Presently a database exist for nordic barley material but not for oats.

With regard to genetic resources collections of oats, the Nordic Gene Bank have 608 accessions in total registered. The database holds information on at least some accessions for the following 84 descriptors:

- | | |
|------------------------------|-----------------------------------|
| - original record number | - donors' code designation |
| - donors' number designation | - designation, other than donors' |
| - donors' source | - genus, latin name |
| - family, latin name | - subspecies-1 |
| - species, latin name | - accession name |
| - subspecies-2 | - landrace/local variety name |
| - commercial variety name | - year of release in Sweden |
| - breeding company, name | - introduction country |
| - breeding company, country | - pedigree or source |
| - introduction year | - relative plant height |
| - genetic origin | - leaf sheath, hairiness |
| - plant height, cm | - nodes, hairiness: density |
| - growth habit | - flag leaf, rigidity |
| - leaf margin, hairiness | - panicle, shape |
| - stem thickness | - panicle, erectness |
| - whip leaf, turning | - panicle, waxiness |
| - type of panicle 1 | - paleae attached or not |
| - panicle, branches: angle | - relative length of panicle |
| - with or without awns | - lemma, colour |
| - paleae/pericarp colour | - callus, hairiness |
| - glumes, length | - rachilla, length |
| - kernel covering | |
| - lemma, hairiness | |
| - rachilla, hairiness | |

- rachilla, grooves
- covering ability
- test weight, kg/100 l
- heading
- growing time, days
- earliness
- flag leaf, length
- straw stiffness 1
- lodging
- straw breaking, height
- resistance straw brittleness
- tendency to tiller formation
- relative grain yield
- coefficient of sensitivity
- rel. adjusted DBC value, %
- hull content
- cereal eelworm, *H. avenae*, Ha 12
- source for nem. *H. avenae* res
- crown rust, *Puccinia coronata*
- *Erysiphe graminis avenae*
- seed sample sent to NGB
- establishment
- 1000 grain weight, gram
- ear emergence
- growth speed
- time of maturity
- ripening temperature
- seed dormancy
- straw stiffness 2
- straw, breaking at maturity
- shattering resistance
- grain yield
- relative straw yield
- N content in grain
- fat content in grain
- cereal eelworm, *H. avenae*, Ha 11
- BYDV, barley yellow dwarf virus
- *Puccinia graminis avenae*
- valuable characters, line no

The Central European Oat Database is being developed by Institut für Pflanzenbau und Pflanzenzüchtung of FAL in Braunschweig, BRD. In the report from the meeting in 1986, the CEOD contained 9056 accessions of the whole genus Avena, including about 25 species from 12 ECO-countries and in addition Canada and USA. As expected, a large number of accessions were duplicates, among named accessions 2831 out of 7915 occurred more than once, i.e. 36 per cent. According to the ECP agreement, this database will be available to interested parties on electronic media.

COMPARISON OF THE GRAVIMETRIC BULK SELECTION METHOD AND THE PEDIGREE PLANT SELECTION METHOD IN PRODUCING QUALITY OATS.

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A. INTRODUCTION.

The Gravimetric Bulk Selection Method was described by Uriel Maldonado at the Second International Oat Conference, therefore I will not describe it at this conference. We have not used this method as yet here in the Mountain Valleys of Chihuahua, but in the future we probably will. The oat lines selected by the gravimetric bulk method evaluated in our experiments were selected by Ing. Carlos Jiménez in México State (near México City) where cereal grain seeding begins about a month earlier than here. Because of this reason, not all the gravimetric bulk method lines have the earliness desired for our region where earliness is an important characteristics. In this paper the oat varieties Cusihuiríachi (Cusi) and Páramo selected by the pedigree plant selection method in the states near México City, the variety Rarámuri selected in the states of Guanajuato, Chihuahua and Coahuila by the same method are compared to the varieties Papigochi, Babícora and Pampas selected by gravimetric bulk method in the states of Guanajuato and México State near México City. The States of Chihuahua and Coahuila are in Northern México which is a dry region with low rain fall in summer. The States of Guanajuato and México State, are in central México where the rainfall generally is higher than here in summer. In Guanajuato the oats is seeded in winter irrigation land and in México State in summer on dryland or irrigation. In the State of Chihuahua the oats is always seeded on dryland in summer. Therefore, there is also some enviromental Interaction when the varieties selected near México City are seeded here in the Mountain Valleys of Chihuahua.

The data presented is taken from the experimental plot data taken during the years 1984-87.

B. COMPARISON OF.

1.0 Yield.

Table 1 indicates that the yield of the varieties Papigochi, Babícora and Pampas, developed by the Gravimetric Bulk Selection Method (GBSM), according to the DMS analysis, is similar to the yield of the varieties Raramuri and Cusi developed by the Pedigree Plant Selection Method (PPSM). The five new varieties yield 16 to 30 percent more than Páramo.

TABLE 1. YIELD COMPARISON OF VARIETIES SELECTED BY THE GBSM, THE PPSM AND THE CHECK PARAMO.

VARIETY	SELECTION METHOD USED	kg/ha	Y I E L D	
			COMPARED TO CHECK PARAMO	
Papigochi	GBSM	2,384*	130%	
Babícora	GBSM	2,116*	116%	
Pampas	GBSM	2,154*	118%	
Rarámuri	PPSM	2,285*	125%	
Cusi	PPSM	2,248*	123%	
Páramo (check)	PPSM	1,828	100%	

*GBSM = Gravimetric Bulk Selection Method; = PPSM = Pedigree Plant Selection Method MSD at 5% = 301.38 kg/ha, C.V. = 19.01%, General Mean 2'169,256 kg/ha.

2. Earliness

Earliness, as was already mentioned, is an important oat characteristics for this region. This was one reason why Páramo, which has this trait, was accepted in this region. New varieties have to be early as well. Of those presented in Table 2, the varieties Cusi, Raramuri and Babícora have maturity similar to Páramo. Because Papigochi is a late variety, it will be released as forage oats for regions where it will be seeded under irrigation or when the rain starts early for dairy cattle feed.

TABLE 2. COMPARISON OF DAYS TO MATURITY OF VARIETIES SELECTED BY THE GRAVIMETRIC BULK METHOD, THE PEDIGREE PLANT SELECTION METHOD AND THE CHECK PARAMO.

VARIETY	SELECTION METHOD USED TO DEVELOP VARIETY*	DAYS TO PHYSICAL MATURITY
Papigochi	GBSM	96
Babícora	GBSM	90
Pampas	GBSM	91
Rarámuri	PPSM	88
Cusi	PPSM	84
Páramo (check)	PPSM	87

*GBSM = Gravimetric bulk selection method PPSM = Pedigree Plant Selection Method.

3. Kernel Size and groat percetn

Table 3, indicates that all the new varieties have a lower hull content than Páramo, but in the 1,000 kernel weight two, Pampas and Cusi, produce lighter kernels than Páramo. However, because their groat percent is high, they produce less hulls than the check. The varieties with highest groat percent and 1000 kernel weight are Babícora, and Rarámuri, the first one is selected by the gravimetric bulk method and the second by the pedigree plant selection method. This data indicates that plant selection by both these methods produce good kernels. Again it is also noticeable that a mechanical selection is just as good as a visual one. As the table indicates further selection is needed to develop new varieties with higher groat percent and high 1,000 kernel weight.

TABLE 3. COMPARISON OF GROAT PERCENT AND 1,000 KERNEL WEIGHT OF VARIETIES SELECTED BY THE GBSM, THE PPSM AND THE CHECK PARAMO.

VARIETY	METHOD USED IN MARDING SELECTIONS*	GROAT PERCENT	1,000 KERNEL WT. (gm)
Papigochi	GBSM	63.2	35.8
Babícora	GBSM	68.4	36.0
Pampas	GBSM	63.1	34.4
Rarámuri	PPSM	66.7	35.8
Cusi	PPSM	66.1	28.6
Páramo (check)	PPSM	59.0	35.9

*GBSM = Gravimetric bulk selection method; PPMS = Pedigree plant selection Method.

4. Disease Resistance.

During seasons with high rainfall, and therefore high humidity, high outbreaks of stem rust occur. As can be observed from Table 4 all the new varieties are moderately susceptible to stem rust in comparison to Páramo which is susceptible. This data also indicates that selections for disease resistance can be done mechanically as well as it is done visually and manually by the pedigree plant selection method. Other diseases such as crown rust, leaf blights, BYD and scald which generally cause very little damage, except in experimental plots, also occur in humid, high rainfall years. Susceptible lines to these diseases are eliminated in such years.

TABLE 4. COMPARISON OF STEM RUST RESISTANCE OF THE VARIETIES SELECTED BY THE GBSM, THE PPSM AND THE CHECK PARAMO.

VARIETY	SELECTION METHOD USED*	REACTION TO <u>Puccinia graminis avenae</u> (Stem Rust)
Papigochi	GBSM	14 MS
Babícora	GBSM	21 MS
Pampas	GBSM	17 MS
Rarámuri	PPSM	17 MS
Cusi	PPSM	12 MS
Páramo (check)	PPSM	44 S

*GBSM = Gravimetric bulk selection method; PPSM = Pedigree plant selection method

5. Groat protein percent

The analysis for this characteristic is done chemically, therefore either selection method would be just as effective in making selections for high protein. Of the varieties selected by the GBSM and PPSM both produce groats with medium and high protein percent. The protein percent is generally higher in varieties with small groats as is the case with Cusi and Pampas (Table 5), However, the varieties with large kernels (groats), Babícora and Rarámuri, that originated from the gravimetric bulk and the pedigree plant selection methods respectively also have high groat protein content (Table 5).

TABLE 5. COMPARISON OF GROAT PROTEIN PERCENT OF VARIETIES SELECTED BY THE GBSM, THE PPSM AND THE CHECK PARAMO.

VARIETY	SELECTION METHOD	GROAT OF VARIETIES	PROTEIN PERCENT MORE THAN PARAMO (CHECK)
Papigochi	GBSM	18.05	-0.85
Babícora	GBSM	20.15	1.25
Pampas	GBSM	21.10	2.22
Rarámuri	PPSM	20.46	1.56
Cusi	PPSM	22.86	3.46
Páramo (check)	PPSM	18.90	0.0

*GBSM = Gravimetric bulk selection method; PPSM = Pedigree plant selection method

6. Conclusiones.

Since the five new varieties developed by these two methods are very similar, what advantage does the gravimetric method have over the pedigree plant selection method? Jiménez (1) lists several besides higher yield. First, it requires little time. Very little data has to be recorded and the harvest operation requires less time than the pedigree method. This factor would be very important when harvesting is done during inclement weather when there is a possibility of losing the oats before selections can be made. Secondly with the G.B.S.M. all possible selections are made that may be overlooked in the P.P.S.M. Thirdly, few personnel are required to do the work and they require no plant breeding experience. Fourthly, because of this fact, expenses are reduced 30% in comparison to the PPSM. The Gravimetric Bulk Selection Method, therefore, has some very good advantages over the pedigree method.

R E F E R E N C E

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Evaluation of combining ability of oat varieties

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The aim of breeding in combination crossing is to exclude unfavourable alleles and to achieve the gene linkage, which could ensure a stable performance of economically important traits, improved in comparison with the state existing until now.

The evaluation of parental materials and their hybrids, made already in the initial stages of breeding, is considerably important for a proper strategy of subsequent selection (Zenisceva 1973, Velikovský Machan 1984). The most frequent genetical methods, enabling this evaluation, are represented by analysis of general and specific combining abilities (Hayman 1954 a,b; Griffing 1956). GCA is associated with a genetic additive variance, while SCA provides an estimation of non-additive compound of genetic variability, containing all effects of dominance, epistasis and genotype x environment interaction (Rojas, Sprague 1952). Therefore, GCA is more convenient in the case of self-pollinators for a basic evaluation of initial material (parents), the importance of SCA increases in a hybrid, the parents of which were selected on the basis of GCA. GCA + SCA rate in a certain traits can serve as a criterion of its potential level, achieved by means of selection (Udacin e.a. 1985). The method of incomplete diallel cross, modified according to Hinkelmann (1966), was used for the evaluation of cross combinations in this work.

Material and methods

The method consists in crossing only male and female cultivars, selected purposefully in advance. When studying the yielding ability and other economically important traits in three cross combinations, the following cultivars were used as female parents:

PAN /CS/ - (Cesky zluty x Goldhafer x D 71 x Rigal; yellow-grained, productive, mid-early cultivar with medium lodging resistance, suitable both for grain and green mass.

PERONA /NL/ - (Cebeco 6081 x Selma); white-grained, productive, mid-early to late cultivar, with high lodging resistance and susceptibility to rusts. It is suitable for green mass too.

FLAMINGSNOVA /D/ - (Pendek x Flämingsstahl); yellow-grained, early, productive cultivar with a short stem and medium lodging resistance.

Male parents were used as follows:

PIROL /D/ - (Endspurt x Luxor); white-grained, productive, early cultivar with a short stem, relatively resistant to the crown rust.

BORRINOVA /D/ - (Eckendorfer Fruh Borriesa x Flämingstreu); yellow-grained, productive, early cultivar with relatively short stem and low proportion of straw.

ALFRED /NL/ - (Marne x Marche Flamande x Mustang); white-grained, medium high, mid-early to late cultivar, high lemma proportion.

MARKUS /PL/ - (Astor x Pendek); white-grained, productive cultivar with medium lodging resistance and low resistance to leaf diseases.

MARGAM /GB/ - (S 222 Cn3/10 x 7717 Cn 3/3 x Condor); white-grained productive cultivar with relatively short stem, mid-early, partly resistant to powdery mildew.

PETKUS 8045 /D/ - (); white-grained, mid-early to late cultivar of productive, lodging resistant oat, with relatively low lemma proportion.

BORUTA /P/ - (MGH 6374 x Cebeco 6717); white-grained, productive, mid-early cultivar with a high lodging resistance.

SAMANTRA /GDR/ - (EMS mutant St. 8072 x Leanda); white-grained, productive, early cultivar with medium lodging resistance.

ERNTEGOLD /A/ - (a hybrid of two German strains); yellow-grained, medium productive cultivar with a short stem, high lodging resistance, susceptible to rusts.

The evaluation was based on F_1 and F_2 generations, sown individually into the beds with spaces of 5 x 15 cm and in 4 replications. Each hybrid combination was sown in the rate of 4 x 30, that is 120 grains, and 4 x 60, that is 240 grains.

Asymmetrical method of incomplete diallel cross evaluation (Design I) according to Hinkelmann (1966) was performed, and the hybrids were obtained from the combinations which were well considered and carefully chosen in advance. The combining ability was evaluated only in hybrids, the parental cultivars were not sown.

The analysis of experimental results was done on the basis of following schema:

$$Y_{ijk} = u + V_i + W_j + S_{ij} + r_k + E, \text{ where}$$

Y_{ijk} = value of a feature selected in a cross of the i -th male parent with the j -th female parent ($i \times j$) in the k -th replication.

u = average value of the total set of crosses.

V_i = general combining ability (GCA) of the i -th male parent ($i = 1, 2, \dots, V$).

W_j = general combining ability of the j -th female parent ($j = 1, 2, \dots, W$).

S_{ij} = specific combining ability (SCA) of the i -th male and j -th female parents.

r_k = replication of experimental members ($k = 1, 2, \dots, n$).

E = error

Auxiliary data:

r_v = number of combinations for each male parent.

r_w = number of combinations for each female parent.

N = total number of combinations (hybrids) in the experiment ($N = Vr_v = Wr_w$ is the number of all hybrids of the father side).

For the evaluation of the relevant components of variability a variance analysis was used, with help of the schema of multifactorial experiment, but with some modifications by Hinkelmann's proposal in comparison with the usual procedure. Corresponding results gained from the evaluation of the above mentioned plant characteristics were by this way processed. Only one trait (i.e. plant kernel weight) in one F_2 generation, however, was due to demanded restriction of this paper.

Results

The cross combinations selected for the evaluation of combining ability and of other components of a general variability are shown in Table 1. The sum values (in g) from F_2 generation and four replications and/also mean values of individual parental cross arrays for plant weight are shown in Table 1.

From the data of male performance in crosses it is possible to see the greatest positive influence of the male parents Markus and Petkus 8045 cv. on hybrid performance increase. In the female cross arrays, the yielding abilities were increased mostly due to the Pan and Perona cv. The both forms contributed to the highest plant kernel weight in subsequent crosses with Alfred and Markus cultivars.

From Table 2 showing variance analysis it is possible to see, that in this case GCA can be considered highly significant ($P=0,01$) in both parental form, SCA was not statistically significant. The evaluation of the intensity of both combining abilities for cross arrays of male and female parents and also of size of additive variance and variance of dominance is shown in Table 3A, 3B. From these tables it is possible to derive an essentially higher GCA for plant kernel weight in the parental forms Markus and Petkus 8045 than in the parental forms Borrinova, Margam, Boruta and Flämingsnova. First of all high SCA for plant kernel weight was manifested by the parental forms Pirol, Alfred and Perona, where as very low expression of SCA was shown by the cultivars Markus, Petkus 8045, Boruta and Flämingsnova. A summary of GCA and SCA in individual male and female parents is given in Table 4. This way was used for evaluation of 10 main traits in all combinations.

Discussion

Hinkelmann's method for evaluating general and specific combining abilities using incomplete diallels, has in comparison with the method of complete diallel cross the special advantage, that it does not necessarily demand the realization of those cross combinations, the usefulness of which in further plant breeding work is obscure. Simultaneously, the method allows to decrease essentially the number of evaluated cross combinations.

The requirement for absolute homozygosity of parents in diallel analysis, cited by some authors dealing with this questions (Hayman 1954a), has been fulfilled by oats.

Analysis of correlation between GCA and some traits by grain yield (Table 5) show, that varieties Pan and Perona have a good influence upon this kernel weight ($P=0,05$, $P=0,01$), while cultivar Flämingsnova had non-significant influence.

Completion of the method of SCA evaluation with further variance components (Hinkelmann 1966), especially with additive genetical variance $\sigma_A^2 = 4$ (Kov(H.S.)) and dominance variance $\sigma_D^2 = 4$ (Kov(F.S.)-2 Kov(H.S.)), contributed essentially to further enlargement and improvement of the recommended analysis. From the above mentioned results and from our experience achieved until now, it is possible to say, that the asymmetrical method of incomplete diallel crossing can be used in analysis of materials elaborated by oat breeders too.

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Tab. 1 SUM AND MEAN DATA FOR GRAIN WEIGHT PER PLANT OF HYBRIDS IN CHOICE COMBINATIONS F_2

♂ \ ♀	PAK	PERONA	FLÄMMINGS-NOVA	ΣV_i	\bar{V}_i	$\bar{V}_i - \bar{N}$
	1	2	3			
1 PIROL	11,439	-	8,568	80,24	10,030	0,072
2 BORRINOVA	9,773	-	6,828	66,40	8,300-1,658	
3 ALFRED	13,015	9,823	-	91,35	11,419	1,461
4 MARKUS	12,640	12,695	-	101,34	12,668	2,710
5 MARGAM	9,563	-	7,218	67,12	8,390-1,568	
6 PETKUS 8045	11,963	12,513	-	97,90	12,238	2,280
7 BORUTA	-	6,703	7,796	66,00	8,250-1,708	
8 SAMANTRA	-	10,010	8,873	75,53	9,441-0,517	
9 ERNTEGOLD	-	10,158	7,623	71,12	8,890-1,068	
ΣW_j	273,78	225,60	187,620	717,00	-	-
\bar{W}_j	11,408	10,650	7,818	-	9,958	-
$\bar{W} - \bar{N}$	1,450	0,692	-2,140	-	-	-

TAB.2 ANALYSIS OF VARIANCES FOR GRAIN WEIGHT PER PLANT IN F₂ GENERATION

SOURCE OF VARIATION	D.F.	SUM OF SQUARES	MEAN SQUARES	F - TEST
REPLICATIONS	3	9,805		
GCA OF MALES V_i (ADAPTED)	8	110,669	13,834	10,716 **
GCA OF FEMALES W_j (UNADAPTED)	2	171,880		
S_{ij} = SCA	7	5,348	0,764	0,592
ERROR	51	65,862	1,291	
TOTAL	71	363,564		
REPLICATIONS	3	9,805		
GCA OF MALES V_i (UNADAPTED)	8	193,672		
GCA OF FEMALES W_j (ADAPTED)	2	88,813	44,407	34,397 **
S_{ij} = SCA	7	5,348	0,764	0,592

TAB. 3A EVALUATION OF GENERAL AND SPECIFIC COMBINING ABILITIES AND VARIANCES OF GENETIC COMPONENTS FOR THE FEATURE : GRAIN WEIGHT PER PLANT

ITEMS	M A L E S									
	PIROL	BORIN.	ALFRED	MAHKUS	MANGAM	PETKUS	BORUTA	SAMANTRA	ERNELGOLD	d(min) P=0,05
GCA $\bar{V}_1 - \bar{N}$	0,072	-1,658	1,461	2,710	-1,568	2,260	-1,708	-0,514	-1,068	+1,520
GROUP OF GCA MANIFESTATION	II	III	II	I	III	I	III	II	II	
SCA MEAN VALUE OF \bar{V}_i	10,030	8,300	11,419	12,668	8,390	12,238	8,250	9,441	8,890	
$\frac{1}{T_V} \cdot SCA^2$	2,139	2,168	2,547	0,001	1,375	0,076	0,205	0,323	1,607	71,615
GROUP OF SCA MANIFESTATION	I	I	I	III	II	III	III	II	II	

TAB. 3B EVALUATION OF GENERAL AND SPECIFIC COMBINING ABILITIES AND VARIANCES OF GENETIC COMPONENTS FOR THE FEATURE : GRAIN WEIGHT PER PLANT

ITEMS	F E M A L E S			d(min) P = 0,05
	PAN	PERONA	FLÄMINGSNOVA	
GCA $\bar{w}_j - \bar{N}$	1,450	0,692	-2,140	± 2,782
GROUP OF GCA MANIFESTATION	II	II	III	
SCA	11,408	10,650	7,818	
$\frac{1}{r_w} \cdot SCA^2$	1,749	2,130	0,509	± 1,615
Group OF SCA MANIFESTATION	II	I	III	
VARIANCES OF GENETIC COMPONENTS				
ADITIVE VARIANCE σ^2_A				2,1070
VARIANCE OF DOMINANCE σ^2_D				12,7356

TAB. 4 EVALUATION OF GENERAL AND SPECIFIC COMBINING ABILITIES FOR THE FEATURE :
GRAIN WEIGHT PER PLANT IN THE PARENTS APPLIED

PARENTS		GCA	SCA
MALES	: PIHOL	INTERMEDIATE	HIGH
	BORRINOVA	LOW	HIGH
	ALFRED	INTRMEDIATE	HIGH
	MARKUS	HIGH	LOW
	MARGAM	LOW	INTERMEDIATE
	PETKUS 8045	HIGH	LOW
	BORUTA	LOW	LOW
	SAYANTRA	INTERMEDIATE	INTERMEDIATE
	ERNTEGOLD	INTERMEDIATE	INTERMEDIATE
FEMALES	: PAN	INTERMEDIATE	INTERMEDIATE
	PERONA	INTERMEDIATE	HIGH
	FLAMINGSNOVA	INTERMEDIATE	LOW

=====

TAB. 5 OAT - CORRELATIONS BETWEEN GCA AND SOME TRAITS BY GRAIN YIELD - AVERAGE OF F₁-F₂

GRAIN YIELD	PAN		PERONA		FLÄMINGSNOVA	
	s	s _r	s	s _r	s	s _r
GCA x BIOMASSE WEIGHT	0,9666 **	0,1281	0,8307 +	0,2490	0,6992	0,3197
x NUMBER OF GRAIN PER PLANT	0,9749 **	0,1114	0,7776 +	0,2812	0,7152	0,3126
x HARVEST INDEX	0,9820 **	0,0943	0,7146	0,3128	0,6923	0,3227
x UNIT STRAW HIGH	0,6006	0,3998	0,8107 +	0,2618	0,6230	0,3498

RESISTANCE OF OATS TO RUST DISEASES

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1. Economic importance of rusts
and of the resistance of oats to them

Crown rust and stem rust, incited by Puccinia coronata Cda. var. avenae Fras. et Led. and by P. graminis Pers. f.sp. avenae Erikss. et Henn., respectively, are widespread diseases of oats that occur in most parts of the world where this crop is cultivated (24, 43, 80). Eriksson and Henning reviewed the incidence of rusts in the 1660-1892. In Sweden in 1889, the oat rust outbreak was so high and damaging that the royal government funded research which led to the world-famous work of Eriksson and Henning (43).

Severe epidemics of oat stem rust in North America reviewed Craigie, Roelfs and Roelfs and Long (43). In Europe, Tanić (94) in Yugoslavia, Akerberg (1) and Leijerstam in Sweden estimated the reduction of 1000-grain weight caused by crown rust at 15-20%. In Czechoslovakia, Blatný (67) estimated losses caused by oat stem rust in 1934 at 30,000-40,000 tonnes. As demonstrated, both stem rust and crown rust reduce yields of grain and straw in oats (43, 58, 70, 79, 80) and the protein percentage in grain (70, 78, 80, 87).

Natural resistance is the most feasible and economic means of controlling the rusts, contributing to the stability of grain yield and quality (70).

2. Terms and definitions

Browder (3) under the concept of resistance understands any characteristic of a host plant limiting the damage produced by disease, including escape. Basically, the resistance of cereals to rust diseases has usually been classified as race specific (vertical) and race non-specific (horizontal) (95). Race specific resistance is usually characterized by the visible hypersensitive response. It is effective against some

racess (isolates) of the pathogen but not against others. Race non-specific resistance is supposed to be effective against all races of the pathogen. Harder (24) proposed to use the term race non-specific for the rate-limiting epidemiological types of resistance such as slow rusting. The rate of multiplication of a pathogen is decreased by reduced receptivity (infectibility) of a cultivar, longer latent period and reduced rate and duration of sporulation (24, 30, 38, 80, 99). According to Harder (24) terms 'specific' (vertical) and 'non-specific' (horizontal) characterize forms of resistance which probably do not exist in such explicit terms (24).

The rust tolerance (20, 21, 72, 74, 75, 76, 85) is that property of a cereal cultivar enabling it to compensate an attack by the pathogen to certain extent so that this does not result in a significant loss in grain yield and quality (60). It is supposed that tolerance could be differentiated from rate-limiting resistance by a combination of yield/kernel weight determinations and spore production (24, 56).

Plant breeders are interested in description resistance in terms of its expression, known inheritance and effectiveness. The Pc-genes for crown rust resistance and Pg-genes for stem rust resistance known to 1978 have been catalogued by Simons et al. (83), the Pg-genes known to 1985 by Martens (43) and the latest Pc-genes by Harder et al. (26, 27) and by Wong et al. (101).

3. Specific resistance

3.1. Inheritance of specific resistance

The specific resistance of oats to rusts is mostly conditioned by single dominant or partially dominant, less by recessive independently inherited genes but also by genes in interaction (61, 80, 83). The degree of dominance was found to be dependent on the genic background and also varies with races (isolates) of the pathogen (61, 80).

The dominance and the independent inheritance enable simple manipulation and the transfer of resistance genes to agronomically valuable cultivars (80).

3.2. Relationships between genes for specific resistance and genes for other characters

No linkage between Pc- and Pg-genes and genes for date of heading, number and length of basal hairs, percentage of lower florets awned, strength of awns and plumpness of seed was found by Osler and Hayes (80). Also in the study of Kiehn et al. (29) the genes for seed colour and awn character did not appear to be linked to the Pc-genes in A. sterilis. More recently, Wong et al. (101) in A. sterilis did not find any association between crown rust resistance and some floret characters as well.

However, the Pg-11 gene was found to be associated with yellow-green plant colour, weak straw and reduced grain yield (25, 50). A linkage between a Pc-gene and low yield was found by Simons in A. sterilis (78). On the other hand, Frey and Browning (14) found in A. sterilis Pc-genes associated with significant yield increase.

3.3. Sources of specific resistance

3.3.1. Crown rust

The cv. Victoria was largely used in breeding cultivars released in North America in 1940s. In addition to gene Pc-2, pleiotropic or closely linked with gene Hv-1 for susceptibility to *Cochliobolus victoriae* (80), the cv Victoria contains the other Pc-genes, effective against many races of crown rust (7, 80, 83). The combination of resistance of the cvs Victoria and Landhafer, incorporated into cvs Dodge and Garland and presently being transferred to several Czechoslovak yielding lines of oats are of continuing great importance (63, 66).

The cv Bond, containing Pc-3 and Pc-4 complementary genes (83) was used in breeding cultivars such as Clinton and the others which replaced the Victoria derivatives in the United States after 1945 (80). In Europe, however, the Bond genes, being recently transferred to German (FRG) cvs Delphin and Pirol (61, 68) and several Czechoslovak advanced lines seem to be of some importance up to now.

The cvs Landhafer and Santa Fe were used in breeding programmes in the U.S.A. after appearance of crown rust races virulent on Bond cultivars.

As obvious from race surveys, of hexaploid standard differentials of crown rust (84), cvs Victoria, Landhafer, Santa Fe,

Trispernia and Bondvic have been relatively resistant in Europe (48, 66, 68, 102) and also in Australia (Oates, pers. comm.).

However, more sophisticated approaches to genetic control of rusts in oats, and of crown rust in particular, in North America in the late 1950s, solving problems of long-term stability and the effectiveness of rust resistance, were enabled only by the findings of overabundance of resistance genes in *A. sterilis* oats (10, 22, 45, 96, 101).

The programmes of breeding and cultivation of multiline (14, 15, 16, 17, 18, 20) and multigene cultivars (49) in the United States and in Canada were opened, respectively.

To date, about 30 genes for crown rust resistance were found in *A. sterilis* collected in Israel (10, 97) and in the other Mediterranean and Near Eastern countries (12, 26, 45, 52, 101). The majority of them was already transferred to yielding lines and is applicable in crown rust resistance breeding programmes.

In the United States a high effectiveness of crown rust resistance was shown in genes Pc-14, Pc-36, Pc-38, Pc-39, Pc-50, Pc-52, Pc-53, Pc-57, Pc-58, Pc-59, Pc-61, Pc-X-1 and Pc-X-2, furthermore in gene combinations H 544, H 548, H 561, H 617-751, WI N569-42-52 and in combinations Pc-14+36, Pc-38+39, Pc-36+52 and Pc-51+53 and in cv. Amagalon (Michel, Simons, pers. comm.).

In Canada a high effectiveness has been repeatedly demonstrated in genes Pc-14, Pc-38, Pc-39, Pc-45, Pc-48, Pc-50, Pc-54, Pc-55, Pc-58, Pc-59, Pc-60, Pc-61, Pc-62, Pc-63, Pc-64, Pc-67 and Pc-68 and in cvs Fidler and Dumont (Pc-38+39, Pg-2+13) (Table 1)(8).

In Europe, more than 70% effectiveness was indicated in genes Pc-38, Pc-39, Pc-48, Pc-50, Pc-55, Pc-56, Pc-58, Pc-59, Pc-60, Pc-61, Pc-62 and Pc-63 (Table 2)(67, 103).

Furthermore, at the Winnipeg Research Station (24, 45) and at the Research Institute for Crop Production in Prague (66) a specific resistance to crown rust is supposed to be found in the diploids *A. clauda*, *A. longiglumis*, *A. pilosa*, *A. strigosa* and *A. wiestii*, the tetraploids *A. barbata*, *A. maroccana* and the hexaploids *A. byzantina*, *A. fatua*, *A. ludoviciana* and *A. sterilis* and in species *A. strigosa*, *A. macrocarpa*, *A. ludoviciana*, *A. sterilis* and *A. fatua*, respectively. As indicated,

a rich collection of donors of crown rust resistance was gathered for future use (24).

3.2. Stem rust

Present studies of virulence of *P. graminis avenae* in North America indicate a high effectiveness of resistance genes Pg-13, Pg-16 and Pg-a (Table 3)(23). The Pg-a complex (43, 47) consists of three recessive genes (Erpelding, McMullen, pers. comm.).

In Europe, a wide virulence range in oat stem rust was found in Sweden by Leijerstam (34), MacKey and Mattsson (39) and in Italy by Paradies et al. (55). The latest study of oat stem rust in central Europe indicated a high effectiveness of resistance genes Pg-a, Pg-13 and Pg-16, less effective were Pg-9, Pg-4 and Pg-15 (Table 4)(69).

In the 1987/1988 winter Harder (pers. comm.) began reviving all the old isolates of oat stem rust stored at the Winnipeg Research Station since the early 1960s, purified and re-identified them on the new North American nomenclature system (46). Up to now he has identified 79 NA-races. Genes Pg-16 and Pg-a had effectiveness 98.7 and 96.2%, respectively, the Pg-13 and Pg-8 82.3 and 70.9%, respectively.

There is high similarity in effectiveness of not yet widely used Pg-a, Pg-16 and Pg-13 genes in Canada and in Europe (Tables 3 and 4). In Europe the effectiveness of the genes Pg-9, Pg-8 and Pg-4 was 94.8, 14.4 and 81.4, respectively whereas in Canada in relation to 79 isolates it was 36.7, 70.9 and 48.1%, respectively. The differences might be explainable by the selection effect of some genes used in commercial cultivars in North America in the past and by environmental factors (43).

4. Non-specific resistance

4.1. Expression and recognition

The non-specific resistance, characterized by a reduced rate of multiplication of the pathogen (slow rusting) has been found to occur in oats to crown rust (27, 30, 35, 37, 38, 77, 80) and to stem rust (30, 93) as well.

Luke et al. (38) regard low receptivity (infectibility), expressed at low but not at high levels of infection, as a major component of slow rusting, as demonstrated also by Kochman and Brown (30).

The slow rusting is recognized according to reduced development of rust during an epidemic and determined by comparing disease progress curves (89) or rust severity during the logarithmic stage of development of an epidemic (99). The rates of rust development are calculated with the logistic and Gompertz models. The latter transformation was found to be more consistent at detecting of slow rusting (36).

4.2. Genetics

Slow rusting is a heritable trait (99). Luke et al. (35) found that in Red Rustproof oats the slow crown rusting was controlled by a small number of genes with partial dominance for susceptibility. Kiehn et al. (29) and Harder and McKenzie (27) indicated that crown rust resistance in A. sterilis was conditioned by recessive genes with additive effects. Simons (77) in field resistance of oats to crown rust found heritability values 46-86 and 65-92% in grain yield and seed weight reductions, respectively. However, none of the oats combined maximum yield with maximum field resistance. According to Simons (77, 80) the manipulation of this kind of resistance in breeding requires large populations (80).

5. Tolerance

The reduction in seed weight with reduction in grain yield are supposed to be the best measure of tolerance (72, 80). The rating technique of oat lines for tolerance consists of the comparison of productivities in paired plots, inoculated and treated with a fungicide (20, 80). The tolerance index is calculated by division of grain yield in rusted plot by the grain yield in treated plot (20).

Poljowski and Browning (56, 80) demonstrated that a dilatory resistance (slow rusting) may not be apparent. They found that the cv Otter producing more urediospores, is more tolerant if compared to the cv Cherokee as the yield depression was in these cultivars the same.

According to Simons (75) the tolerance is a complex quantitative trait. Therefore, the selection for rust tolerance should be effective (80).

Sources of crown rust tolerance were found in both cultivated oats (6, 80, 85) and in A. sterilis (76).

6. The precocious formation of teliospores -
a potential component of genetic control ?

The precocious teliospore formation in crown rust seemed to be polygenically controlled in one A. sterilis accession (71). It is supposed that this property might be used in genetic control of those cereal rust populations in which it works. Selection for this trait might be carried out in field or even in seedling tests. More research in both pathogen-host relationships and the effect of external factors on this process has to be carried out.

7. Strategies of genetic control

7.1. Multigene cultivars

The breeding of multigene single line cultivars, consisting of several resistance genes, as an alternative to multiline cultivars, was proposed and has been practised with success at the Winnipeg Research Station (49). It is supposed that the cultivation of multigene cultivars and, especially if connected with spatial (regional) deployment of genes can considerably prolong the effectiveness of the resistance genes (49, 51). The basic assumption of this approach is to be available a group of non-allelic genes.

7.2. Multiline cultivars

As reviewed by Wolfe (100), the control of airborne pathogens by multiline cultivars or cultivar or line mixtures is given by decrease of susceptible plants, the barrier effect of resistant plants and by the induced resistance.

7.3. Cultivar or line mixtures

Are supposed to facilitate the system of utilizing heterogeneity. A disadvantage of a cultivar mixture is overcome by line mixtures (28). A line mixture consists of lines with single resistances and similar in agronomic type (28, 100). Evaluation of the suitability of cultivars or lines for use in mixtures should be more elaborated (100).

7.4. Spatial (regional) and temporal deployment
of resistance genes

Regional deployment of specific resistance genes has been practised with success in crown rust control in the North American Puccinia Path for many years (20). The deploying

different sets of resistance genes into three regions of the Puccinia Path (5) enabled the breakdown of the epidemiological unit of this rust and the reduction of its epidemics in North America.

A system of spatial diversification of cultivars working on a farm scale was proposed and with success has been practised in the U.K. (28).

Furthermore, a temporal deployment of resistance genes is supposed it might enable their recycling and thus higher utilization.

8. Conclusions

Crown rust and stem rust are worldwide diseases of oats.

Resistance is the most feasible and economic means of controlling the rusts in oats.

The inheritance of specific resistance and the relationships of its genes with genes for other characters of plant indicate the wide use of specific resistance in breeding of yielding cultivars. There are many genes for specific resistance, especially to crown rust available in A. sterilis and in other wild oat species.

More genes for specific resistance to crown rust and stem rust indicate a high effectiveness in both North America and Europe.

The non-specific resistance (slow rusting), has been found to occur in oats to both crown rust and stem rust. The manipulation of non-specific resistance requires large populations.

The precocious formation of teliospores might be used in genetic control of cereal rusts.

Strategies of genetic control of oat rusts can consist of the cultivation of multigene and multiline cultivars and cultivar or line mixtures, possibly combined with spatial (regional) and temporal deployment of resistance genes.

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TABLE 1
EFFECTIVENESS (IN %) OF P_c GENES
AGAINST P. CORONATA VAR. AVENAE ISOLATES
IN CANADA IN 1984
(FROM CHONG, 1985)

P _c - gene / cv	effectiveness		
	Manitoba	Ontario Quebec	Total
P _c 35	63.9	47.0	58.0
P _c 38	98.9	98.0	98.6
P _c 39	100.0	100.0	100.0
P _c 40	60.1	95.0	72.4
P _c 45	98.9	96.0	97.9
P _c 46	43.7	88.0	59.4
P _c 48	99.5	100.0	99.6
P _c 50	90.7	97.0	92.9
P _c 54	91.3	91.0	91.2
P _c 55	100.0	100.0	100.0
P _c 56	88.5	65.0	80.2
P _c 58	99.5	100.0	99.6
P _c 59	99.5	99.0	99.3
P _c 60	98.9	100.0	99.3
P _c 61	100.0	100.0	100.0
P _c 62	98.9	98.0	98.6
P _c 63	100.0	98.0	99.3
P _c 64	97.8	93.0	96.1
P _c 67	91.8	99.0	94.3
P _c 68	100.0	100.0	100.0
HUDSON	77.6	79.0	77.7
FIDLER	100.0	100.0	100.0
DUMONT	100.0	100.0	100.0
ASCENCAO	93.4	98.0	95.0

TABLE 2
EFFECTIVENESS (IN %) OF P_c-GENES
AGAINST P. CORONATA VAR. AVENAE ISOLATES
IN EUROPE IN 1977 - 1980
(FROM ŠEBESTA, HARDER, 1983)

P_c-gene	effectiveness
P _c 35	61.2
P _c 38	74.5
P _c 39	95.1
P _c 40	52.4
P _c 45	58.1
P _c 46	70.5
P _c 47	56.1
P _c 48	93.6
P _c 50	93.3
P _c 54	66.4
P _c 55	95.9
P _c 56	82.3
P _c 58	100.0
P _c 59	100.0
P _c 60	83.4
P _c 61	83.1
P _c 62	87.2
P _c 63	76.3

TABLE 3
EFFECTIVENESS (in %) OF P_g-GENES
AGAINST P. GRAMINIS F. SP. AVENAE ISOLATES
IN CANADA IN 1984 (FROM HARDER, 1985)

P _g -gene	effectiveness				
	Ontario Quebec	Manitoba	Saskatchewan	Alberta	Total
P _g 1	12.2	0.6	0.0	0.0	3.9
P _g 2	0.0	2.8	0.0	0.0	1.9
P _g 3	1.4	0.0	0.0	0.0	0.4
P _g 4	0.0	2.8	0.0	0.0	1.9
P _g 8	87.8	0.6	0.0	0.0	25.6
P _g 9	9.5	94.4	100.0	100.0	70.2
P _g 13	93.2	100.0	100.0	100.0	98.1
P _g 15	4.1	81.0	33.3	100.0	58.5
P _g 16	70.3	100.0	100.0	100.0	91.5
P _g a	100.0	100.0	100.0	100.0	100.0

TABLE 4
EFFECTIVENESS (in %) OF P_g-GENES
AGAINST P. GRAMINIS F. SP. AVENAE ISOLATES
IN CENTRAL EUROPE IN 1978 - 1985
(FROM ŠEBESTA, HARDER, ZWATZ, 1987)

P _g - gene	effectiveness
P _g 1	14.4
P _g 2	17.5
P _g 3	21.6
P _g 4	81.4
P _g 8	14.4
P _g 9	94.8
P _g 13	99.0
P _g 15	79.4
P _g 16	99.0
P _g a	100.0

Tolerance of oats to Barley Yellow Dwarf

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The economic importance of barley yellow dwarf virus (BYDV) tolerance in oats is viewed differently by various experts. In the United States, the grain yield of recent cultivars (1975-1988) has been a striking improvement over the yield of previous ones. Most of these recent cultivars have better field tolerance to BYDV. It has been stated that improved BYDV tolerance could not be the primary factor explaining the recent yield increases¹. Personally, I believe that the importance of BYDV tolerance has been underestimated². It has also been stated that resistance to certain fungi is linked to lower yield potential³. The examples below will demonstrate that BYDV tolerance is linked with good yield potential, and that the active pursuit of BYDV tolerance or resistance would probably facilitate the creation of outstanding oat cultivars with better yield.

Before any further discussion, a definition of the terms "resistance" and "tolerance" is needed. We will use the Cooper and Jones terminology in our text⁴. According to them, a plant is resistant when virus infection and/or replication and/or invasion is restricted; a plant is tolerant when little or no disease effect is apparent on the plant. There is no paradox in stating that a plant could be at the same time resistant (by restricting virus multiplication) and sensitive (showing symptoms despite a low virus contents); following the same definitions, a plant could be susceptible (carrying virus levels about as high as may exist) but tolerant (showing little or no yield loss).

As such cases really exist with BYDV, we should get used to this double qualification. Because of this low correlation between resistance and tolerance, ELISA data can be difficult to use to predict tolerance in the field. High or low ELISA values may also be limited to a certain time period or to certain plant tissues. In one publication, tolerance has been related to somewhat lower virus contents in the aerial parts, as evaluated by the ELISA method⁵. This would qualify as intermediate resistance level, but the authors were not convinced that resistance was the most proper term to describe the reaction of oats, and they chose to use "tolerance". The authors were probably right in their preference of this term, considering that the low symptoms of the tolerant plant can be described as tolerance, whether virus contents is high, medium or low. Recent studies also show that ELISA of leaves without ELISA of roots could be quite misleading, and we must pay more attention to virus in roots when attempting to define the virus resistance or susceptibility of tolerant plants of any species⁶.

History of BYDV tolerance

Dr. R.M. Endo started the Illinois breeding project in 1955; shortly after, Dr. H. Jedlinski was hired to continue this work with Dr. C.M. Brown. At the time, cv. Albion was the best source of tolerance and Jedlinski's pioneering work led to the discovery of many other sources in Avena sativa and A. byzantina. The first tolerant cultivars from Illinois were Jaycee and Otee, which had just about the tolerance of Albion, and the yield potential of these was not better than the checks in virus-free situations. In 1976, the line Ill73-2664 entered the Uniform Midseason Oat Nursery (UMSON), in a year of BYDV epidemic. This line, outstanding in yield and straw strength, has become and still remains the most popular cultivar of the last decade in North America under the name "Ogle". It resists moderate drought and remains a top yielder in absence of virus. Strangely enough, a trend started in 1976 in the UMSON: every year except 1977, 1978 and 1984, the negative correlation between yield average and BYDV symptoms was significant or highly significant. Omitting "Ogle" from the calculations did not modify this conclusion. This was evidence that BYDV tolerance may have something in common with high yield.

In Canada, the Quebec BYDV project was started in 1972 and the Winnipeg project in 1975. Sources of tolerance were obtained from Illinois, Michigan and New Zealand, and wild oat species from international collections were also investigated in Quebec. Useful genes were found in Avena sterilis and A. occidentalis, but the best tolerance, which could perhaps be true resistance, was in the perennial oat A. macrostachya. Recently, Dr. J.-P. Dubuc, a colleague from our Research Station, registered two BYDV-tolerant cultivars, "Nova" and "Capital", from crosses that were submitted to artificial BYDV inoculation during the early segregation generations. These cultivars seem to possess a yield potential higher than any BYDV-sensitive cultivar known in Quebec. The Winnipeg project has also been producing cultivars with improved BYDV tolerance and these had good yield potential.

One important spinoff of the Quebec project was a major improvement of the aphid rearing and handling methods⁷, which made possible the artificial inoculation of half a million plants of oats, wheat or barley per year. We investigated spring oats from Europe and found tolerance in French cultivars "Noire de Moyencourt" and "Manoire", but obviously this was bred by chance and not by conscious effort. Cultivar "Norrland" from the Arctic Circle province of Norway was found very tolerant; this line is a tall landrace. Line AA 68-75-s-1 contains the Norrland tolerance (Table 1). Genetic variability was also found in winter oats, but no breeding work was done with these.

Oat quality is reduced by BYDV; increased hull percentage is observed even with late BYDV infection⁸ and fungal attacks are more severe on the panicles of sensitive cultivars, leading to seed discoloration and shattering. Breeding oats for food should emphasize the role of BYDV tolerance to protect seed quality.

The First International BYDV Nursery

The First International BYDV Nursery was launched in 1987 by Comeau, Jedlinski and D. Brown, using a system where every participant must send entries to all others. Collaborators joined in (Qualset, California; Burnett, Mexico; McEwan, New Zealand; Ohm and Foster, Indiana; Brinkman, Wisconsin; Haber, Winnipeg; Comeau, Québec) to produce a unique set of data on available BYDV-tolerant cultivars under artificial and natural BYDV inoculation.

The best lines of the group are shown in Table 1. The artificial inoculation data is probably more reliable because of uniform infection. A principal component analysis revealed that all the artificial inoculation trials were closely related, but the natural infection trials were less closely related to each other and to the artificial trials. The difference between tolerant and sensitive was also much more important in artificial inoculation trials (Table 1).

Quebec and Winnipeg lines were the best in the artificial inoculation, but Illinois lines were the best in natural infection sites. It is possible that natural infection trials favored lines that were less attractive to aphids or lines showing antibiosis to aphids; if this was the case, there could be a possibility for gene pyramiding by crossing Il 79-4924, best in natural infection trials, to 76 s6-1454, best in artificial infection trials. The four lines 76 s6-1454, Q.O. 215.1, Q.O. 209.58 and C.I. 9311 were in the top ten in both types of BYDV trials.

Relationships between BYDV tolerance, yield, and other factors

The First International BYDV Nursery data contained germplasm whose main quality was BYDV tolerance, with only one sensitive check; this nursery did not provide yield and agronomic data. However, the 1987 UMSON trials which is a pre-registration trial for U.S.A. contained yield, BYDV and rust data, and interesting correlations could be obtained with lines that represented a broad spectrum of agronomic value and disease reaction (Table 2).

It was most puzzling that, despite the exclusion of three sites where BYDV and rust damage was judged too severe, the average BYDV symptoms had a correlation of -0.72 with mean yield calculated over 20 sites in Northeastern USA and Canada. This correlation was raised to -0.80 by a fourth power transformation of the BYDV data. This meant a determination coefficient of 0.64 , about four times higher than the determination coefficient given by the correlation of mean rust to mean yield. In a trial done in 1973, BYDV infection had decreased the severity of rust, so one could perhaps have foreseen a negative correlation between BYDV and rusts⁹. But not even one single negative correlation was significant or near significant in the 1987 UMSON data set.

.Instead of the expected negative values, many highly significant ($P < 0.01$) and significant ($P < 0.05$) positive correlations were found between rusts and BYDV symptoms. This could mean linkage between BYDV tolerance genes and rust resistance genes has become a frequent case; it could also mean that BYDV predisposes oats to rapid invasion by certain rust strains. To be more accurate, positive significant correlations existed in about one third of the 96 correlations calculated between rust and BYDV data (from one given site or using means of many sites). For the majority of cases, correlations were not significant. Perhaps collaboration between BYDV and rust specialists would be warranted, in the immediate future, to bring some light on this most unexpected relationship between the two main diseases of oats.

Hypotheses and breeding strategy

Two hypotheses were formulated in 1974 about the high yield of BYDV-tolerant lines in various cereal trials. The Comeau hypothesis was that symptomless BYDV damage is always significant and reduces yield without being identified properly. The St-Pierre hypothesis was that BYDV-tolerant plants are selected for better translocation efficiency, better resistance to drought, cold, heat, fungi, and mineral deficiencies. After many years of heated debate with my colleague, I have to admit he could be partly right. The BYDV epidemics certainly do reduce the stress resistance of oats; by shortening the root system, the virus aggravates drought damage and mineral nutrition problems. Shorter straws bring more fungal infection on panicles and the Septoria problems were historically related to BYDV epidemics in Quebec. However, field sampling with ELISA also showed the first hypothesis was often true in Quebec: a lot of BYDV damage goes unnoticed. Only the heaviest epidemics produce the classical symptoms.

A breeding project cannot avoid the problem caused by interactions between diseases and stresses; trying to select for each disease or stress separately may be against nature. Probably that, in a humid year, one should select for the BYDV-tolerant lines that remain clean from fungi. In a dry year, it would be time to select lines that can maintain a healthy, functional root system despite the BYDV and drought.

BYDV tolerance is generally additive, and involves 3 to 5 segregating factors¹⁰. This imposes serious constraints to plant breeders. The simplest breeding strategy would be to produce F_2 lines and inoculate artificially with BYDV. This could work only if both parents possess BYDV tolerance with good agronomic potential. When one crosses a poorly adapted tolerant line (T) with a registered cultivar (G), one cannot expect enough useful progeny because tolerance is quantitatively inherited¹⁰. The recurrent selection methods would be appropriate, but another method that works well is to backcross the $T \times G F_1$ again with the

G parent, obtain F₂ of the backcross, and inoculate artificially for two or three selfing generations. If the virus is applied uniformly at the tillering stage, this process should at least eliminate all the sensitive progeny. Large initial plant populations being necessary, it is wise to inoculate the F₂ with a weaker BYDV strain, or to inoculate it late, about in the middle of the active growth period, to avoid destroying too much of the genetic variability. The F₃ and F₄ could be inoculated with severe BYDV strains, between the 5-leaf stage and tillering, as plant populations should be adequate by then to allow for harsh selection without excessive loss of genotypes.

Conclusion

The correlation between high yield and BYDV tolerance should encourage breeders to work together with entomologists and virologists to develop BYDV tolerant oat lines. Sources of tolerance are available to breeders, but the method for rearing viruliferous aphids is still poorly mastered except in a few research institutions. Learning this method is the first step before developing a large-scale project. Whether BYDV is or is not the number one disease of oats remains more or less a matter of personal opinion and a subject for further debate. The discussion could necessitate in-depth research if the present trend continues, BYDV-tolerant cultivars showing the best yield in many areas of North America. Some physiological attributes of the lines showing tolerance could actually be useful even in the absence of viral disease. Positive correlations observed between two main diseases of oats, namely leaf rusts and BYDV, warrant immediate investigation.

Acknowledgment

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Table 1. Best tolerant lines out of 51 evaluated in the First International Oat BYDV Nursery

Artificial inoculation (5 trials) ^a			Natural BYDV infection (3 trials) ^b		
<u>Line</u>	<u>Symptoms^c</u>	<u>Origin</u>	<u>Line</u>	<u>Symptoms^c</u>	<u>Origin</u>
76S6-1454(T)	3.0	Quebec	Il. 79-4924	2.3 & R.R.	Illinois
83 Rust Area Test 28	3.4 & R.R.	Winnipeg	C.I. 9311 (T)	2.9	Illinois
Q.O. 215.1	3.5 & R.R.	Quebec-Winnipeg	C.I. 9303 (T)	3.0	Illinois
Q.O. 209.58	3.5	Quebec-N.Z.	84 Quaker 95	3.0 & R.R.	Wisconsin-Texas
AA 68-75-s-1	3.5	Quebec	W 83577	3.0	Winnipeg
C.I. 9311 (T)	3.7	Illinois	76108RB1-7-1-4-5-3	3.0	Indiana
84 Rust Area Test 23	3.7 & MR.R.	Winnipeg	Q.O. 215.1	3.1 & R.R.	Quebec-Winn.
Q.O. 209.40	3.7	Quebec-N.Z.	Ogle	3.2	Illinois
84 Rust Area Test 32	3.9 & R.R.	Winnipeg	Q.O. 209.58	3.2	Quebec-N.Z.
Q.O. 209.43	3.9	Québec-N.Z.	76 S6-1454 (T)	3.3	Quebec
Clintland 64 (sensitive check)	7.8		83 Quaker 185	3.3	Wisconsin-Texas
			Lamar x CAV 3604.3	3.4	Quebec
			Clintland (sensitive check)	4.8	

a Two trials in Indiana and one in Illinois, Winnipeg, Sainte-Foy. All were with various PAV-type strains except for one trial with RPV in Indiana.

b Data from New Zealand, California and Mexico, with a few missing data in the last two sites (damaged plots).

c BYDV symptom scale: 0 = healthy looking; 5 = moderately heavy damage with leaf yellowing, slight dwarfing, loss of about 30% of tillers, head size reduction; 9 = very heavy damage, severe dwarfism, no heads. Lines marked R.R. were resistant to leaf rust in Wisconsin; the one marked MR.R. was moderately so. The lines indicated with (T) are the BYDV-tolerant checks.

Table 2. A selection of the most significant correlations (r) and determination coefficients (r^2) observed between data sets obtained or calculated from the 1987 Uniform Midseason Oat Nursery

	r	r^2
Mean all BYDV & Mean yield ^a	-0.72**	0.51
(Mean all BYDV) ⁴ & Mean yield ^b	-0.80**	0.64
Mean leaf rust & Mean yield ^a	-0.41*	0.17
<u>Leaf rusts and BYDV</u>		
PC 59 & (Mean all BYDV) ⁴	+0.57**	0.33
PC 59 & Illinois PAV	+0.45**	0.20
Ames 264B & Indiana RPV	+0.53**	0.28
Winnipeg seedling rust & Mean all BYDV ^a	+0.43**	0.18
Winnipeg seedling rust & Ind. PAV	+0.57**	0.33
Winnipeg seedling rust & Ind. RPV	+0.56**	0.32
Mean rust ^a & Indiana PAV	+0.46**	0.21
Mean rust & Indiana RPV	+0.46**	0.21
(Mean all BYDV) ⁴ & Mean rust	+0.32*	0.10

^a Mean yield includes 20 sites/23; 3 were excluded because of severe BYDV. The "Mean all BYDV" mean includes 4 data sets of natural infection plus 4 from artificial inoculation. The "Mean rust" includes all readings from artificial and natural leaf rust infection, totalling 15 data sets. For the r values, the negative sign indicates that higher symptoms (BYDV or rust) go together with lower yield.

^b (Mean all BYDV)⁴ is the mean above, raised to the fourth power.

* P < 0.05

**P < 0.01

FRIT FLY RESISTANCE IN OATS

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INTRODUCTION

The frit fly *Oscinella frit* (Linnaeus) is the most important stem boring pest of cereals in southern Sweden. Great economic damage occurs in oats, especially in fields where spring sowing has been delayed. The fly normally produces three generations a year. The first (late spring) and second (mid summer) generations mainly develop in oats (seedlings and panicles respectively). The third (overwintering) generation develops in grasses and winter cereals. Greatest economic damage is caused by the first generation larvae.

The best strategy for frit fly control in oats should be to reduce the population of larvae attacking the seedlings. The present paper discusses the mechanisms of resistance to frit fly attack and the possibilities of breeding for frit fly resistance in oats.

THE PERIOD OF SUSCEPTIBILITY - A CRUCIAL FACTOR

Very young oat seedlings are resistant to frit fly attack because they do not offer suitable egg-laying sites. Old seedlings, on the other hand, are resistant because the larvae fail to penetrate the shoot. The period of susceptibility starts when the seedlings become attractive to the egg-laying females. This event normally coincides with the early two-leaf stage. The period of susceptibility is not ended until resistance to larval penetration is fully developed. This normally happens at the five or six leaf stage. The length of the period is consequently determined by two key factors related to 1) the oviposition behaviour of the adult frit fly female and 2) the host plant penetration attempts by the newly hatched larva.

Oviposition behaviour

The frit fly female strongly prefers to lay eggs in the narrow crevice behind the loose coleoptile of cereal seedlings. Oat plants are maximally attractive around the two-leaf stage. This is when the coleoptile spontaneously starts to detach. On younger seedlings the coleoptile is closely affixed around the leaf base and does not permit the female to insert her soft ovipositor.

Coleoptile disconnection occurs quite suddenly at the two-leaf stage and the variation in this pattern is small among oat cultivars. Therefore, it seems impossible to reduce the period of susceptibility by manipulating the coleoptile character.

Larval penetration

The newly hatched frit fly larva burrows into the main shoot and enters the meristematic region. With increasing age the oat shoot becomes more resistant to larval attack. This gradually increasing resistance to penetration seems to be a general tendency in oats. Some cultivars, however, obviously acquire this type of resistance more rapidly than others. The main factor responsible for the increasing resistance to larval penetration seems to be the vascular bundles of the first leaf sheath. These act as a mechanical barrier and may stop the newly hatched larva from entering the central part of the shoot. Oat cultivars with rapidly developing vascular bundles show the highest level of resistance.

If resistance to larval penetration is induced early, the period of susceptibility will be reduced. This effect is of great practical importance, since late frit fly attacks are more serious and more common than early attacks.

BREEDING FOR RESISTANCE - SOME EXPERIMENTAL RESULTS

The selection method

The plant character associated with resistance to larval penetration is easy to observe: At late three-leaf stage (3 - 4 wks after sowing in the greenhouse), the first leaf sheath of the seedling is cut off just above the coleoptile apex. The vascular bundles are then counted under a binocular microscope at moderate magnification, either directly or after bleaching in 70 % alcohol for a few days. If the leaf sheaths are cut off carefully, the plants will recover and produce seed. By this rapid and non-destructive method segregants with desirable anatomical characters may be selected from large breeding populations.

Selection effects

Selections based on the vascular bundle character have been made in experimental breeding populations. Positive selections (a high density of vascular bundles) and negative selections (a low density of vascular bundles) were tested for frit fly resistance both in the greenhouse and in the field. The results indicate a small but consistent increase of the level of resistance in the positive selections.

The results obtained so far strongly indicate that it is biologically possible to improve frit fly resistance by plant breeding. It seems uncertain, however, whether a sufficiently high level could be obtained by the methods described above. From a commercial point of view, resistance should of course be good enough to "stand on its own feet". The value of a partial resistance should not be underestimated, however.

INTEGRATED PEST MANAGEMENT

Partial resistance may be a powerful ingredient in a system of integrated pest management. Even a moderate or low level of resistance may - if supported by other methods of pest control - contribute substantially towards a reduced need for pesticides. In the case of frit fly control in oats, early sowing in the spring is probably the most important factor. Choice of large, high quality seed which produce vigorous seedlings may also be important. If these measures are taken with an oat cultivar which rapidly passes through the susceptible growth stages, the risk of a frit fly attack would be highly reduced. A reliable method of predicting the risk of an attack would also help the farmer to decide whether insecticides should be used.

SUMMARY

Oat seedlings are maximally susceptible to frit fly attack around the two leaf stage. Younger seedlings are resistant because they do not offer suitable egg-laying sites to the frit fly females. The gradually increasing resistance of older seedlings, on the other hand, is caused by a reduced ability of the larvae to penetrate the shoot. The utilization of a direct resistance to larval penetration seems to be the most promising way of improving the resistance to frit fly attack in oats. An early development of resistance to larval penetration is associated with a rapid build-up of additional vascular bundles in the leaf sheath of the first leaf. This anatomical character can easily be observed in individual plants and hence be selected for in a segregating breeding population. Experimental studies indicate that the level of frit fly resistance can be increased in this way. Total resistance, however, is probably impossible to achieve by this method. Nevertheless, a breeding strategy aiming at a reduced period of susceptibility during the seedling stage would be of practical interest. If combined with an early sowing date, choice of large, high quality seed, and a possibility of predicting the risk of frit fly attacks, a partially resistant oat cultivar may contribute substantially towards a reduced need for chemical insecticides. This view is based on the conviction that partial host plant resistance can be a powerful ingredient in a system of integrated pest management.

TOLERANCE OF OATS TO HERBICIDES

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Much of the world's small grain production is routinely sprayed with a herbicide. Oats are more sensitive to herbicides than the other small grains. Therefore, they have a greater potential for injury. Herbicide injury is known to occur, however determining the reason for the injury or the amount of loss is often difficult.

Most of the literature pertaining to herbicides on oats discusses 2,4-D since it was an early herbicide and is still the most widely used on small grains. A limited number of reports discuss MCPA, atrazine and Hoegrass (diclofop-methyl). Other chemicals briefly discussed include: 2,4,5-T, NAA, IPC, paraquat, and toxaphene. Many tests of chemicals are contained in regional reports and have limited distribution.

The effectiveness of a herbicide depends upon 1) the absorption by roots, shoots or stems, 2) its translocation, 3) the molecular fate of the herbicide and 4) what affect it has on the metabolism.

Herbicide efficiency

There are four major categories of factors which determine the effect of herbicides on oats. These are 1) the chemical, this includes the kind, form and application rate, 2) the growth stage at which the herbicide is applied, 3) the environment which includes temperature, moisture and soil fertility, and 4) the variety.

On oats, the 2,4-D amine is the recommended form to apply because the ester form causes more injury. Much of the research with 2,4-D used the ester form because a primary concern was detecting differences between crops or varieties. This makes the assumption the amine and ester forms affect the plant in the same manner. The stage of development of the crop when 2,4-D is used is the second most important factor determining injury. The only factor of greater importance is the herbicide rate. Several researchers studied the effects of 2,4-D on oats when applied at different stages of growth.

Environmental conditions, such as temperature, moisture, and fertility have a major effect on plant growth. Plants are considered to be more susceptible to herbicide injury when growth is rapid. Several studies have shown oat varieties differ in their injuries from herbicides. The current situation exists because most of the studies showing differential variety susceptibility were done in the 1950's when herbicides were introduced. With the new varieties and new herbicides, the response of a specific variety to a herbicide is often unknown.

Variety response

In 1987, we tested 14 herbicide treatments using 5 chemicals on 5 oat varieties. The results from Watertown will be used as an example of what can happen. Seven treatments had a significant yield reduction. Four of these treatments are commonly recommended while the other three are often used for specific weed problems. The four common treatments also had significant reductions in test weight. Lodging was significantly increased by all three 2,4-D treatments.

The same test was planted at two other locations. At one location, only three treatments had significant yield reductions.

The two following tables show some of the detailed results of the 1987 results at Watertown using 2,4-D amine, MCPA and Banvel. All plots were sprayed at the recommended 3-4 leaf stage. The varieties show a differential response to 2,4-D with a wide response range at each herbicide rate. All varieties were tolerant of MCPA. However, the response to the Banvel + MCPA mixture showed some varieties to be tolerant while others were quite sensitive. This shows a variety may respond quite differently to various recommended herbicides. The only way to determine tolerance/susceptibility at the present time is to test each variety and herbicide combination. This is very unlikely to be done due to the number of tests required.

Table 1. Percent yield reductions of five oat varieties.

	Ai/ha	Variety				
		Hytest	Lancer	Noble	Sandy	Steele
2,4-D	0.56	10	21	5	16	29
	0.84	15	20	11	21	42
	1.12	6	16	10	10	41
MCPA	0.56	+4	+4	0	1	6
BANVEL .18; MCPA .28		2	17	23	8	21

To provide an annual reference on herbicide effects we cooperate with the extension people and use one oat variety and several herbicide treatments each year. The variety 'Lancer' is used because it has been shown to be sensitive to 2,4-D which is our most widely used small grain herbicide. 2,4-D ester at 0.56 kg/ha caused a 46% reduction in yield in 1987 while the amine form caused no reduction that year.

Table 2. Herbicide effects on oat yield components. Values are averages of five varieties.

	Rate Ai/ha	Per culm		1000 KW	Culms/m
		grain	seeds		
	kg	g	No.	g	No.
	0	1.11	39.3	28.5	62
2,4-D	.56	.97	33.7	28.9	61
	.84	.93	32.7	28.5	67
	1.12	.92	31.7	29.2	69
MCPA	.56	1.02	36.1	28.2	69
BANVEL .18; MCPA .28		.91	32.5	27.7	66

Table 2 shows herbicide treatments can reduce the average grain weight per panicle. Under our conditions, the reduction in number of kernels per panicle is often the most visible effect prior to harvest. Under these conditions the number of seeds per panicle was decreased more than the weight per panicle. As the number of kernels per panicle decreased, the average kernel weight often increased. Similar results were reported by Kent and Hutchinson who found treatments of 2,4-D or MCPA which decreased yields often increased kernel

weight and decreased the number of kernels per unit area. If a plant is not severely injured, it is easy to see how a reduction in kernel number per panicle results in slightly heavier kernels. Therefore, herbicide injury does not always cause poorer quantity grain. Most of the treatments in Table 2 also caused an increase in the number of grain-producing culms per unit area. Increasing the number of grain-producing culms per unit area did not compensate sufficiently to negate yield-reducing factors. These additional culms were usually small and produced only a few seeds.

Environment

When you have differences in herbicide effects and varietal responses, it becomes quite difficult to predict effects. This is particularly true when considered across different environments. The major variable in determining how oats respond to recommended herbicides is the local environment. The importance of the environment interaction has also been shown for other herbicides. When 20 oat varieties were tested for atrazine tolerance, yield reductions of 70 and 33% were reported for consecutive years by Brinkman et al. Prior studies with atrazine by Smith and Buchholtz reported 3 of 20 varieties responded differently in 2 years. Severe injury by MCPA was reported for one year in New Brunswick by Everett. The cause was not determined, but it was more severe on early varieties. We produced about 60% blasting in selected lines with bromoxynil plus MCPA one year when very wet fields delayed spraying slightly. This treatment on most years causes little damage. Therefore, the cause of injury was apparently due to the specific physiologic condition of the plants when sprayed. Since the spring had been very wet, there was probably a reduction in the size of the root system. The differential blasting was due to genetic differences.

Herbicides on oats have been reported to have the following effects: 1) lower grain yield, 2) increase lodging under certain conditions, 3) increase tillering, 4) reduce height, 5) delay heading, 6) cause rolling or burning of leaves, 7) panicles elongated or compacted, 8) reduce kernels per plant or area, 9) decrease seed viability, 10) increase protein, 11) stunt roots and 12) cause embryo changes. Lodging is greatly increased by 2,4-D at individual locations in some years. We don't know the prerequisites for this to occur. Friesen and Olson reported 2,4-D sometimes caused severe lodging. Total lodging of treated oat plots was reported by Erickson and Gault who added 2,4-D to the soil. The increase in lodging may be related to effects on the root system. Large and Weston reported injury to oat crown roots caused by 2,4-D. Studies on wheat by Johanson and Muzik reported abnormal root growth and suggested it may be the cause of decreased yields.

Oat plants are considered resistant or susceptible to 2,4-D depending upon their stage of growth. Losses can occur when they are sprayed at the wrong stage. Spraying at the least sensitive time is not always easy. For example, weather conditions or equipment failure can delay spraying. Varieties also have their individual patterns in rate of panicle primordia differentiation and panicle elongation. Ross reported early oat varieties had fewer leaves visible at panicle initiation time than later varieties. Tillering of small grain also makes it difficult to spray only at the best time. Cisar and Shands reported the first tiller is initiated 2 1/2 to 3 days later than the main stem. If a plant has two tillers the panicle initiation will be spread over six days. Differentialism of the spikelets in a panicle is spread over about 18 days according to Bonnett. The specific effects can vary considerably depending upon the factors already discussed.

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RESISTANCE OF THE NEW OAT VARIETIES TO CROWN RUST

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Oat crown rust is the most aggressive and harmful among other grain rust. On the data of American phytopathologists yield losses caused by this disease may reach up 70 % (Estimated losses caused by rust in small grain cereals in the United States - 1918-1976, 1978).

The causal agent of crown rust - *Puccinia coronata* Cda doesn't overcome winter in urediostage on the USSR territory, the sexual stage takes place on species of *Rhamnus* annually. This results to increase of a whole pathogen adaptation and great immunological diversity of populations. Diversity of faces and virulences combinations is very high on the whole parasit areal. That is why many attempts to create varieties with vertical resistance failed and led to arising of new virulent races. So, varieties with different resistance genes were infected in 2 - 3 years after developing (Stewart, Robert, 1970, Simons, 1986), for crown rust control nonspecific (horizontal resistance and tolerance) resistance should be regarded as basic one, and specific (vertical) resistance plays a supplementary role.

Problem of tolerance determination is in close connection with investigations of disease harmfulness. Information about economical damage, the level of pathogen harmfulness on definite varieties is necessary for breeder to improve a program developing varieties, their distribution in different regions taking into account epiphytity frequency.

The last 50-60 years a great number of papers has been devoted to methods of tolerance determinations. One of the most precise method is the pair plot's method suggested by Simons (1966), which allows to evaluate crop losses on various varieties.

Recently the new resistant varieties were developed in MPO "Podmoskovie".

Therefore, our aim was determination of the level crown rust resistance of wide-spread and new varieties and revealing of resistance role in decreasing economical damage due to disease.

Materials and methods.

Widely spread varieties - Astor, Nemchinovska 2, Gambo and the new, developed in KPO "Podmoskovie" - Drug, Skakune and 27h377 were investigated. Economical damage, caused by *Puccinia coronata* on these varieties and tolerance level were determined by the pair plot's method (Simons, 1966). Plots were randomized in 4-replications, 2-blocks. Plot size 3m². Inoculation was carried out with local populations of *Puccinia coronata* in tillering stage. Control was sprayed with tilt two times a season with interval 3 weeks.

Account of disease severity was carried out 5 times a season using the score Stakman E. C., Levine M. N., Baily (1923), corrected by Murphy (1953). The first score was carried out in two weeks after inoculation, the following ones - in 7 - 12 days in accordance with environmental conditions. Level and type of resistance were determined in field and laboratory trials according to the generally accepted method.

Laboratory cultivation of crown rust based on benzimidazol application.

Besides that the modified laboratory method was approbated on investigated varieties. The essence of it is the following: seedlings in Petry dishes on benzimidazol solution were inoculated by equal quantity of urediospores, which are virulent to all studied varieties. When postules appeared on contral sensitive varieties separately from each varieties urediospores were collected, suspended in tuein solution and accounted. Ratio between spore number from susceptible and resistant varieties is the index of horizontal resistance.

Coefficient of correlation of field laboratory data fluctuated from 0,87 up to 0,91 for different isolates.

Proteine content was determined by Kjeldahl metod.

Results and discussion

Nowadays nonspecific (horizontal) resistance determination is a rather complicated problem. There is not standart method of definition. Contemporary methods, which embraced identification of latent disease period, postules size and spores number, can't give the full

idea about the level of resistance. Laboratory methods, which consist of determination of postules number on unit's surface of seedlings and on flag-leaves are used only for separating susceptible samples from resistant ones. Consequently, a level of horizontal resistance can be determined on several indices. That's why in our work different methods of resistance identification were used, including above mentioned modified method.

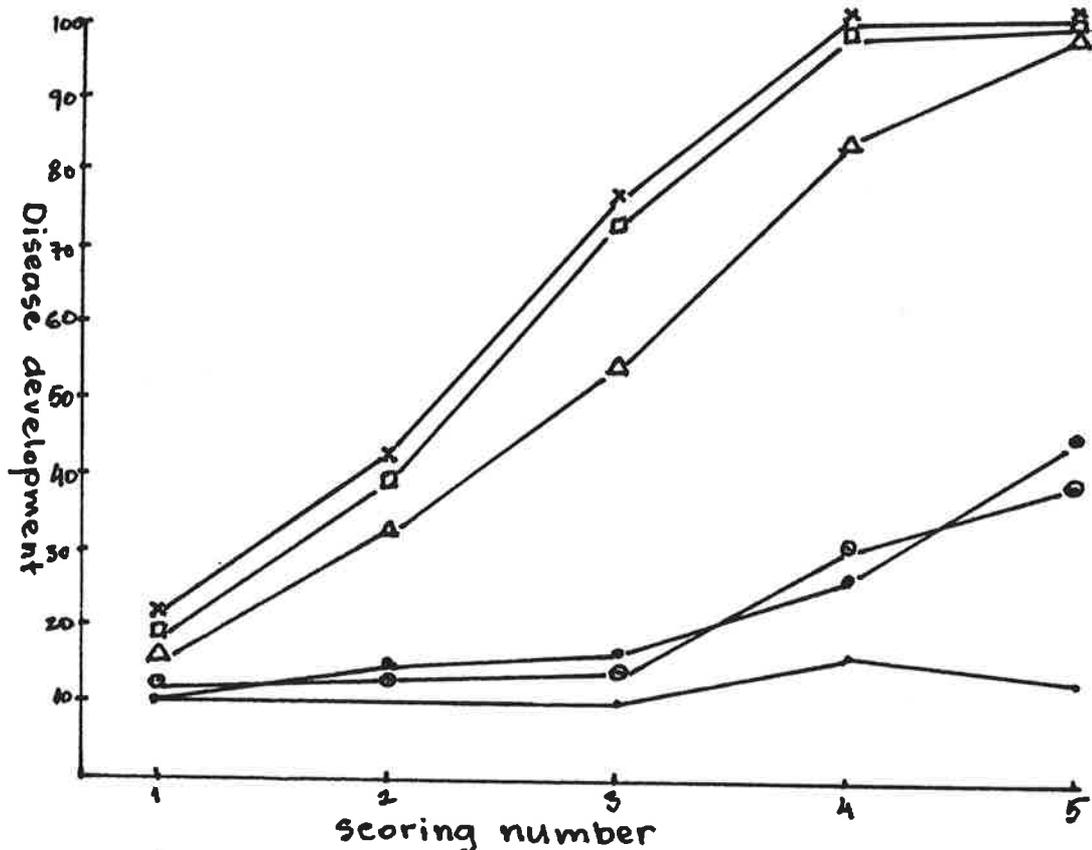
Field estimating on artificial inoculation background showed, that varieties Gambo, Astor and Nemchinovski 2 are susceptible, and Drug, Skakun and 27h377 are resistant to crown rust. Slow rate of infection on resistant varieties allows to conclude, that they have a horizontal resistance (fig. 1). For checking this suggestion 50 monopustule lines from fungal populations were isolated and all 6 varieties were infected separately by each of 50 isolates using the laboratory benzimidazol method. Simultaneously isolates were tested on 10 Pendec lines. In total isolates infected all lines except Pc 39. Thus, all six varieties, including Drug Skakun. 27h377 proved to be susceptible to all 50 isolates of pathogen. Resistance type of these varieties, determined by modified method (sporulation measuring) confirmed a suggestion about horizontal resistance.

Taking into consideration disease progress curve (fig. 1), susceptibility to all tested pathogen isolates, less rate of sporulation it may be concluded, that Drug, Skakun and 27h377 have horizontal resistance. For resistant varieties possible losses at maximum level of infection were determined (table 1). They consist of 7 to 23 %. It should be remarked, that 27h377 at the level of disease development 7 % didn't practically reduce yield.

Crown rust influence on oat yield

Table 1

Variety	Infection %		Yield losses %		
	Average	max	1986	1987	by average
Astor	90 S	100 S	61	91	76
Nemtsinovski 2	80 S	100 S	68	90	79
Gambo	85 S	90 S	45	72	58
Drug	37 SR	40 SR	18	28	23
Skakun	25 SR	28 SR	23	24	23
27h377	12 RS	15 RS	5	9	7



Crown rust severity of susceptible and resistant varieties in dynamics

- | | |
|-------------------|------------|
| □ - Astor | --- Drug |
| x - Nemtsinovka 2 | ○ - Skakun |
| △ - Gambo | — 27 H 377 |

Susceptible varieties losses were from 58 % to 79 %. No one from them didn't show satisfactory level of tolerance. Tolerance coefficient of Astor and Nemtsinovski 2 was only about 0,2. Variety Gambo is more tolerant, but also this level of tolerance is not sufficient for effective protection of yield.

Except of direct losses, crown rust causes indirect harm. On the data of many investigators, crown rust decreased 1000 keneral weight and starch in 20 %, content of nitrogen and 35 % increased husk content.

Our studies confirmed these data. As a result of structural analyses it is determined, that ratio of grain and straw weight, productive tillering and proteine content decreased.

Resistant varieties, which has not been infected by rust and protected with fungicide, didn't differ on of the most of indeces.

Crown rust influence on yield structure and grain quality of resistant and susceptible out varieties.

Table 2

Variant	Variety	Plant height cm	Prod. tillering	yield t/ha	Percentage of grain to sheat wheat	husk %	Proteine content %	1000grain weight g
A		<u>Susceptible</u>						
Infected by crown rust	Astor	89,8	1,09	0,98	33,2	33,2	10,5	27,3
	Nemtsinovski 2	95,3	1,00	0,91	27,9	32,1	9,8	27,3
	Gambo	101,7	1,15	1,89	29,1	30,2	10,4	28,0
	<u>Resistant</u>							
	Drug	125,8	1,04	3,82	31,2	26,6	10,9	35,7
	Skakun	100,6	1,19	3,97	37,9	26,7	11,0	34,4
	27h377	104,4	1,22	5,78	41,7	25,0	11,9	34,4
B		<u>Susceptible</u>						
Control (treated by tilt)	Astor	99,3	1,18	4,45	39,3	28,2	11,1	33,8
	Nemtsinovski 2	103,9	1,14	4,94	38,0	24,3	10,8	33,5
	Gambo	102,8	1,30	5,06	39,4	25,2	11,1	35,1
	<u>Resistant</u>							
	Drug	131,9	1,04	5,00	30,3	24,6	12,8	38,4
	Skakun	103,9	1,28	5,70	37,5	24,6	11,8	36,1
	27h377	101,9	1,26	6,20	45,0	25,0	13,6	33,1
	LSD 5 % (general)		0,84 t/ha					
	LSD 5 % (varieties)		0,63					

It is only observed slight yield and 1000 grain weight decrease of Drug and Skakun. This fact proves, that their level of resistance can satisfactory protect plants. It should be remarked, that low yield losses were demonstrated on a very strong artificial inoculation background. Under natural conditions disease appears at a heading stage, while in our trials inoculation was carried out at tillering stage and, accordingly, disease developed earlier.

As it is well known, the development of disease on varieties with horizontal resistance is low. This thesis is illustrated in our trials on specific varieties (fig. 1).

So, under conditions of natural epiphytoty the infection level of Drug, Skakun and 27h377 will be much less, than it is established in field trials. Yield losses will be also not considerable. In this connection fungicides application can be intirely eliminated.

Conclusion

Widly cultivated varieties Astor, Gambo and Nemptsinovski 2 are susceptible to *Puccinia coronata*. At the heavy infection they reduce yield in 76, 58, 79 % correspondingly. Grain quality decreases.

Drug, Skakun and 27h377 have level of resistance which is preliminary determinated as a horizontal. These varieties practically don't loss yield and can be without any fungicide application.

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DOMINANCE OF RACE 276 OF Puccinia coronata avenae ON Avena sterilis POPULATIONS IN ISRAEL.

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The oat crown rust fungus develops in Israel in its natural habitat and cycles between its main hosts, a few wild species of *Avena* and different species of *Rhamnus* as alternate host.

The host population of *Avena* in Israel consists mainly of wild indigenous hexploid *Avena sterilis* which is the progenitor of cultivated oats and readily crossable. This wild grass is found in every geographic niche in Israel.(11)

These natural ecosystems are undisturbed by human interference and do not include man-guided evolution in agrosystems.

These conditions are best suited to study various traits of the pathogen, such as virulence and the biotic and abiotic factors influencing their evolution. Surveys have been made in the past 5 years, in which we have annually collected isolates in about 100 different locations that represent various geographic regions of Israel. Analysis of the results of the surveys show that there was a high frequency of isolates of race 276, which appears to be the most prevalent race over the whole country, while race 263 occurs infrequently (1,9,11,12). The present study was undertaken to examine some of the factors that may be responsible for the dominance of race 276 over 263 in nature.

MATERIALS AND METHODS

In each experiment ten isolates of race 276 and ten of race 263 were compared. Each of the isolates studied were chosen from a sample of 20 - 30 monouredial isolates secured from different locations of country-wide distribution.

The locations ranged from the Upper Galilee and Golan Heights, with cold winters and abundant rainfall in the north, to the arid Negev desert with high temperatures, in the South.

Isolates were identified on a set of differential cultivars of oats according to Simons and Michel (10).

Components of pathogen fitness of the isolates were compared in different temperatures in the green-house and in the field. The studies were made on the oat cultivar Markton, which is universally susceptible to crown rust, thus eliminating the possibility of selective influence of the host genotype on parasitic strains.

To start with a series of inoculations by using one mixture of 2 isolates of races 263 and 276 taken from the same region has been done, as described elsewhere (2).

RESULTS

Shift in race populations. The races of 276 and 263 differed in their ability to survive in mixture when inoculated on a susceptible cultivar in a greenhouse at a temperature of 20 C. Race 276 increased its initial level when mixed with race 263. After the third generation, (each generation being 14 days) there were significant differences in the number of uredia between the two races. In the first experiment initial inoculations were carried out using five pairs of isolates of the races tested, race 276 consisted of 250 uredia out of 400 samples (62.5%) after four generations (Table 1).

Temperature-effect on urediospore infectivity and productivity. Infectivity of urediospores maintained for 6 to 21 days at various RH values at 28°C were higher in the case of race 276. Although survival rates decreased with an increase in storage period and RH values, infectivity for race 276 was significantly higher than that of race 273 (Table 2).

After 21 days of storage at 0% RH, the infectivity of race 276 was 14.4% as compared to 6.5% for race 263. A similar direction in the resulting infectivity was obtained at 45% RH (7.3% and 3.1% for race 276 and 263, respectively) and at 85% RH (2.4% and 0%, respectively) (Table 2).

At all temperatures tested, race 276 produced more pustules per leaf area unit and more urediospores per pustule. At 15°C, 8.1 and 3.9 pustules per cm² and at 20°C, 8.5 and 4.0 pustules per cm² were produced for races 276 and 263, respectively (Table 3). In addition, race 276 produced more urediospores per pustule than race 263. At 15°C race 276 yielded 27.9% more urediospores than race 263 (29552 vs. 23105). At 20°C race 276 yielded 40.5% more urediospores than race 263 (29973 vs. 21327), and at 25°C race 276 yielded 14.9% more urediospores than race 263 (21225 vs. 18461) (Table 3).

Epidemiological field experiment. Disease severity of plants in field plots infected with race 276 was higher than with race 263 at each disease assessment period throughout the experiment. Twenty-three days after inoculation, disease severity of plants in field plots infected with race 276 was significantly higher than those infected with race 263 (15% vs. 7%) (Fig. 1). Similar results were found in the number of urediospores trapped in the air. In field plots infected with race 276, 35 days after inoculation, the cumulative spore concentration per liter of air was 550×10^3 as compared to 320×10^3 for race 263 (Fig. 2).

DISCUSSION

Crown rust race surveys conducted in Israel annually have ascertained that race 276 of P. coronata avanae has been consistently dominant countrywide in populations of the indigenous, ubiquitous wild species A. sterilis. In contrast, race 263 has been found to be distinctly less common (1,9,11,12). The performance of both races on seedlings of standard differentials for race identification is similar except for the virulence of race 276 on the differential Ukraine, which is resistant to race 263 (10).

The objective of this study was to explain some of the factors that may have been responsible for the preferential competitive ability (or aggressiveness) of race 276 in relation to race 263. There is a broad consensus that prevalence of a pathogen in a plant population is conditioned not only by its virulence, but also by its survival ability and reproductive success (5,6,7).

Roane et al. (7) have stressed that a "distinction must be made between genes for virulence and those for ability to grow and reproduce rapidly". Similarly, on the basis of extensive studies on diseases of cereal crops, Sebesta (8) has concluded that the "virulence of a race on a variety does not prove significant harmfulness of the parasite".

Studies by U. Brodny, Z. Eyal and I. Wahl (unpublished) reject the possibility of a differential screening effect of A. sterilis populations on races 276 and 263. Moreover, the studies reported herein were carried out on the oat cultivar Markton, which is universally susceptible to crown rust, thus eliminating the possibility of selective influence of the host genotype on parasitic strains.

This research has dealt with the effect of some elements of parasitic fitness on the development of races 276 and 263. A similar approach was adapted by Brown (3), Martens (4) and Nelson (6).

Our results reveal that race 276 is superior to 263 in urediospore competitiveness in mixture (Table 1) and in urediospore viability over a period of hostless conditions (Table 2). The number of uredia and the number of spores per uredium produced by race 276 was higher than race 263 (Table 3). In field tests infectivity and duration of urediospore yields for isolates of race 276 showed a higher rate of pathogenic development than those of race 263 (Figures 1 and 2). The cumulative effect of these factors over a number of generations may influence the capability of the pathogen to survive and propagate in A. sterilis populations.

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TABLE 1. Number of uredia produced by mixtures of races 263 and 276 grown for four uredial generations on the variety Markton at 20 C

Experiment no.	Generation ^a no.	Uredia (no.) ^b		χ^2 values (1:1) ^c
		276	263	
I	1	207	193	0.49
	2	209	191	0.81
	3	220	180	4.00
	4	238	162	14.44
II	1	202	198	0.04
	2	216	184	2.56
	3	234	166	11.56
	4	250	150	25.00

^aOne generation means a cycle from inoculation to sporulation at an interval of 14 days.

^b400 Pustules were sampled randomly in each generation to detect significant differences between proportions of the two tested races at $P < 0.05$.

^cThe expected χ -square value, $P = 0.01$, is 6.63.

TABLE 2. Infectivity of urediospores of *Puccinia coronata avenae* race 276 and 263 after storage in various conditions of relative humidity and time at 28 C

Days of storage	Percentage of infection ^b after exposure to the following relative humidities (RH) ^c					
	RH 0%		RH 45%		RH 85%	
	Race 276	Race 263	Race 276	Race 263	Race 276	Race 263
6	92.9	87.1	60.8*	48.4*	37.2	30.2
15	71.3*	40.9*	33.7*	23.7*	26.1*	17.6*
21	14.4*	6.5*	7.3*	3.1*	2.4*	0.0*

^aRelative humidities of 0, 45, and 85% were obtained by maintaining inoculum in closed containers over dry P_2O_5 and saturated solutions of $Ca(NO_3)_2$ and $ZnSO_4$, respectively. Data are averages of six replications with 16 replicants in each.

^bPercentage of infection was determined in each treatment by comparing it to plants inoculated with fresh spores.

^cAsterisks indicate significant differences between the two races ($P = 0.05$), as determined by the Waller-Duncan k -ratio t test.

TABLE 3. Number of pustules per square centimeter (cm²) leaf and cumulative number of urediospores per pustule produced on leaves of Markton inoculated with races 276 and 263 of *Puccinia coronata avenae*

Temperature (C)	Pustules per cm ² /leaf ^{a,b}		Cumulative no. of urediospores ^{b,c} produced per pustule	
	Race 276	Race 263	Race 276	Race 263
15	8.1 a	3.9 b	29552 a	23105 c
20	8.5 a	4.0 b	29973 a	21327 b
25	4.9 bc	3.6 b	21225 b	18461 d

^a Each race was represented by 10 isolates; the given values are means of six replicates of each of the 10 isolates, each replicate containing 20 replicants.

^b Means within a column followed by different letters differ significantly ($P = 0.05$) according to the Waller-Duncan k -ratio t test.

^c Data are averages of six replicates of each of the 10 tested isolates. In each replicate, urediospores were collected from all pustules occurring on a 3-cm segment of leaf surface from five leaves (6–10 pustules per leaf). Spores were collected four times, at 2-day intervals, beginning 9 days after inoculation.

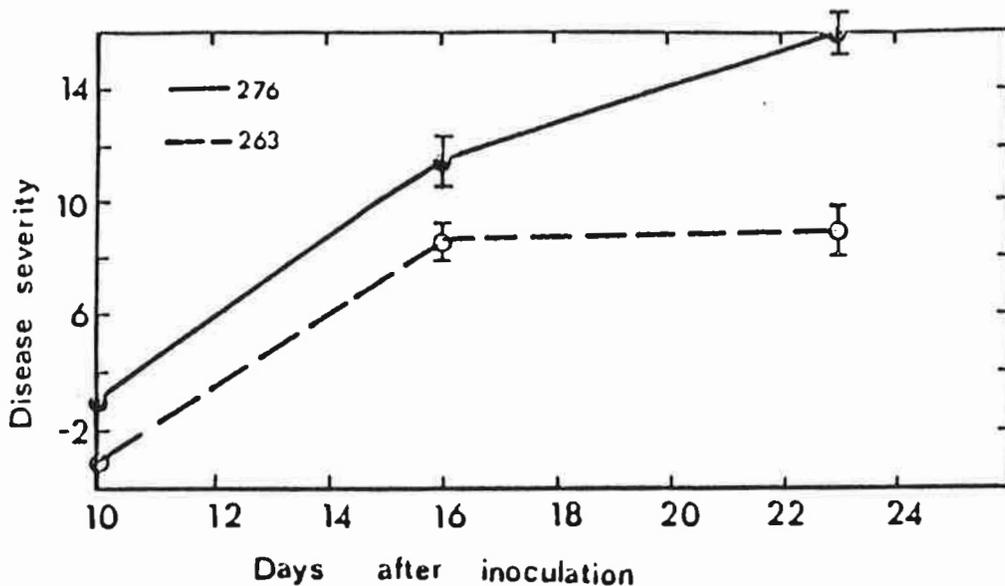


Fig. 1. Development of telia in races 263 and 276 of *Puccinia coronata avenae* at 25 C. A, Time of telia formation of the two races. Twelve isolates of each race were tested. B, The respective percentage of coverage of leaves by telia of races 276 and 263. Each data point is an average of 20 plants with two replicates. Vertical bars indicate \pm SE of the mean.

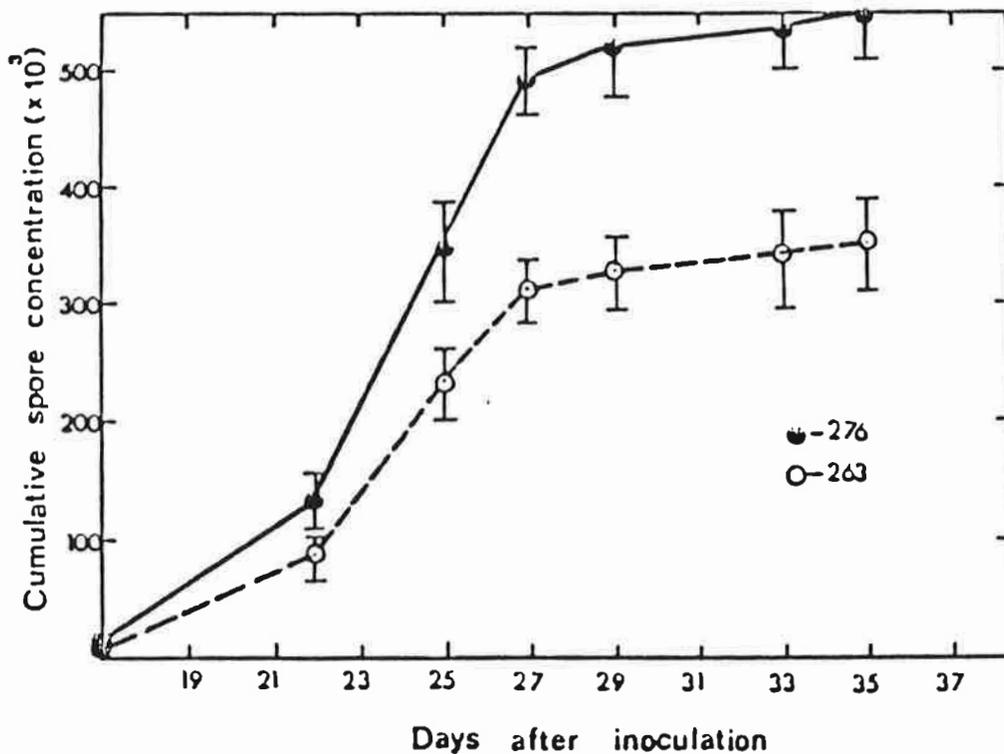


Fig. 2. Rate of disease progress in field plots inoculated with races 276 and 263 of *Puccinia coronata avenae*. Each data point is an average of five plots in two experiments. Vertical bars indicate \pm SE of the mean.

DICLOFOP-METHYL TOLERANT OATS IN THE WINNIPEG BREEDING PROGRAM

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Wild oats (*Avena fatua*) is an important weed in western Canada causing reductions in both yields and grades. Due to genetic similarities, no herbicide is recommended for control of wild oats in cultivated oats (*A. sativa*) in Canada. One of the reasons given by farmers for not growing oats is that the reduction in the wild oat population, achieved from herbicide use under previous cereal cropping regimes, is lost when the uncontrolled wild species in oat crops produce large quantities of seed which shatter and perpetuate the weed problem. The dormant scattered seed perpetuate the weed problem and heighten the necessity for annual use of wild oat herbicides. If an oat variety tolerant to one of the wild oat herbicides were available, oats could be kept free of wild oats through herbicide application and the weed problem could be minimized.

Several sources of tolerance to wild oat herbicides have been reported. The best appears to be 'Savena 1' (Barr, 1985), a recently registered Australian oat variety, which is tolerant to the wild oat herbicide diclofop-methyl (registered under the names "HoeGrass", "Hoelon" or "Illoxan"). The pedigree of this variety, developed by Andrew Barr of the South Australian Department of Agriculture is West*2/New Zealand Cape. Savena 1 has been used as a source of tolerance to diclofop-methyl in the Winnipeg oat breeding program.

In an attempt to determine how widespread tolerance to diclofop-methyl in the oat population was, a diverse group of genotypes was screened. This group consisted of advanced lines from oat breeding programs in North America, Canadian varieties of current and historical interest and an *A. fatua* line reported to have the greatest tolerance out of a collection of 88 *A. fatua* and *A. sterilis* accessions. Based on visual and dry matter ratings none of the lines tested had a tolerance as good as Savena 1, although a few had an intermediate tolerance while most were killed by the herbicide. This work indicated that tolerance to diclofop-methyl, both in tame and wild oat populations is not widespread.

To determine the mode of inheritance of tolerance to diclofop-methyl, four adapted, advanced lines in the Winnipeg breeding program were used in crosses and reciprocal backcrosses to Savena 1. Duplicate plantings of material from these crosses were sprayed with diclofop-methyl at either 0.4 or the recommended 0.7 kg/ha when the plants were in the 3 leaf stage. Diclofop-methyl injury symptoms could be read two weeks after spraying although differentiation of expression was clearer after four weeks. Symptom expression was clearer on those plants treated at the higher rate of application.

There were clear extremes in reaction to diclofop-methyl but lines showing segregation or an intermediate reaction made it difficult to fit a genetic model for all of the generations of all the crosses. Despite this difficulty, several general conclusions about the inheritance of tolerance to diclofop-methyl could be drawn. Because the reciprocal backcrosses produced similar ratios, it was concluded that this trait was not cytoplasmically controlled. Although data from some generations of the cross involving OT233 and Savena 1 did not support the hypothesis, most data indicated that tolerance to diclofop-methyl was controlled by two independent recessive genes (Warkentin et al. 1988). Nearly uniformly tolerant lines resulted after one or two generations of spraying. The results of this study indicate that it should be possible to incorporate tolerance to diclofop-methyl in an oat breeding program.

Some of the lines which were obtained from the inheritance study also form part of the oat breeding project at Winnipeg. Lines of interest were those that were tolerant to diclofop-methyl and were also resistant to stem and crown rust. To compare the yield potential of these lines, trials involving sprayed and unsprayed control plots were performed in 1986 and 1987 at the Agriculture Canada Glenlea research farm. In addition to 22 diclofop-methyl tolerant lines, all five parents involved in developing these lines and the variety Dumont were included in the tests. When the plants were at the 2-3 leaf stage, one of the tests was sprayed with diclofop-methyl at the recommended rate of 0.7 kg/ha.

The plants were sprayed under excellent conditions but because of heat (1986) or moisture (1987) stress after spraying, the herbicidal action was not as great as it could have been under ideal growing conditions. Nevertheless, differences were observed. All of the experimental lines and the parents in the sprayed test were shorter than in the unsprayed, control test. This is an observed effect of the action of diclofop-methyl (Crowley et al., 1978). In all but two of the experimental lines, the height reduction was less than 10%. There was no relationship between the reduction in height and the reduction in yield due to the herbicide.

Lodging in the sprayed test was not as great as in the control test. This might be due to the reduction in stature although in some cases it might also be due to a thinner stand of plants. As with the height reduction, there was no relationship between the reduction in lodging and the reduction in yield due to the herbicide.

In all cases, the test weights of seed harvested from the plots that were not sprayed with diclofop-methyl were slightly greater than the sprayed plots. For most plots, this difference was less than 5%.

Yields were influenced by this herbicide. The greatest yield reductions (approximately 40 %) were observed in the herbicide sensitive parents. The experimental lines varied in their yield reaction. Some showed yield reductions similar to the sensitive parents but 13 of the 22 lines had a yield reduction of less than 20 % in the presence of the herbicide compared with their yield in the unsprayed tests. Three of the 13 lines had a mean yield reduction of less than 10%. When sprayed with the herbicide, all but three of the

experimental lines yielded more than the check cultivar, Dumont. In the absence of the herbicide, six of these diclofop-methyl tolerant lines yielded equal to or better Dumont.

This yield trial showed that, on the basis of a small number of early generation lines, the herbicide tolerance of Savena 1 can be combined with the rust resistance and most of the yield potential of the recurrent parent. By backcrossing and selecting only the best of the lines surviving after spraying, a commercially acceptable variety could be developed for farmers to control wild oats in their cultivated oat crops.

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CONTROL OF WILD OATS IN CULTIVATED OATS WITH HERBICIDE SAFENERS

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1. INTRODUCTION

Approximately 100 herbicides are available for use in cereals in the UK. In wheat and barley about ten control wild oats (*Avena fatua*, L.). In the oat crop, there is no herbicide which can selectively control wild oat in the UK, although one, chlorfenpropmethyl, is available in Germany. Such a situation has led to the decline of oats in recent years and has inhibited its increase as an alternative crop (1). Although crop genetic engineering offers some hope in solving this problem (2), another possible approach employs the concept of herbicide safeners (2,3).

This paper describes some results of a three-year study at the former Weed Research organization, Begbroke Hill, Oxford into the potential use of pre-emergence herbicides in conjunction with safeners. Similar work with post-emergence herbicides was reported on at the second international oat conference (4).

The pre-emergence studies were done in three phases, each of one-year duration (i) initial and subsequent screening of potential herbicides, safeners and a wide range of oat cultivars, (ii) investigation of the influence of biotic factors on safening, (iii) improvement of the degree of safening by manipulation of chemical and physical factors.

2. MATERIALS AND METHODS

Experiments were carried out generally in 9 cm. diameter plastic pots containing a sandy loam soil, sown with five oat seeds at a depth of 1cm. Safeners (see Table 1) were applied prior to sowing by shaking appropriate weights of seeds and safeners in glass beakers. (0.5% w/w a.i. of seed weight, 0.25% for flurazole). Herbicides were applied generally to the soil surface with a laboratory track sprayer travelling at constant speed ($0.5 \text{ m}_1 \text{ sec}^{-1}$), 30 cm. above the stationary pots delivering a volume of 370 l ha^{-1} at a pressure of 2.1 kg.cm^{-1} . Plants were kept in a temperate glasshouse, being watered from overhead as necessary for germination and growth. Assessments were made by counting surviving plants, scoring for vigour and recording the fresh weight of shoots. There were at least three replicates per treatment together with appropriate controls, including safened and unsafened.

TABLE 1. List of safeners, their chemistry and formulation

NA	1,8-naphthalic anhydride	98% a.i. technically pure solid
R25788	N,N diallyl-2,2-dichloroacetamide	20% a.i. water soluble powder
M32988	2,2-dichloro-N-(3-methyl-4-thiazolin-2-ylidene) acetamide	technically pure solid
Flurazole	benzyl-2-chloro-4-(trifluoromethyl)-5-thiazole carboxylate	48% liquid

3. RESULTS AND DISCUSSION

(i) Screening of herbicides, safeners and oat cultivars.

Of the 52 herbicides tested, ten showed a positive safening response with one or more of the safeners. These were TCA, metolachlor, propachlor, ethofumesate, benfuresate, 1-flamprop-isopropyl, flamprop-methyl, trimexachlor, EPTC and tri-allate, the two latter being applied as incorporated treatments. Generally NA was the most effective safener, both in terms of the number of herbicides showing safening responses and in the degree of safening. In the cultivar trial some natural selectivity was found between cultivated and wild oat with some of the ten herbicides, cvs. Elen, Madog, Milford and 07260 Cn III often being tolerant at doses where the weed was controlled. Safening was almost entirely confined to one type of herbicide, i.e. those which inhibit mitosis in their mode of action. There was little response with photosynthetic inhibitor type herbicides, such as ureas or triazines, in common with safening in other crops (3). Of the various herbicide 'families' there was a tendency for safening to be found with acetanilides, e.g. metolochlor, another feature in common with safening found in other crops (3).

(ii) Factors affecting safening of NA.

These included factors such as N, P, K, pH/liming, soil type, sowing depth, NA dose, seed moisture content and soil moisture. The soil moisture had the greatest influence, both as regards safening and herbicide efficacy (Table 2). Plant growth improved with increasing soil moisture. NA also promoted better growth, more so at higher soil moisture contents. Results with 1-flamprop-isopropyl and other herbicides showed greater activity at field capacity (22%) and above. The degree of safening tended to be higher at field capacity for all herbicides tested.

Increasing the dose of NA applied to seeds also tended to improve safening but only to a certain level.

TABLE 2. Effect of soil moisture on safening of oats by NA with 1-flamprop-isopropyl (g/plant fresh weight)

Dose (kg/ha)	Soil moisture content (%)						
	17		22*		27		
	-NA	+NA	-NA	+NA	-NA	+NA	
1-flamprop	0	0.44	0.54	0.63	0.76	0.74	0.99
isopropyl	1.5	0.41	0.56	0.35	0.79	0.55	1.19
	3.0	0.15	0.54	0.10	0.72	0.22	0.89

S.E. \pm 0.06

* = field capacity

(iii) Improvement of safening by manipulation of chemical and physical factors. Considerable variation in safener performance was experienced during the course of these experiments. Much of this was thought to be due to the problem of adhesion of the NA powder to the seeds. This was especially evident in a field experiment where much of the NA was lost in the seed drill. Even so, a significant degree of safening was found with TCA and tri-allate. Much effort was consequently spent concentrating on the physical and chemical aspects of adhesion of the safener to the seeds. Some experiments with chloroform and surfactants showed that disturbance of the wax on the seed coat could enhance safening. Inclusion of the fungicide, thiram was found to increase the degree

of safening. These findings culminated in experiments in which the ordinary method of seed dressing, as described earlier, was compared with a commercial seed coating process (Filcoat) kindly prepared by Germain's UK Ltd. The latter was slightly more effective (Table 3). Unfortunately, bad harvesting conditions in a field trial in 1985 prevented any firm conclusions being drawn; but from interim observations, the commercial preparation seemed more effective, as expected after performing better in the seed drill.

TABLE 3. Degree of safening with Dula oat seeds dressed normally with NA or coated (% shoot fresh wt. increase as compared to unsafened)

	dose (kg/ha)	<u>Normal</u>		<u>Coated</u>		
		NA rate %	0.5	1.0	0.5	1.0
Ethofumesate	0.3		37**	64***	43**	67***
Flamprop- methyl	2.0		23*	34**	43**	46**
	4.0		50***	72***	52***	86***

*, **, *** = significantly different from unsafened at P 0.05, 0.01 and 0.001 respectively

One of the most encouraging experiments was with a two-way (binary) chemical combination of safeners. Most promising was the NA + M32988 mixture with TCA and ethofumesate (Table 4). Both safeners alone showed partial safening, but together, crop tolerance was maximised. One implication of this is that a herbicide may have more than one recognized mechanism of action while a single safener may have the potential to block only one of these processes.

TABLE 4. Effect of two safeners, alone and in combination, on herbicide activity to oats (mean fresh wt. g/plant as % of control)

	dose (kg/ha)	-NA	+NA	+M32988	+NA/M32988
TCA	3.0	20	41	70**	89***
Ethofumesate	0.3	0	22	23	87***

** , *** = significantly different from unsafened at P 0.01 and 0.001 respectively

Finally, the effect of delaying the application of the herbicide by up to four days after sowing safener treated oat seed, resulted in improved safening with NA. While this may not always be possible in practise, perhaps other similar, physical changes would be worth further study.

4. CONCLUSION

While it is agreed that safeners have not yet reached an adequate level of effectiveness in oats (2), the results of these experiments suggest that if the processes involved were better understood, further research may yet lead to the solution of such an intractable problem as wild oat control in cultivated oats. Biochemical and other studies into the mechanism of action of safeners continue in various laboratories throughout the world and will undoubtedly lead to a greater understanding of their potential use. However, it is felt that more

research into the physical and chemical nature of the whole process of seed coating of safeners, in conjunction with other chemicals, such as fungicides and plant growth regulators, could help to solve this problem.

5. ACKNOWLEDGEMENTS

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TOLERANCE OF OATS TO DROUGHT

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1. INTRODUCTION

Supply of water is one of the most important ecological events affecting grain production. Grain crops are relatively often exposed to drought stress also in temperate and rather humid regions. Rainfall deficiency periods fluctuate from year to year, within years and between different locations. Spring and early summer droughts are an almost annually recurrent problem for the farmers in the central and eastern parts of Sweden.

It is known among breeders that some old types of oats, as the central Swedish black oats, had a better ability to endure periods of early summer drought than modern white oats (1,2,3,4). Black oats, which were on the market to about 1960, were grown in these areas long before modern plant breeding had commenced in Sweden. They were suggested for cultivation in these regions already two hundred years ago (5). At present, one objective for the breeders is to transfer the characteristics of drought resistance from the black oats to the new modern types of oats.

Drought resistance of cereal plants is, however, related to many phenological, morphological and physiological factors. Genetic variation in plant root system is probably one of the most important ones. The use of root characters in evaluation of drought resistance of breeding materials has been suggested repeatedly (6,7,8,9,10). For breeding purposes, however, root characteristics have been of limited value due to methodical difficulties. Performance of root investigations in growing crops is very laborious and time consuming. Breeders are looking for simple and fast methods which enable them to handle large plant populations.

In an earlier paper (4) such an early test has been proposed, which involved the assessment of a drought resistance index based on measurements of shoots and roots of juvenile plants.

A laboratory drought resistance index (DRI) was proposed as a criterion for drought resistance. DRI was calculated using measurements of two traits of seedlings, root length and leaf area, according to the formula:

$$\text{DRI} = (\text{root length} / \text{leaf area}) 100 / c$$

where, c is a constant referring to these traits in the reference cultivar 'Victory'. Leaf area in the formula does not represent the exact area, but a 'generalised leaf area' calculated from (i) the combined length of the first and the second leaves, and (ii) the width of the first leaf.

The next step in this investigation in oat have been to compare the results from this seedling test to yield data in controlled field trials. By using rain shelters it has been possible to expose the plant material to controlled water soil conditions, and evaluate the usefulness of the seedling test for screening of drought resistance.

2. MATERIALS AND METHODS

A total of 22 black and white oat (*Avena sativa* L.) cultivars and breeding lines of varying origin were examined in this study (Table 1). The cultivars were chosen to represent different types of oats, which have been cultivated in Sweden during the last eighty years.

TABLE 1. Representative groups of oats used for the experiments.

Oat types	No. of cultivars/lines
A. Old cultivars of black oat	4
B. Old cultivars of white oat	3
C. Modern cultivars of white oat	7
D. Breeding lines, Sang x Selma	5
E. Breeding lines, Stormogul II x Sang	3

The black oat cultivars (A) originate from old land-races, which earlier have been grown in the central parts of Sweden. The four black oat cultivars used here were all known to exhibit a higher yielding capacity during years of drought than white oats.

White oat cultivars have recently replaced the black oats in cultivation. The modern white oats are higher yielding in seasons less affected by drought than black oats. Knowledge about the drought resistance of these modern white cultivars is limited, mainly due to the fact that most of them have only been cultivated in Sweden during a relatively short period.

Two groups of breeding lines (groups D and E) were also included in this experiment. These breeding lines were all selected, among other traits, for higher DRI using the technique described by Larsson (4). In the first group (D) two modern white cultivars, 'Sang' and 'Selma', were used as parents in crosses. In the second group (E) one parent was the black cultivar 'Stormogul II' and the other the white cultivar 'Sang'.

The rain shelter experiments were performed in 1985 and 1986 at Ultuna close to the Swedish Agricultural University at Uppsala in central Sweden. The experiment was run on two adjacent places with different soil types, a heavy clay indigenous to this area, and an artificial sand profile. The sand profile was prepared two years earlier using new sand soil material. The natural clay soil was in this case replaced by the new sand profile to a depth of 1 m.

Both adjacent experimental places were equipped with rain shelters. The rain shelters were automatically regulated by a rain sensor connected to electric motors which pulled the shelters over the experimental areas when it started to rain, and returned them into parking position when it had stopped raining. The amount of water, supplied from the irrigation systems to the experimental plots, was estimated using measurements of the actual evaporation and the soil water content.

The trials were arranged according to a completely randomized design with four replications. The separate plots consisted of five rows that were 1 m long and 12 cm apart. Each row had space for 20 plants. The experiment was combined over two years, two soil types, and two irrigation levels.

During the first two months after sowing, the supply of water to the experimental plots was regulated by the drip irrigation system and by the movable rain shelters. At the beginning of the experiment, all plots were irrigated with 10 mm of water to obtain uniform initial growth for all plants (Table 2). After this initial phase only the control plots were irrigated during the first two months. At the beginning of July the rain shelters were disconnected and both the control and the water-stressed plots were irrigated to field capacity. Thereafter the crops were left to natural conditions until maturity.

TABLE 2. Irrigation levels (mm of water added) during the first six (seven) 10-days periods of the vegetation in rain shelter experiments.

Years	Soil	Irrigation	10-days periods:							Total
			1*	2	3	4	5	6	7**	
1985	sand	control	10	10	40	30	30	40	-	160
	"	stress	10	-	-	-	25	40	-	75
	clay	control	20	10	25	25	25	45	-	150
	"	stress	20	-	-	-	-	20	-	40
1986	sand	control	10	10	20	30	55	40	15	180
	"	stress	10	-	-	-	15	45	15	85
	clay	control	10	10	15	25	30	55	25	170
	"	stress	10	-	-	-	-	-	50	60

* - sowing dates : 7 May 1985, 5 May 1986

** - 1986, 4 days

The experimental plots were harvested by hand. The plant material was subsequently dried indoors at room temperature and threshed.

3. RESULTS

Means of characters measured at the seedling stage are shown for all oat genotypes in Table 3. The data indica-

ted longer roots and markedly higher drought resistance index (DRI) for the old black oat cultivars (group A). The second highest values of DRI and RL were exhibited by a group of breeding lines (E), which originated from crosses between black and white oats. Old white cultivars generally formed the shortest root system and possessed the smallest values of DRI. New breeding lines originating from Sang x Selma crosses (D) had higher drought resistance indices than modern white cultivars (C) and also somewhat longer roots.

TABLE 3. Means of seedling stage indices for the different oat types in relative values to cv. 'Victory', which is set to 100. DRI = drought resistance index, RL = root length.

Oat types	DRI	RL
A. Old cultivars of black oat	161	118
B. Old cultivars of white oat	98	97
C. Modern cultivars of white oat	106	102
D. Breeding lines, Sang x Selma	118	110
E. Breeding lines, Stormogul II x Sang	138	115

TABLE 4. Grain yield averaged over oat types, soils and irrigation regimes. Mean values over 1985 and 1986. C - irrigated control plots, S - water stressed plots.

Oat type	Grain yield, g/m ²						Total mean
	Sandy soil		Clay soil		Mean		
	C	S	C	S	C	S	
A	506d	427a	569c	398cd	537d	413b	475c
B	623c	372b	588bc	369d	605c	371c	488c
C	684ab	378b	674a	450bc	679ab	414b	547b
D	734a	397ab	682a	509a	708a	453a	581a
E	675bc	400ab	644ab	500ab	660b	450a	555b
mean	653	394	641	450	647	422	534

a-d - means within columns followed by the same letter are not significantly different by Duncan's multiple range test at P<0.05 level.

As is evident from the data (Table 4), modern white oat cultivars (C) and new breeding lines (D,E) were on an average 20% higher yielding than old black (A) and white (B) ones. Breeding lines of D and E groups, which were chosen after selection for higher seedling drought resistance indices and higher yields in trials at Svalöv, were found to produce notably higher grain yield on the water

stressed plots than the modern white cultivars (C).

Mean grain yield of all cultivars on different types of soils was reduced with about 35% when stressed. Grain yield losses were markedly higher on sandy soil (40%) than on clay soil (30%).

As indicated in Table 4, black oat cultivars were the most stable ones at the irrigation levels used. The combined tests on the two soils showed (Table 5) that black oats had the lowest field drought susceptibility index (S).

Field drought susceptibility index (S) were calculated from the grain yield data according to the equations :

$$S = (1 - YD/YP) / D \quad (17)$$

where, YD is grain yield of the genotype under drought, YP is grain yield of the genotype without drought, and D is drought intensity [= 1 - (mean YD of all genotypes)/(mean YP of all genotypes)].

TABLE 5. Averaged field drought susceptibility index (S) for grain yield of oat types examined in the rain shelter experiments. Calculated over 1985 and 1986.

Oat types	index S		
	sand	clay	total*
A	0.382	1.012	0.668
B	1.007	1.253	1.113
C	1.263	1.110	1.122
D	1.152	0.850	1.034
E	1.030	0.743	0.913

* - combined for both soils

This was particularly evident on the sandy soil. The grain yield reduction for black oats on the stressed sandy soil was only 15%, whereas in other genotypes the reduction ranged from 40% to 60%.

On the clay soil, however, the breeding lines of group D and E indicated the lowest field drought susceptibility index (S). Modern as well as old white cultivars were found to be most sensitive to the drought conditions used.

Figure 1 shows regressions of the field drought susceptibility of all oat cultivars (n=22), as an average over all soils and years, on the relative DRI and RL. RL and DRI were strongly correlated with the field drought sensitivity index (S) ($r=-0.72^{**}$ and $r=-0.91^{**}$, respectively). RL showed looser association with drought susceptibility than DRI.

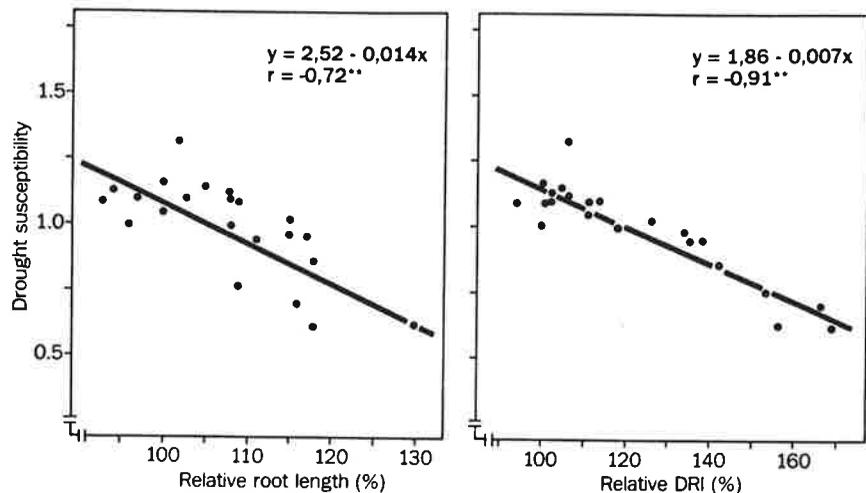


Figure 1. Relationships between the drought susceptibility of oat cultivars in the field (S), as averaged over all environments, and relative seedling stage indices (RL and DRI).

4. DISCUSSION

The results showed that if water was a restricting factor in early summer, juvenile shoot and root characteristics associated with a rapid and deep soil penetration as well as with a better seedling establishment would be of great advantage for oat plants, particularly for those growing on sandy soil. The data confirm findings made by Stucker and Frey (11), Åkerberg (12) and Salim et al. (13) in oats and those made by Hurd (8), Irvine (14), Jaradat and Duwayri (15), Górný and Patyna (16) and others in wheat and barley. They pointed out that improvements in the root system, and particularly in the seminal root system, consequently ought to result in increased water use efficiency, drought tolerance, and also in higher grain yield.

On the other hand, data from this study did not indicate any clear relationship between the seminal root length or DRI and grain yield of oat genotypes on the clay soil. On clay soils, it seems that the geometry, distribution, rooting density, and other characteristics of the root system in top soil layers seem to be of more significant advantage than a rapid and deep seminal root system.

In the present study, the old black oat cultivars exhibited the highest DRI index and the lowest drought sensitivity on the sandy soil. Both the old black and the old white cultivars showed distinctly lower yield fluctuations under different soils and watering regimes. The black oats therefore appeared to be rather suitable gene

donors for breeding programs with the aim to improve oat yield stability in central and eastern Sweden.

Numerous crosses with different black oat cultivars have been made to improve the drought resistance in modern white oat genotypes. This work was started by Persson (2) at The Swedish Seed Association in Svalöv. However, most attempts to improve the drought resistance in the white oat selections have so far failed due to lack of simple and rapid screening methods.

Results of the present study indicate that the drought resistance index (DRI) and seminal root length (RL) may be a good criterion for selection of drought resistant oats genotypes on sandy soils. A simple and relatively rapid method for laboratory estimation of DRI, as proposed by Larsson (4), appears to be useful for oat breeders.

It is interesting that oat breeding lines of group D and E, which were initially selected for higher DRI, also exhibited a higher yield potential in this study. These lines had the lowest drought sensitivity among all oats examined on the clay soil and a distinctly higher drought tolerance than modern white cultivars (C) on the sandy soil. It is evident from the data that selection was effective for higher DRI. This program was begun some years ago in populations originating from crosses between white and black oats (18). Several off-springs from these crosses are now included in the ordinary breeding material and tested for yield and other characteristics.

It may be concluded that the use of the seedling stage indices as indirect selection criteria appears to be a profitable tool for improvement of yielding capacity of oats. Because of limited information about the heritability of DRI and root length in oats, it is impossible at the moment to know which one of the two is the most usable characteristic. Since yielding potential was more strongly correlated to DRI than to RL, the use of DRI seems to be more advantageous. On the other hand, the use of RL alone has an economical implication with respect to time and costs of an examination. Further investigations on segregating populations are needed to clarify these questions.

5. CONCLUSION

Comparisons were made between drought resistance characteristics of juvenile plants and drought responses in yield of crops grown in field. By using automatic movable rain shelters in combination with a drip irrigation systems, both high and low irrigation regimes could be effected in the field experiments.

Black oat cultivars were more stable under water deficiency conditions, particularly on sandy soil. They possessed the highest drought resistance indices both in the laboratory and field. Modern white oat cultivars were found to be most drought sensitive.

Drought resistance index (DRI) and seminal root length (RL), as assessed in seedling stage, were strongly correlated with field drought susceptibility index (S). It is suggested that DRI and RL could be used as selection criteria to increase drought resistance of oats.

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TRANSLOCATION AND GRAIN DEVELOPMENT IN OATS

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Grain development in oats is dependent upon the translocation system to provide essential nutrients for the synthesis of starch, protein, lipid, cell wall and other components of the endosperm and embryo. Carbohydrate is provided mainly in the form of sucrose, and nitrogen is transported as amino acids and amides. These solutes are transported primarily through the phloem. Scientists interested in improving the productivity and quality of oats are concerned about the extent to which grain development is limited or regulated by the provision of solutes from other tissues and organs. Both the rate and duration of grain filling may be affected by translocation. Definitive experimental data are technically difficult to obtain, and less is known about oats than wheat, rice and barley. There is evidence that the synthesis of starch and of protein are not affected in the same way by the availability of transported solutes.

Remobilization of Carbohydrates and Nitrogen

Numerous experimenters have investigated the decline in nonstructural carbohydrates and nitrogen in vegetative tissues in relation to the increase in dry matter and protein in developing grain. These experiments give a crude estimate of the extent to which materials stored in the plant prior to anthesis can provide for grain filling. These estimates are approximate at best because respiratory losses are usually not measured, and in field experiments, roots are usually not sampled. To estimate the importance of remobilized assimilates for grain fill, genotypic comparisons are made or the plants are manipulated to alter the ratio of source to sink.

In a field study of six oat cultivars varying in groat protein concentration, Peterson et al. (1) found that the ratio of N to dry matter remobilized from the leaf and culm tissues into the panicles was significantly correlated with groat protein concentration. In another study by Welch and Hayward, low straw protein at maturity was associated with high grain protein in comparisons among North American and among European cultivars, indicating a relationship between remobilization of nitrogen and grain protein concentration (2). In a comparison of two high-protein Avena sterilis lines, one was efficient in remobilization of nitrogen, but the other was not (3). The investigators suggested that the former line may have useful characters that could be incorporated into adapted strains of A. sativa to increase groat protein. The high- and low-protein cultivars, Dal and Orbit, were grown in environmental chambers to compare their physiological characteristics (4). Remobilization of nitrogen was similar in both cultivars, but Orbit remobilized more carbohydrates, resulting in increased yield but lower protein concentration. These studies point to translocation of nitrogen from the vegetative tissues as an important factor in grain protein content, but indicate that translocation of both nitrogen and carbohydrates must be considered together.

In a similar manner, changes in total nonstructural carbohydrates can be measured to assess the contribution of remobilized carbohydrates from vegetative tissues to the developing grain. Peterson et al. (1) found that reduction of total nonstructural carbohydrates in vegetative tissue from anthesis to maturity was only 15-24% of the increase in panicles over the same time span. These values are similar to those obtained for other cereals (5). Recently, we have examined in detail the changes in carbohydrate fractions in the vegetative plant parts of field-grown oats during the period from anthesis to maturity, and related these to increased grain starch. The total contribution of carbohydrate was about equal for flag leaf, all lower leaves, and the culm, and together they accounted for about 18% of the increase in starch of the panicle (Table 1). In the flag leaf blade and sheath, the greatest loss of carbohydrates was from the fructan fraction, whereas loss of sucrose was at least as great as loss of fructans from the lower leaves. Loss of hexoses was predominant from the culm. These results do not indicate the predominance of any single plant part or carbohydrate fraction in providing remobilized carbohydrates for the developing grain. The soluble sugars were almost completely depleted from each plant part, whereas considerable fructan remained in the vegetative tissues at maturity.

Table 1. Changes in carbohydrate fractions (mg/plant part) between anthesis and maturity in Froker oats.

Plant part	Fraction					Total
	Fructan	Sucrose	Glucose	Fructose	Starch	
Flag leaf	-55.5	-29.3	-7.8	-1.9	ND	-94.5
Lower leaves	-43.2	-48.9	-13.9	-7.7	ND	-113.7
Culm	-10.4	-22.8	-52.9	-21.7	ND	-107.8
Peduncle	+27.3	+0.7	-17.1	-5.8	ND	+5.1
Panicle	-0.1	-21.0	-12.6	-25.8	+1670.8	+1611.2

Relationship between substrate supply and grain growth

Experiments have been conducted to assess the possible relationship between the availability of substrates (sucrose, amino acids) for endosperm synthesis, and the rate and duration of grain growth. Evidence seems to show that starch accumulation is not critically dependent upon sucrose availability, whereas protein accumulation can be controlled by amino acid availability (6). The dry weight increase of excised oat panicles cultured in nutrient solutions did not exceed that of intact controls, regardless of sucrose concentration in the media (7). Neither the level of sucrose within the endosperm nor the rate of starch synthesis of cultured, detached wheat spikes responded to media sucrose concentrations above 100 mM, and at that concentration, these parameters were similar to intact controls (8). These data indicate a limit on the rate of transport of sucrose into the developing grain (9), which could operate at the level of phloem loading, transport or unloading (10).

In contrast to starch accumulation, protein accumulation in excised oat panicles could be increased as much as 70% over that in an intact control plant by elevating the concentration of the media nitrogen source (6). Protein increases of lesser magnitude were reported for wheat (11) and barley (12). In a field experiment, oat spikelets were removed to reduce the sink size relative to the source. This resulted in a disproportionate increase of protein, as compared to dry weight in the remaining kernels (13), as has been shown for other cereals. These results further reinforce the idea that protein but not starch is regulated by the supply of assimilates.

Recently, it has been possible to sample the contents of peduncle sieve tubes of wheat plants by collecting the exudate from excised aphid stylets (14). Concentration of total solutes in the sieve tube sap increased during grain fill and was greater in phosphate deficient plants, in which rate of grain fill was reduced, than in normal ones. The sieve tube sap concentration appeared to be under developmental control, and unrelated to grain fill rates or to photosynthetic capacity. These results support the view that grain growth rate and its termination are not controlled by supply of assimilates. No similar studies have been conducted with oats.

Anatomy of Transporting Tissues

The minor veins of the leaf blades contain sieve tubes and companion cells that are involved in loading of assimilates from the leaf mesophyll. These vascular bundles are continuous with those of the leaf sheath. At the base of the leaf sheath, they join with those of the culm, which are formed into two concentric circles, the inner circle containing the larger bundles. At each node in the panicle, some bundles are directed into the branches, leaving fewer within the main panicle axis. The average number of vascular bundles per spikelet ranged from eight for the terminal spikelet to less than two for spikelets originating from the lowest panicle node (15). The authors speculated that the prevalence of blasting of spikelets on the lower panicle nodes may be a consequence of being served by fewer vascular bundles, thus suffering from a restricted supply of assimilates. Within each floret, the caryopsis contains a single vascular bundle which extends its entire length within the pericarp on the dorsal (crease) side. In cross section, its position is peripheral to the chalaza (pigment strand) and nucellar projection. It is evident that solutes unloaded from the sieve tubes of the phloem must cross the chalaza and nucellar projection to enter the endosperm cavity and become available to the developing endosperm.

Transport Mechanisms

The movement of solutes from a source, such as a leaf, to a sink, such as a developing grain, through the phloem is believed to occur via a mass flow mechanism, as originally stated by Münch (16). This hypothesis states that sugars are actively loaded from the mesophyll into the sieve tubes of the minor veins of the leaves, resulting in their accumulation at high concentration (17). The production of high osmotic pressure in these sieve elements leads to an influx of water, generating the motive force for phloem translocation. It has been postulated, based upon evidence from the rice caryopsis, that assimilates unloaded from the phloem in the vascular bundle of the pericarp, are transported symplastically through the chalaza and nucellar projection through numerous plasmodesmata (18). There are no plasmodesmata connecting the nucellus with the aleurone, indicating that the assimilates must cross the plasmalemma into the apoplast at that point.

Minerals from the roots are translocated primarily in the xylem via the transpiration stream. However, a special tracheary element was shown to block the continuity of the xylem stream between the rachilla and the pericarp of wheat (19). A similar structure is presumed for other cereals. This means that minerals must be transferred from the xylem to the phloem for movement into the developing grain.

Regulation of Phloem Transport

The control of the movement of assimilates from leaf mesophyll cells to endosperm cells could be exerted at several points along this pathway (20):

- 1) Availability of sucrose and its active uptake into the sieve tubes in the leaf minor veins.
- 2) Structural features of the path determining resistance to flow and leakage from the sieve tubes.
- 3) Phloem unloading in the caryopsis and transport through the adjacent tissues into the endosperm.
- 4) Conversion of transport molecules into polymers in the endosperm.

Phloem loading. Evidence from a number of observations indicates that sucrose is released from the mesophyll cells into the free space and then actively loaded into the sieve tubes. The loading process involves a plasma membrane ATPase which provides energy to pump the sucrose into the sieve tubes against a concentration gradient. The sucrose concentration in the free space could limit phloem loading, as could the capacity of the sucrose carrier. Loading of amino acids may also be energy dependent, but may involve different carriers. In oats, the mass transfer rate of sucrose was about 50 times greater than that of several amino acids, indicating a much higher affinity of the carriers for sucrose (21). Does the availability of sucrose limit the amount transported into the grain? Recent experiments indicate that sucrose concentration of the vegetative tissues changes during the grain filling period, and becomes quite low as maturation nears (Fig. 1). Although this suggests that the availability of sucrose for phloem loading may be limiting late in grain filling, direct measurements of sieve tube sap osmolality in wheat peduncles showed an increasing trend until the cessation of grain filling (14). These measurements have not been done with oats. If oats are similar, it appears that the availability of sucrose at the source may not be an important limiting factor.

Phloem capacity. The possibility that the capacity of the vascular system to transport assimilates might limit yield of oats was considered in a series of experiments (15, 22). Parameters of vascular bundles in the peduncle, such as bundle number and area and sieve tube number and area, were significantly correlated with kernels/panicle and yield/panicle among several oat cultivars grown in Wisconsin and Indiana, indicating a strong relationship between vascular capacity and grain filling (22). However, kernel weight did not correlate with any vascular measurements. These results indicated that vascular capacity may limit kernel establishment but does not affect filling of established kernels. A similar conclusion was reached for cultured wheat spikes (23).

Phloem unloading. Solutes unloaded from the phloem of the vascular bundle in the pericarp of the kernel are thought to move via plasmodesmata through the chalaza and into the nucellar projection which extends into the endosperm cavity. Final movement of solutes into the endosperm involves passage from the symplast into the apoplast. This pathway has been deduced from anatomical studies, and was verified by the movement of fluorescein into isolated

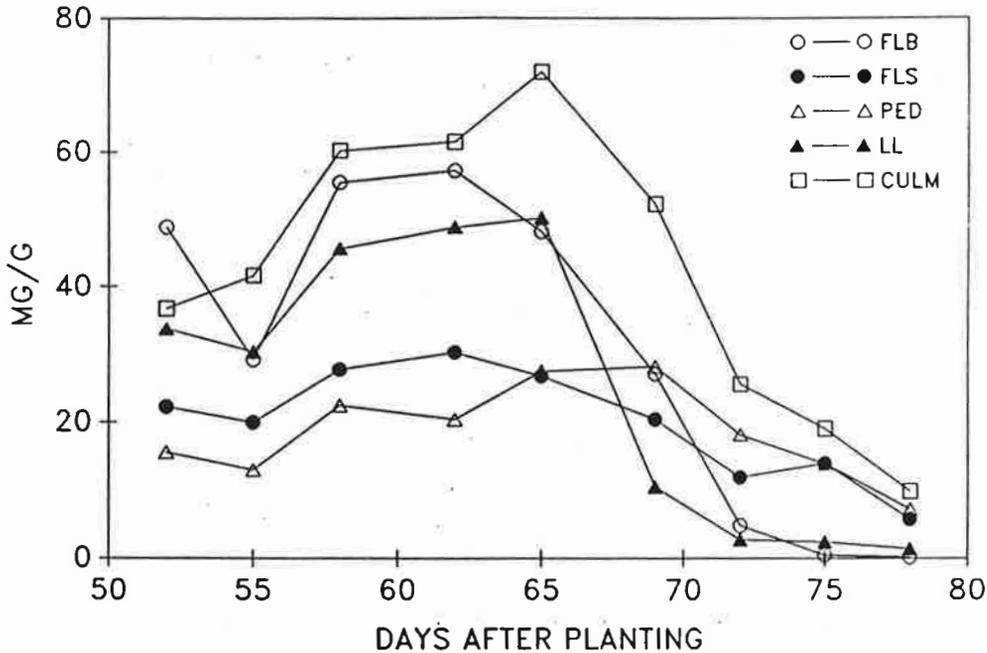


Fig. 1. Changes in sucrose concentration of Froker oat plant parts from heading to maturity. FLB, flag leaf blade; FLS, flag leaf sheath; PED, peduncle; LL, lower leaves, CULM, culm.

caryopses of wheat and barley (24). The demonstration of a solute gradient across the grain crease tissues between the sieve tubes and the endosperm cavity led to the postulate that important control points for grain filling exist within these tissues (25).

Accumulation and conversion of sugars in the endosperm. Sugars and other solutes are available to the endosperm cells from the endosperm cavity. Their concentration must reflect a balance between import from the sieve tubes and uptake by the endosperm cells. A high concentration of osmotically active solutes in the sink apoplast is a characteristic of strong sinks (10). Experiments with isolated wheat endosperm show that uptake and incorporation of sucrose responds positively to external sucrose concentration up to 150-200 mM (26). These data have been interpreted to indicate substrate limitation to grain filling in vivo, as endosperm cavity sucrose concentration is much lower. However, Fisher and Gifford (27), using indirect methods of measuring in vivo mass transfer rates into the grain, failed to demonstrate any association between sucrose concentration in the endosperm cavity and grain filling rate. While it is conceivable that one or more of the steps in conversion of sucrose to starch in the endosperm is rate limiting, there is very little evidence to support this theory under non-stressed conditions.

Conclusions

While much remains to be learned about the regulation of transport and its relation with grain development in oats, we can make some tentative conclusions. It seems most likely that factors regulating assimilate import

into developing grain reside in the grain itself, and not in the source tissues under normal environmental conditions. This regulation must involve some aspect of phloem unloading, transport to the endosperm, or utilization within the endosperm cells. The case for protein is very different, and evidence indicates that more amino acids can be utilized for protein synthesis in the endosperm than are normally provided.

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GROWTH RATE OF OATS

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INTRODUCTION

Traditionally, the components of grain yield of cereals were considered to be number of heads (panicles or spikes) per unit of land area, number of seeds per head, and weight per seed (Grafius, 1956). These traits, however, represent components of only the "sink" of the cereal plant in which assimilates are stored. To account for contributions of both "source" and sink to grain yield of cereals, Takeda and Frey (1976) suggested that the equation for grain yield should be

$$\text{Grain yield} = \text{Growth rate} \times \text{Growth duration} \times \text{Harvest Index}$$

Takeda and Frey (1976), indeed, showed that more than 90% of grain yield variation in interspecific matings was accounted for by growth rate and harvest index, and the relative contribution of growth rate was 1.27 times that of harvest index. Subsequent research by Frey and his colleagues (Takeda et al., 1979a, 1980; Frey, 1984; Takeda and Frey, 1985; Gupta et al., 1987), who applied this conceptual formula to oat (*Avena sativa* L.) breeding, showed that growth rate was the only component in this equation that could contribute substantially to improving grain yield of cultivars for midwestern USA. Growth duration of oats was limited to 100-110 days because of late-summer heat and diseases, and a harvest index of 45-50%, which is typical of current cultivars, is optimum for high grain yield. Therefore, the rest of this paper will be devoted to a summary of growth rate research.

MEASURING GROWTH RATE OF CEREALS

The typical method for measuring growth rate of cereals is to make periodic harvests (usually weekly) of the vegetation from a unit of land area (usually 0.1-1.0 m² with a standard number of plants), measure the dry weights of these samples, and compute the growth rate as the linear increase in dry weight over the growth cycle. For harvests made after anthesis, it is common to separate the plant material into vegetation and seed, which are weighed separately. Mean dry weight accumulation for five oat cultivars measured via this method by Frey et al. (1967) is shown in Figure 1.

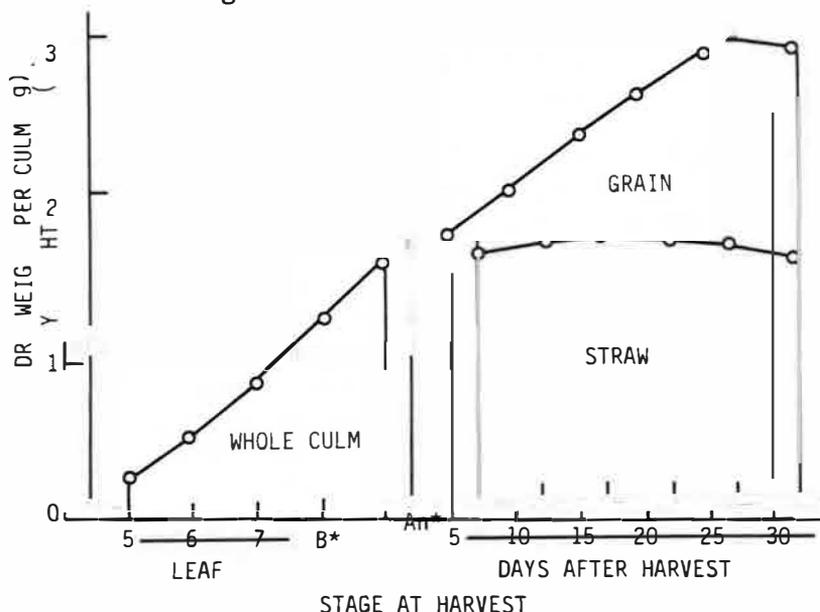


Figure 1. Mean dry weight of vegetative and grain portions of oat culms in five varieties at several stages of plant development (B = boot stage and An = anthesis).

Note that between harvests 2 and 10, which represents the period between the 5th leaf stage and 25 days post anthesis, that dry weight accumulation was linear.

Measuring growth rate of oats via the weekly sampling method leads to accurate estimates, but it is too laborious and expensive to use in a breeding program in which hundreds and even thousands of entries must be evaluated. Further, Takeda and Frey (1976) reasoned that a growth rate, to be used in the grain-yield equation, should be estimated independently from the grain-fill interval. Perusal of Figure 1 showed that dry weight of the oat vegetation (i.e., straw) did not change materially after anthesis, so Takeda and Frey (1976) reasoned that straw weight at harvest divided by days to anthesis would provide an estimate of growth rate that (a) required no extra plots, (b) was inexpensive to measure, and (c) was measured independently of the grain-fill interval. This is the method that has been used extensively in growth rate research at Iowa State University.

Wych et al. (1982) have shown that genotypes of oats and experimental environments may cause straw dry weights to increase or decrease differentially between anthesis and maturity. Therefore, they recommended that growth rate would be more accurately estimated if computed from dry weight at anthesis divided by days to anthesis. Gupta et al. (1986, 1987) showed that growth rates measured at anthesis (GRA) and at maturity (GRM) were significantly and positively correlated in intra- ($r = 0.35^{**}$) and inter-specific ($r = 0.42^{**}$) matings of oats. Gupta et al. (1987) found that GRM and GRA were genotypically correlated with $r = 0.64$.

Bramel-Cox et al. (1984) developed a rapid method for measuring growth rate of pearl millet (Pennisetum americanum L.). They measured dry weight per m^2 at 14-day intervals from 21 days after emergence to physiological maturity on 16 diverse genotypes. Because pearl millet tillers nonsynchronously, growth rate estimated by dividing straw weight by days to anthesis + 10 was more accurate than that estimated by dividing straw weight by days to anthesis. The correlations between growth rates measured via linear regressions over all harvests and growth rates measured via straw yield at maturity divided by days to anthesis + 10 were 0.91^{**} in a dry season and 0.61^{**} in a wet season.

GENETICS OF GROWTH RATE Sources of Genetic Variation

Takeda et al. (1979a) studied 23 matings among A. sativa genotypes--nine were adapted x exotic strains, eight were adapted x semi-exotic strains, and six were adapted x adapted strains (Table 1). The proportion of plus transgressive segregates (those that exceeded the high-parent by one LSD) for growth rate over all 23 matings was 3.4%, a value well within the 5% expected to be transgressive by chance. Certain matings, however, produced sizable percentages of transgressive segregates. Of the seven matings with more than 5% plus transgressive segregates, five had Tippecanoe cultivar as one parent. These five matings had a mean of 9.2% plus transgressive segregates, whereas all other matings had a mean of 1.9%. These results suggest that Tippecanoe is the only A. sativa genotype among the 19 used that has substantially unique growth rate alleles.

In marked contrast to the results from matings among A. sativa genotypes, interspecific matings of A. sativa x A. sterilis produced very large proportions of plus transgressive segregates for growth rate. Takeda and Frey (1977) obtained an average of 22% plus transgressive segregates from eight interspecific matings. Matings involving the A. sativa lines CI 7463 and CI 8044 averaged 29 and 16% plus transgressive segregates, respectively. Cox and Frey (1984a) found that minus transgressive segregates for growth rate were nearly

Table 1. Matings among A. sativa genotypes, their parentage, and percentages of plus transgressive segregates (one LSD above high parent) for growth rate (adapted from Takeda et al., 1979a).

Mating number	Parentage	Percentage plus transgressive segregates
<u>Adapted x Exotic</u>		
1	CI 7970 x Tedere	2.1
2	Goodfield x Tedere	0.0
3	Tippecanoe x Tedere	14.6
4	CI 7970 x Pusa Hybrid	2.1
5	Goodfield x Pusa Hybrid	2.1
6	Tippecanoe x Pusa Hybrid	6.3
7	CI 7970 x SA 15	0.0
8	Goodfield x SA 15	0.0
9	Tippecanoe x SA 15	0.0
<u>Adapted x Semi-exotic</u>		
10	CI 7970 x Abegweit	0.0
11	Goodfield x Abegweit	6.3
12	Tippecanoe x Abegweit	10.4
13	CI 7970 x Sturdy	8.3
14	CI 7970 x Col-C1	0.0
15	Goodfield x Col-C1	0.0
16	Tippecanoe x Col-C1	6.3
17	CI 7970 x LMHJ	0.0
<u>Adapted x Adapted</u>		
18	Goodfield x Tippecanoe	8.3
19	Bonham x Clarion	0.0
20	Clintland x Newton	4.2
21	Clintland 60 x Marion	2.1
22	Burnett x Cherokee	4.2
23	Clintland 60 x Beedee	2.1
	Mean	3.4

nonexistent in either inter- or intra-specific matings, whereas plus transgressive segregates were frequent (Table 2). On average, there were nearly twice as many plus transgressive segregates from inter- as from intra-specific matings (i.e., 9 vs. 5%).

It is evident that only occasional matings among A. sativa genotypes will give segregates with significantly positive transgressive growth rates, whereas such segregates are rather common from A. sativa x A. sterilis matings.

Table 2. Percentages of segregates with growth rate means one $LSD_{0.05}$ below the low parent mean or one $LSD_{0.05}$ above the high parent mean in inter- and intra-specific matings pooled by A. sativa parents (adapted from Cox and Frey, 1984a).

Parents	Transgressive segregates	
	Minus	Plus
<u>Inter-specific</u>		
Wright	0	12
Nodaway 70	0	4
Ogle	0	2
Benson	0	3
CI 9170	0	13
Tippecanoe	0	21
Mean	0	9
<u>Intra-specific</u>		
Nodaway 70	1	1
Ogle	2	3
Benson	0	5
CI 9170	0	7
Tippecanoe	0	7
Mean	1	5

Inheritance

In 16 of 23 matings among A. sativa genotypes, Takeda et al. (1979a) found the gene action operative for growth rate was additive, whereas in the other seven, nonadditive (dominant and epistatic) gene action was operative for this trait. Tippecanoe had a set of alleles for growth rate that "nicked" with alleles from other genotypes to give marked positive heterosis. Helsing and Frey (1983) studied growth rate inheritance in 12 matings between A. sativa cultivars and A. sativa-like lines with superior growth rate due to introgression of A. sterilis alleles. Additive gene action accounted for the growth rate inheritance in seven matings, but in five nonadditive gene action was operative. A series of A. sativa x A. sterilis matings studied by Takeda and Frey (1977) showed extreme positive heterosis for growth rate, with a mean of 22% of segregates being significantly higher than the midparent value, so they concluded that gene action for this trait in interspecific matings was nonadditive. Cox and Frey (1984b) made a Design II set of matings among six A. sativa cultivars as females and ten A. sterilis accessions as males and measured growth rate of F_2 -derived lines from the 60 matings. The percentage of sums of squares for matings accounted for by A. sterilis (males) was nearly five times greater than that for A. sativa (females), which reflects that A. sterilis accessions had a greater range of growth rates than did the A. sativa cultivars

Table 3. Percentages of mating mean squares accounted for by males (A. sterilis, GCA), females (A. sativa, GCA), and males x females (SCA) for growth rate (adapted from Cox and Frey, 1984b).

Source	Percentage of mean square
Males	60.6
Females	12.7
Males x females	26.7

Both general combining ability (GCA) and the specific combining ability (SCA) were significant, but collectively GCA accounted for three-fourths of the variation among matings. Ogle, among the A. sativa cultivars, and PI 411560, among the A. sterilis accessions, had the greatest positive GCA effects, and the mating with the highest positive SCA effect was CI 9170 x PI 324748.

In all studies, the inheritance of growth rate of oats was polygenic, and gene action was both additive and nonadditive. The number of effective factor pairs by which parents in intraspecific oat matings differed for growth rate ranged from 5 to 21, with a mean of 7 according to Takeda et al. (1979a). In interspecific matings, the number ranged from 3 to 9, with a mean of 6 (Takeda et al., 1979a).

Heritability of growth rate on a plot basis for matings among A. sativa genotypes reported by Takeda et al. (1979a) was 0.22 when averaged over 23 matings, whereas a comparable mean for interspecific matings reported by Takeda and Frey (1977) was 0.40 when averaged over 16 matings. Helsel and Frey (1983) reported that heritability of growth rate on an entry-mean basis was 0.54 when averaged over 12 matings.

ASSOCIATION OF GROWTH RATE WITH OTHER TRAITS

Because growth rate, growth duration, and harvest index are the three components of grain yield, associations among these traits and of them with grain yield are of special interest. Phenotypic correlations between growth rate and growth duration tend to zero, but genotypic correlations are positive, ranging from 0.31 to 0.56 (Table 4). Phenotypic correlations between growth rate and harvest index ranged from -0.03 to -0.38, with two being significant, whereas genotypic correlations ranged from 0.15 to -0.44. Thus, growth rate has a moderate positive genotypic association with growth duration and a small negative association with harvest index. The moderate genotypic correlation between growth rate and growth duration is modified by environment so that no phenotypic association occurs between these two traits. Contrariwise, the genotypic and phenotypic associations between growth rate and harvest index are similar, which indicates that environment has little or no effect on the association between these two traits.

The time in the growth cycle when growth rate is measured (i.e., at anthesis or at maturity) does not change the direction of association between

Table 4. Phenotypic and genotypic (in parentheses) correlations among growth rate (GR), growth duration (GD), and harvest index (HI) measured on segregates from interspecific (Inter) and intraspecific (Intra) matings of oats.

Authors	Genetic materials	Traits correlated	
		GR-GD	GR-HI
Takeda and Frey (1977)	Inter	-0.10	-0.03
Takeda et al. (1979a)	Intra	(0.31)	(0.15)
Takeda et al. (1980)	Intra	(0.56)	(-0.44)
Helsel and Frey (1981)	Intra	0.06 (0.35)	-0.38** (-0.02)
Cox and Frey (1984a)	Inter	-0.12	-0.04
	Intra	0.15*	-0.34**

growth rate and growth duration and harvest index, but it has a marked effect on the magnitude of association (Table 5).

Table 5. Phenotypic correlations of growth rate measured at anthesis (GRA) and at maturity (GRM) with growth duration (GD) and harvest index (HI) among segregates from interspecific and intraspecific matings of oats (adapted from Gupta et al., 1986).

Type of mating	Traits correlated			
	GRA with		GRM with	
	HD	HI	HD	HI
Interspecific	0.70**	-0.06	0.34**	-0.29**
Intraspecific	0.69**	-0.36*	0.25	-0.69**

All associations between growth rate and growth duration are positive, but when growth rate is measured at anthesis, the two traits are highly correlated, and when measured at maturity, they are only moderately correlated. In contrast, all associations between growth rate and harvest index are negative, and they are strengthened by delaying the measurement of growth rate from anthesis to maturity.

In general, the correlations of growth rate measured at maturity with growth duration and harvest index range from zero to moderate; thus, it should be possible for an oat breeder to manipulate growth rate upward while holding the other two components nearly constant, especially in A. sativa x A. sterilis matings. Growth rate when measured at anthesis was quite strongly and positively correlated with growth duration in both inter- and intra-specific matings.

GROWTH RATE AND GRAIN YIELD Correlations

Of course, the ultimate purpose for studying growth rate of oats is to

determine its value for increasing grain yield. Early on, Takeda and Frey (1976) and Takeda et al. (1979a) showed that growth rate and harvest index accounted for 92 to 97% of the grain yield variation among segregates of interspecific matings and 83 to 94% in intraspecific matings.

The phenotypic correlation between grain yield and growth rate over many studies ranged from 0.45 to 0.68, and all were highly significant (Table 6).

Table 6. Phenotypic and genotypic correlations of growth rate with grain yield of oats.

Authors	Material	Correlations	
		Phenotypic	Genotypic
Takeda and Frey (1976)	Interspecific	0.68**	0.76
Takeda and Frey (1977)	Interspecific	0.67**	--
Takeda et al. (1979a)	Intraspecific	--	0.73
Takeda et al. (1979b)	Varieties	--	0.82
Takeda et al. (1980)	Intraspecific	--	0.67
Helsel and Frey (1981)	Intraspecific	0.59**	0.73
Cox and Frey (1984a)	Interspecific	0.60**	--
	Intraspecific	0.60**	--
Gupta et al. (1986)	Interspecific	0.45**	--

Genotypic correlations ranged from 0.67 to 0.82. The magnitude and positive direction of these correlations show that sizable increases in grain yield of oats could be expected from selecting for growth rate.

Gupta et al. (1986) found that the correlations of grain yield with growth rate measured at anthesis and at maturity were 0.37** and 0.45**, respectively. These correlations do not differ.

Yield Increases from Growth Rate Selection

Changes in relative grain yield of oats expected from selecting for growth rate and harvest index singly or simultaneously are presented in Table 7.

Table 7. Relative grain yield predicted from selecting for changes in harvest index and growth rate singly or simultaneously in inter- and intra-specific matings of oats (adapted from Takeda and Frey, 1976 and Takeda et al., 1979a).

Mating type	Harvest index (%)	Growth rate g/da/plot			
		0.7	0.8	0.9	1.0
Inter	40	100	114	128	142
	45	118	132	147	161
Intra	40	100	110	120	130
	45	118	128	139	149

Note that, even with a harvest index of 45%, increases of 43 and 31% in grain yield can be expected from increasing growth rate from 0.7 to 1.0 g/da/plot in inter- and intra-specific matings, respectively.

Johnson et al. (1983) selected for four criteria in a population of F_2 -derived lines of oats and then measured the mean grain yield of selected samples of lines. The criteria were harvest index, growth rate, grain yield, and harvest index + growth rate and the selection intensity for each was 10%. Selecting for growth rate and for grain yield per se resulted in 8 and 7% gains which shows that growth rate was a major trait contributing to grain yield (Table 8).

Table 8. Means for grain yield (q/ha) and percentage gains for samples of oat lines selected for high trait values according to four criteria (adapted from Johnson et al., 1983).

Selection criterion	Grain yield (q/ha)	Gain (%)
Harvest index	49.8	4
Growth rate	51.7	8
Grain yield	51.2	7
Harvest index + growth rate	50.8	6
Random	47.9	-

An index of growth rate + harvest index results in only a 6% gain. Takeda and Frey (1985) found that independent culling at 25% selection intensity for harvest index followed by an 8% intensity for growth rate gave the same gain in grain yield as did a 2% selection intensity for grain yield per se, and the two groups of lines were very similar for all agronomic traits. Gupta and Frey (1987), by selecting for increased growth in the F_3 and F_4 generations of interspecific oat matings, increased this trait 7 and 6%, respectively. The correlated changes in grain yield were a 24% increase from selection in the F_3 and a 3% decrease in F_4 .

A different result was reported by Payne et al. (1986) who found an 11% increase in yield of oats accomplished via recurrent selection without any change in vegetative growth rate.

SUMMARY

Growth rate, growth duration, and harvest index are the components of grain yield of oats. For midwestern USA, the only component that can be manipulated to increase oat grain yield is growth rate. Of the *A. sativa* genotypes tested to date, only Tippecanoe cultivar possesses high growth-rate alleles that are unique. However, a large proportion of *A. sativa* x *A. sterilis* matings produce plus transgressive segregates for growth rate. Growth rate in both intra- and inter-specific matings is inherited polygenically with parents differing by 3 to 21 effective factor pairs for this trait. Gene action for growth rate is both additive and nonadditive.

Genotypic association between growth rate and growth duration is moderately positive, whereas that between growth rate and harvest index is low and

negative. Growth rates computed from dry weights at anthesis and maturity are positively and significantly correlated. Stage of plant growth when growth rate is computed has a modest effect on the associations of growth rate with growth duration and harvest index.

Phenotypic and genotypic correlations of grain yield and growth rate of oats are 0.60 and 0.75, respectively. Simulated and actual selection experiments have shown that grain yield can be increased by selecting for growth rate.

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SHOOT:ROOT INTERRELATIONS IN OATS

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Efficient breeding for increased yield of a crop plant implies access to genetic variation as well as knowledge how to construct the desirable ideotype for the given niche. The Swedish oat breeding programme, running now for one hundred years, illustrates this statement very well (Fig. 1).

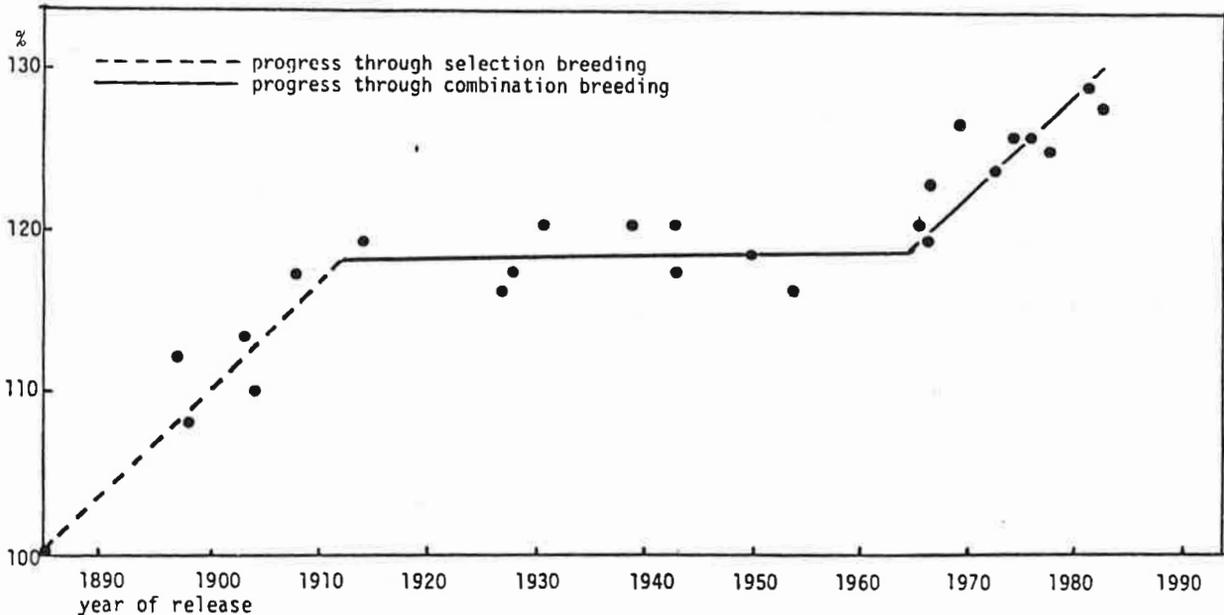


Fig. 1. Progress in Swedish breeding of spring oats. Relative grain yield for all released cultivars of the Probstei type. Unbred landrace Älvsborg = 100 (as to calculation cf. MAC KEY 1979a).

Individual plant selection from heterogenous landraces resulted in monocultures allowing generatively more productive types to compete on equal premises. Recombination breeding hardly offered any substantial improvement over the first forty years. This was much because of too restricted a genetic gene pool but also because of unawareness of modern ideotype concepts. First when the principle behind harvest index was fully understood, progress was able to continue.

Unconsciously, oat breeders of the past tried the right way. Lodging resistance was of major importance, straw shortening is here the easiest way to proceed, generally leading to improved harvest index. Attempts to develop reliable cultivars failed, however, due to loss in drought tolerance. Improvements arrived first when consciousness gave persistency enough.

This case story illustrates well the importance to understand the correlative constraints in plant growth and stand development. A considerable interdependence between shoot and root growth was pointed out by MAC KEY already in 1966, but it is not until more recently that KLEPPER et al. (1984) in detail described the synchronized development between leaf, tiller and main root development of small grains.

It is an old knowledge that oat cultivars may vary not only as to shoot but also as to root pattern (cf. MAC KEY 1959). To what extent the two parts show a correlated growth was, however, less well understood. Studying six oat lines in a water tank, CARRIGAN and FREY (1980) were able to demonstrate a high correlation between shoot and root weight. Using a more elaborate hydroponic system (MAC KEY 1973, 1980, 1986), a representative world collection (n = 93) covering different oat ecotypes and *Avena* species gave i.a. the following correlations:

number of tillers and crown roots.....	r = 0.43***
number of leaves and crown roots.....	r = 0.53***
plant height and number of crown roots.....	r = 0.42***
plant height and root depth.....	r = 0.50***
root dry weight and root depth.....	r = 0.45***
dry weight of shoot and root prior to seed set...	r = 0.87***

The interrelations observed support the observed difficulties to combine a reliable root system with a short-strawed, vegetatively restricted, more generatively emphasized ideotype. A direct search for correlation breakers must be highly justified. Ordinary yield trials will easily be too tedious and vague through mere watching phenotypic stability.

Fig. 2 shows convincingly that a systematic search for the combination between short straw and deep enough roots ought to be suc-

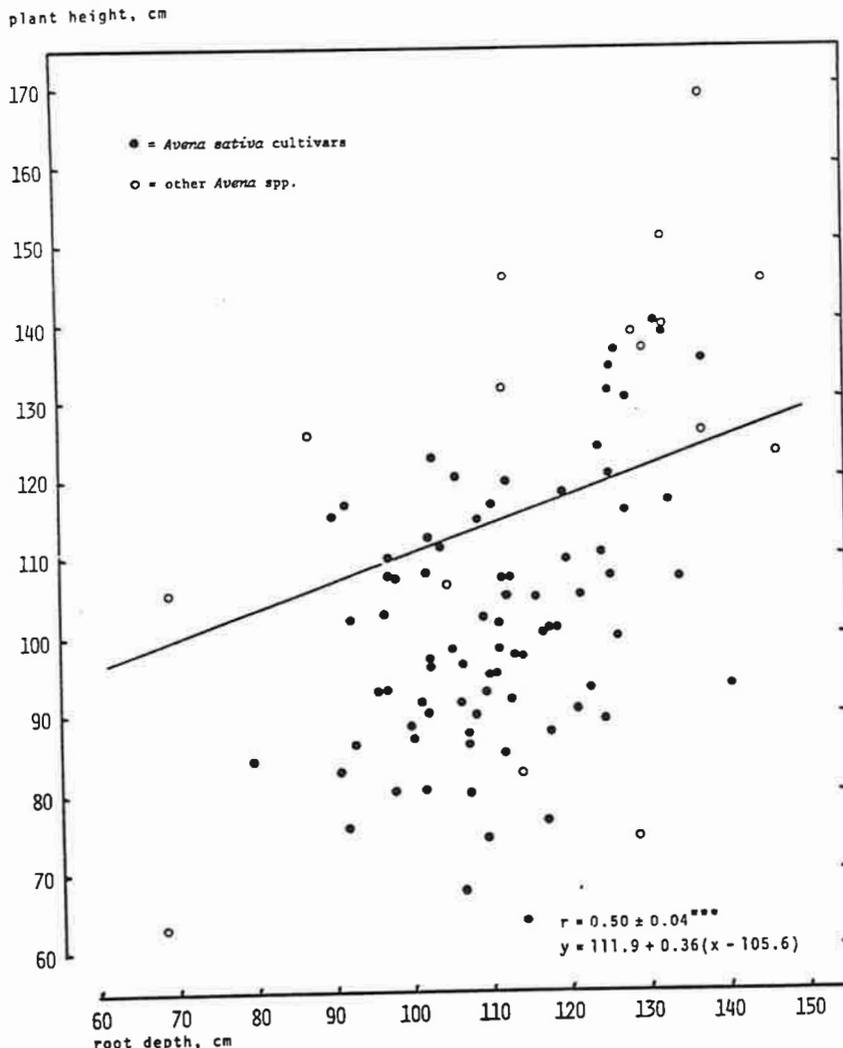


Fig. 2. Relation between plant height and root depth in a world collection of spring oats (n=93). 8 replications per accession.

cessful. Especially the gene pool outside *Avena sativa* offers potentials. It is apparently much more difficult to maintain root volume and weight unchanged, if a surplus of straw and leaf production is to be shifted towards more grain (Fig. 3). Since there also

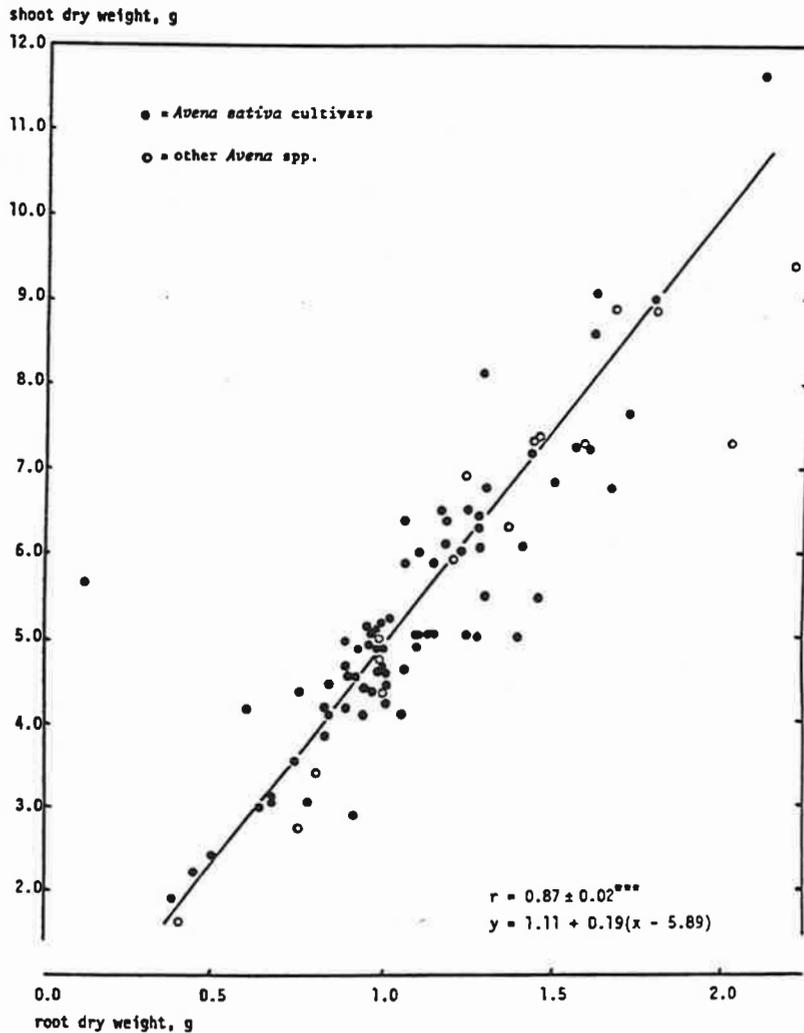


Fig. 3. Relation between dry weight of shoot and root in a world collection of spring oats ($n = 93$). 8 replications per accession.

exists a correlation between root dry weight and root depth, a general trend seems to be that modern, short-strawed oat cultivars have a larger part of their root mass more concentrated to the top soil (Table 1). Their advantage thus highly depends on the more intensive management of today.

The root profile is also dependent on the actual number of roots and their type. Seminal roots go deeper, are thinner and more branched than crown roots, i.e. they are more efficient per unit of dry

Table 1. Change in root profile with decreasing plant height within Swedish spring oats.

Swedish oat cultivar	Plant height cm	Root depth cm	Percentage of root mass at			
			0-20 cm depth	20-40 cm depth	40-60 cm depth	>60 cm depth
Roslags.....	139.9	131.7	19	15	13	53
Sörba.....	110.8	124.5	30	25	16	29
Selma.....	101.1	117.9	38	29	16	17
Hedvig.....	83.4	90.6	42	33	19	6

weight. Contrary to crown roots, they are independent of tillering as to number but probably also in oats related to seed size or more correctly endosperm size. Such a correlation is found in wheat ($r = 0.71^{***}$; MAC KEY 1979b) as well as in barley ($r = 0.22^{**}$; APEL et al. 1981).

The crown roots are, however, directly involved in the synchronized developmental pattern of the plant. Oats show a higher variation in number of crown roots per tiller than observed in wheat ($r = 0.67^{***}$) or barley ($r = 0.67^{***}$). Under the favourable conditions for root growth in the used hydroponic system, the Swedish oat cv. Stormogul II produced as an average 6.3 crown roots per tiller compared to the Australian cv. West with 2.7 and the Dutch cv. Gambo with 2.5. From the correlations given above, short-strawed types with a reduced number of leaves per stem should be those with a lower number of crown roots per tiller.

The efficiency of the crown root system is of course not only dependent on number and depth, two features by themselves negatively correlated according to the principle of competing sinks (MAC KEY 1986). For the same reason, number is negatively correlated with root diameter. Seminal roots go almost vertical, but crown roots can orient differently. Early developed crown roots tend to resemble seminal roots, while very young crown roots may go rather horizontally and unbranched, thus functioning more as prop roots. According to BALYK (1982), small grains including oats may have different, general patterns of crown root orientation. The crown roots may tend to go first more vertical and then spreading, or first growing at an angle and then more vertical or first more horizontal and at a depth of 5-8 cm starting to go more vertical. The different patterns will influence lodging by bending or by uprooting differently. No observation is, however, available whether there exists a correlation with the way tillers grow. They may immediately go straight upwards or more slowly curving upwards thus spreading the plant base. The latter tendency is undesirable, since ability to endure a thick stand is in oats an important yield component. It should also be recognized that the length of the root crown have relevance to root anchorage (cf. MAC KEY 1959).

In contrast at least to examined wheats and barleys, some oat lines show a tendency not entirely to cease root growth at beginning of grain filling. It is a feature already observed by CARRIGAN and

Table 2. Shoot:root development in a defoliation experiment with spring oats (means of cvs Sun II and Leanda, each 8 replications).

T r a i t	Untreated control, abs. values	Defoliation except flag leaves started			Total defoliation started		
		4 weeks after sowing,	6 weeks after sowing,	8 weeks after sowing,	4 weeks after sowing,	6 weeks after sowing,	8 weeks after sowing,
		relative values (%)					
No. of tillers.....	5.9	89	89	97	64	70	89
No. of crown roots.....	43.1	52	61	64	28	23	40
Plant height, cm.....	119.2	63	68	72	44	45	68
Root depth, cm.....	134.6	88	91	95	60	75	95
Shoot dry weight, g.....	7.0	19	26	33	5	7	18
Root dry weight, g.....	1.27	19	27	35	6	8	22
% roots in zone, 0-20 cm..	37	39	37	39	50	41	33
" " " " , 20-40 " ..	17	22	20	23	27	23	25
" " " " , 40-60 " ..	14	14	15	15	15	16	16
" " " " , 60- " ..	30	25	28	23	8	20	26

FREY (1980), occurs more in wild but also in cultivated oats and appears to be associated with an initially slow growth as more characteristic of true winter oats.

The firm interrelation between shoot and root as indicated above can also be demonstrated by different mutilation experiments. Table 2 reports on a defoliation experiment. The reduced assimilation is equally affecting shoot and root dry weight. The balance is obviously maintained but with a somewhat different pattern. Since roots are developed a certain time lapse after the corresponding tiller or leaf in the synchronized growth pattern (in wheat approx. three phyllochrons), the number of crown roots becomes more reduced than number of tillers. Since number and size tend to have an inverse relationship, each tiller will have more reduced growth potential than each main root. As a consequence shoot height is more reduced than root depth. Defoliation thus confirms how the interrelation between shoot and root operates and simulates also influences caused by other above-ground damages such as by hail, leaf diseases and attacks of leaf-eating insects and larger animals.

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RELATIONSHIPS OF GROAT PERCENTAGE WITH KERNEL WEIGHT, GRAIN WEIGHT PER PANICLE, AND BIOMASS PER TILLER IN SPRING OATS

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Cultivar development requires the manipulation of many traits to produce superior genotypes. In addition to grain yield, reaction to diseases, protein concentration, and straw strength, selection for physical grain quality traits such as high test weight and high groat percentage is practiced in most oat (*Avena sativa* L.) improvement programs. Many of these traits are correlated, and knowledge of these interrelationships is important in order to make decisions about parental choices, test environments, and test methods.

In the Wisconsin oat breeding program it has been noted repeatedly that vigorous, productive breeding lines often produce hully kernels, i.e. kernels with below-average groat percentage. This observation led to an investigation of the relationships of groat percentage with kernel weight, grain weight per tiller, and biomass per tiller and of the inheritance of these traits.

The environment has a major effect on groat percentage(5,6,16), primarily on the development of the groat. Groat percentage, however, was less variable over years than grain yield(7).

Relationships between groat percentage and other traits have varied from study to study. Yield and groat percentage were negatively correlated among 11 cultivars while little or no relationship was found in segregating populations(13); however, in another study groat percentage was positively correlated with both yield and test weight(2). A significant positive correlation was found between yield and groat percentage during a high rust year, but these traits were not correlated during a normal year(1). A negative correlation was reported between groat percentage and straw yield(8). Selection for high groat percentage in three populations resulted in positive correlated response for yield in one population, no change in one population, and a decrease in the third population(11). In this same study, selection for high groat percentage resulted in increased kernel weight in two populations and no change in the third. Negative correlations between groat percentage and kernel weight have been observed(8,9,13); however, other studies have reported no association(12), and even positive associations (2,4).

Inheritance of groat percentage has been studied in only a few instances. In a pair of studies(14,15) the means and frequency distributions for three crosses indicated that multiple factors influence groat percentage and that the effects are primarily additive. A significant midparent heterosis was observed for grain yield per plant and slight midparent heterosis was observed for primary kernel weight. Heritability estimates in standard units, from the F_2 and F_3 generations, ranged from 0.38 to 0.92 for groat percentage of primary kernels and 0.31 to 0.82 for primary kernel weight.

The first objective of this study was to determine the relationships of groat percentage with plant growth and grain production in plants evaluated in an early generation head row series. The second objective was to examine in depth the relationships of groat percentage with kernel weight, grain weight per tiller, and biomass per tiller in segregating lines from two crosses between parents divergent for these traits.

Head Row Study

This study, summarized below, was designed to fulfill our first objective and began in 1982 with the gathering of panicles from a group of early generation head rows (F_3 to F_6) which were very diverse for physical kernel quality traits and plant vigor. Correlation analysis was performed between primary kernel groat percentage of these parent panicles and vegetative weight and grain weight from primary culms of their progeny, which were grown in an unreplicated head row series during 1983. Panicles which represented a large diversity of phenotypes were in turn collected from these plants, and their progenies were grown in a head row series with two replicates during 1984. Correlations were calculated between primary kernel groat percentage from the 1982 and 1983 progenitors and several primary culm traits of their 1983 and 1984 progenies.

Correlation coefficients of groat percentage with grain weight, panicle weight, vegetative weight, biomass of the primary culm, and primary kernel weight were generally negative (Table 1) and all were significantly negative when 1982 and 1983 groat percentages were correlated with 1984 productivity traits. The 1984 correlations between groat percentage and the productivity traits on a line mean basis were also all significantly negative.

Table 1. Correlation coefficients between groat percentage and several other traits. Parental data correlated with that of their progeny lines (1982-1983 and 1983-1984) or of their families (1982-1984). Line means were used in calculation of within-year (1983 or 1984) correlations.

	Head rows			Pure lines		
	parent/progeny			line means		
	1982- 1983	1982- 1984	1983- 1984	1983	1984	1984
Groat percentage correlated with:						
Grain wt.	0.09	-0.30**	-0.38**	-0.01	-0.55**	-0.57*
Panicle wt.	-0.03	-0.29*	-0.30**	-0.11	-0.55**	-0.49
Vegetative wt.	-0.25*	-0.39**	-0.35**	-0.26*	-0.55**	-0.19
Biomass	-0.13	-0.35**	-0.37**	-0.19	-0.57**	-0.41
Primary kernel wt.	-0.35**	-0.21	-0.41**	-0.46**	-0.28**	-0.35
	n = 69	n = 69	n = 82	n = 69	n = 82	n = 15

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

Pure Line Study

A second experiment conducted in 1984 involved the same measurements on 15 pure line cultivars or advanced selections. The correlation coefficients calculated among traits in this study (Table 1) revealed results similar to the head row study. Due to the low number of lines tested, however, fewer correlation coefficients were statistically significant.

After finding these negative relationships at the single culm level in early generation material and in the 15 pure lines, our next step was to examine these relationships in a broader context of elite material at the forefront of the U.S. cultivar development process. Rankings for groat percentage of the five highest yielding entries in the 1983, 1984, and 1985 USDA Uniform Midseason Oat Performance Nurseries (UMOPN) were examined. The five top-yielding cultivars in 1983 ranked only 15 to 28 (of 35) for groat percentage; however, in 1984, two of the five top-yielding cultivars had high groat percentages and in 1985 four of the five top-yielding cultivars had groat percentage ranks of 10 or better. These variable results caused us to shift our attention to the relationships between groat percentage and the productivity traits among segregating lines from crosses between material diverse for these traits, the focus of the following investigation.

Genetic Study

Materials and Methods

In each of the two crosses used for this study, X4614-1/X5243 and X4614/X3962-7, parent 1 was a line with high groat percentage, small kernels, and relatively low grain weight and biomass of the primary tiller, while parent 2 was a line with low groat percentage, large kernels, and relatively high grain weight and biomass of the primary tiller. The crosses were made in the field during 1985 and F_1 plants were grown in the greenhouse during the 1985-1986 winter.

The F_2 plants were grown during the 1986 field season on the University of Wisconsin-Madison Charmany Farm in 3-m rows 30 cm apart with 5-cm spacing between plants. Several rows of each parent were planted among the F_2 rows. Half of each parent row was planted at 5-cm spacing and half of the row at 2.5-cm spacing in order to identify the effect of spacing on the various traits. The 1986 growing season was characterized by typical temperatures and adequate moisture.

At maturity, over 100 healthy F_2 plants were harvested from each cross. The F_2 and parent plants from the 1986 field were threshed by hand, the grain weight of the primary tiller was recorded, and 10 primary kernels were weighed and then hand dehulled for groat percentage determination. An F_3 plant from each F_2 plant was grown in the fall greenhouse, and two F_4 plants from each F_3 plant were grown in the winter-spring greenhouse. Seed from the F_2 field plants and F_3 and F_4 greenhouse plants were planted in 1987 field nurseries at two locations, the University of Wisconsin-Madison Charmany Farm and the University of Wisconsin Arlington Farm. A randomized complete block design with two replicates of families and generations within families was used at each location. Seed from the F_2 field-grown plants was divided to grow F_3 lines at both locations. Seed from the greenhouse-grown F_3 and F_4 plants was sufficient for only one location, therefore, the F_4 lines were grown at Arlington and the F_5 lines were grown at Madison. At least one F_5 line was grown for each family, and a second F_5 line was grown if the second greenhouse F_4 plant had sufficient seed. Up to 30 seeds were planted into the center of a 1.5-m row at approximately 2.5-cm seed spacing. 'Stout' was planted as filler at each end of the row, and several rows of each parent were included at random locations within each replicate. The 1987 growing season was abnormally hot and dry.

At maturity all of the plants in each F_3 , F_4 , and F_5 line (row) were harvested, bagged, and air dried. Data collected on the healthy tillers from each row included tiller number, biomass, grain weight, 100 kernel weight, and groat percentage.

Results and Discussion

Analyses of variance for grain weight per tiller, biomass per tiller, kernel weight, and groat percentage revealed highly significant variation among families for all four traits at both locations for both crosses. Significant variation was detected between generations within families for all traits in both crosses at Madison (F_3 & F_5) and Arlington (F_3 & F_4) (except for grain weight per tiller for Cross 1) indicating continued segregation after the F_2 generation. The lack of significant variation for grain weight in Cross 1 may be more an indication of the effects of environment on this trait than an indication of lack of segregation. The reason for this remains unresolved. Significant variation between F_5 lines nested within families was detected for kernel weight for Cross 1 and groat percentage and biomass for Cross 2. This variation suggests genetic

segregation for some traits among F_4 plants from the same F_3 plant. Analysis of variance of F_3 lines and parents grown at both locations revealed no significant variation between locations except for groat percentage in both crosses. Location means indicated that groat percentage was much higher at Arlington than at Madison. Another interesting observation was that the groats of the Madison-grown material consistently broke into many pieces when dehulled with the impact dehuller while the Arlington-grown groats remained relatively sound. This is another indication of environmental influence on groat development and composition. Significant variation was present between parents for all traits except grain weight per tiller between the parents of Cross 2.

Frequency distributions of individual F_2 plants or of F_3 to F_5 line means showed near-normal patterns with very few plants or lines outside the range of the parents. These distributions are typical of traits controlled by several factors with mainly additive effects. The major exception was for grain weight per tiller where the mean of F_2 plants showed considerable heterosis, and the F_3 and F_4 line means were larger than the parental midpoint. Slight midparent heterosis was seen for kernel weight of the F_2 plants in both crosses. These multifactor segregation patterns for groat percentage, large heterosis for grain weight, and slight heterosis for kernel weight are consistent with results reported in the literature(14,15).

The means for grain weight and biomass per tiller of the parents at the 5-cm spacing were significantly higher than parental means at the 2.5-cm spacing indicating strong environmental influence on these two productivity traits. No difference was detected between the plant spacings for groat percentage or kernel weight for either cross, indicating that these two plant densities did not differentially affect the two kernel traits.

Heritability estimates by parent-offspring correlation(3) were generally in the medium range (Table 2).

Table 2. Heritability estimates by correlations between various generations.

Generations	Groat percentage		Grain weight per tiller		Kernel weight		Biomass per tiller	
	Cross: 1	2	1	2	1	2	1	2
F_2 F_3 (M)†	0.53	0.48	0.50	0.21	0.68	0.56		
F_2 F_3 (A)	0.46	0.48	0.58	0.50	0.75	0.56		
F_2 F_4 (A)	0.48	0.46	0.53	0.30	0.55	0.35		
F_2 F_5 (M)-a	0.31	0.42	0.22	0.13	0.55	0.47		
F_2 F_5 (M)-b	0.37	0.45	0.27	0.21	0.49	0.50		
F_3 (M) F_4 (A)	0.49	0.40	0.28	0.20	0.57	0.40	0.64	0.50
F_3 (M) F_5 (M)-a	0.40	0.33	0.62	0.47	0.68	0.63	0.77	0.50
F_3 (M) F_5 (M)-b	0.48	0.52	0.57	0.39	0.67	0.63	0.66	0.48
F_3 (A) F_4 (A)	0.50	0.53	0.64	0.53	0.68	0.66	0.73	0.53
F_3 (A) F_5 (M)-a	0.44	0.32	0.11	0.15	0.60	0.60	0.55	0.24
F_3 (A) F_5 (M)-b	0.44	0.39	0.04	0.23	0.52	0.56	0.39	0.40
F_4 (A) F_5 (M)-a	0.55	0.43	0.29	0.38	0.76	0.75	0.65	0.60
F_4 (A) F_5 (M)-b	0.48	0.55	0.17	0.42	0.79	0.65	0.63	0.60

† Abbreviations for locations: Madison (M) and Arlington (A).

The highest estimates were found for kernel weight and biomass per tiller. Heritability estimates using F_2 data correlated with the other generations were surprisingly similar to the other generation pairs (F_3 - F_4 ,

F_3 - F_5 , and F_4 - F_5) since only single plants (or primary culms) were measured for the F_2 generation. Heritability estimates for groat percentage and biomass were fairly consistent across estimates involving the F_2 generation. Heritability estimates for grain weight showed some location effect in that those involving the F_2 plants with F_3 lines at Arlington were larger than those involving F_2 plants with F_3 lines at Madison. Estimates of heritability from correlation of F_3 data with F_4 and F_5 data were similar to those involving F_2 data. Estimates between two generations in the same environment were larger than those between two generations in different environments especially for grain weight per tiller. The estimates for groat percentage and kernel weight were affected less by environment than those for grain weight. These results emphasize the need to reduce genotype x environment interaction and its bias on heritability estimates.

Many of the r values of groat percentage with grain weight, kernel weight, and biomass were significantly negative for cross 1, both between and within generations. The significant r values ranged from -0.20 to -0.57 with only two correlations stronger than -0.50 . For Cross 2, however, only a few of the mostly negative correlation coefficients were significant and those were between groat percentage and kernel weight and ranged from -0.23 to -0.34 . These cross differences are partly due to the larger diversity between the phenotypes of the parents of cross 1 and partly due to the fact that some crosses exhibit correlations between some traits and other crosses do not (11). These negative correlations of groat percentage with kernel weight and grain weight per tiller are especially important because kernel weight is one of the three standard yield components and grain weight per tiller encompasses two of the three yield components.

Based on 82 line means from 33 different crosses in the head row study we found a correlation of -0.55^{**} between groat percentage of primary kernels and grain weight of the primary tiller. Another disappointing observation was that in the head row material sampled, rare outliers with both high groat percentage and high grain weight per tiller were not found (Fig. 1A). The parents used for our genetic study were genotypes from the upper and lower ends of this distribution (Fig. 1A arrows). Both crosses produced several lines with both relatively high groat percentage and high grain weight per tiller (Fig. 1B).

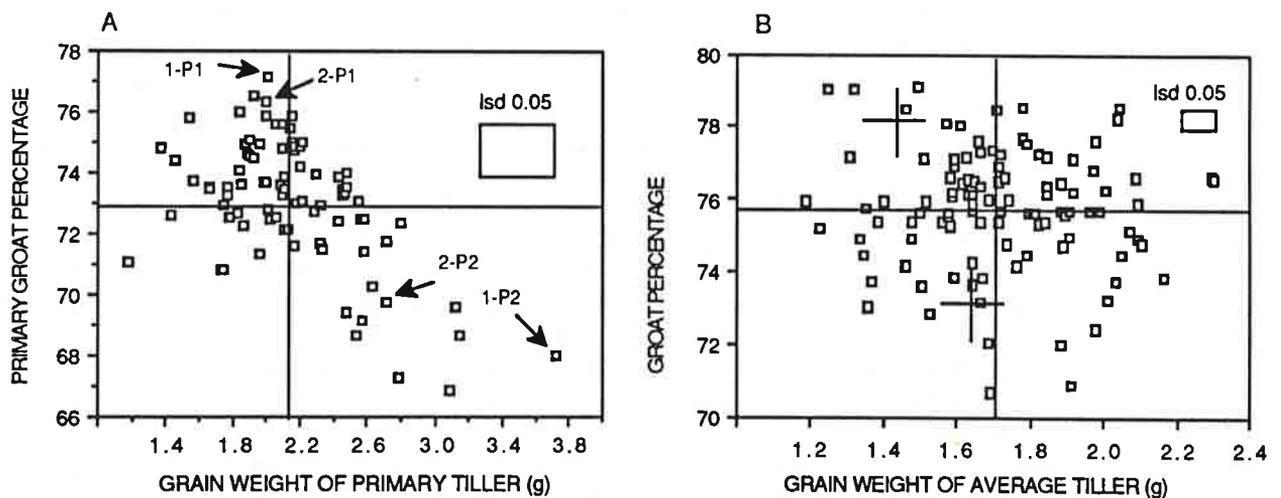


Figure 1. A. Line means of material from the 1984 head row series study. The parents for the genetic study are identified by the arrows. B. F_4 line means for Cross 2 from the 1987 Arlington field nursery. Each large '+' indicates a parental mean for this environment. The vertical and horizontal reference lines represent the overall means for each trait. The lsd box indicates the least significant difference between line means.

Many of the families above the mean for both groat percentage and grain weight at Arlington in the F₄ generation were also above the overall means for both traits in other generation/environment combinations, however, no families were above both means for all generation/environment combinations. Although a significant negative correlation between groat percentage and single culm grain weight was found in the head row study and among the 15 pure lines, our results indicate that these crosses between genotypes with high groat percentage and medium to low grain weight per tiller and those with low groat percentage and medium to high grain weight per tiller can produce offspring with high groat percentage and high grain weight per tiller. Different correlation patterns and estimates of heritability can be expected from different crosses, locations, and plant spacings illustrating the importance of genetic diversity, environmental influence, and selection procedure in a breeding program.

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DEVELOPMENTAL STABILITY IN OATS (*Avena sativa* L.)Magne Gullord¹⁾ and Are Halvor Aastveit²⁾Introduction

Genotype-environment interaction occurs in all plants, crop plants included. Several methods have been applied to measure and describe cultivar response to environments (Finley and Wilkinson 1963, Eberhart and Russel 1967, Aastveit and Martens 1986).

The use of physical measurements of environmental factors in order to explain genotype-environment interaction has been stressed by several authors (Nor and Cady 1979, Saud and Francis 1983, Aastveit and Martens 1986 and Gullord and Aastveit 1987).

Variation in the weather during the course of plant development may effect the overall response of genotypes to environments. A detailed identification of weather variables associated with the genotype-environment interaction is therefore required. The objective of this study was (1) to identify relationships between yield stability on one hand and climatic and edafic factors on the other, and (2) to find a basis for increased efficiency of the cultivar testing programme in oats.

Materials and MethodsExperimental

Twenty two oat lines selected from crosses between adapted North-European cultivars for high grain yield, lodging resistance and earliness and three commercial varieties were included in the series of trials (Table 1).

The oat lines were evaluated in totally 36 yield trials at nine locations in the southern part of Norway during the period of years 1981-84.

All field plots consisted of ten eight-metre rows, spaced 13 cm apart, of which 5.4 to 7.0 metres were harvested. The lines were arranged according to a five by five lattice design replicated 2 times. The sowing rate was 200 kg per hectare.

For each plot grain yield and moisture content at harvest were recorded. At most of the locations the day of heading and the day of yellow ripeness, per cent lodging and straw length were also recorded.

The growing season was divided into seven periods. The time between planting date and tillering was divided into two periods (1 and 2) of equal length, while the phase from tillering to heading and from heading to yellow ripeness were both divided into two equal periods (3, 4, 5, and 6 respectively). The last period was from yellow ripeness to harvest. For each period the mean temperature in °C (T1 - T7) and the mean daily rainfall in mm (N1 - N7) were calculated. These data were partly from adja-

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cent weather stations of the Norwegian Meteorological Institute, and partly from recordings at the test sites. Soil, pH, p-Al, k-Al, soil type and the amount of fertilizer applied at each test site were also recorded

Statistical

In order to study the genotype-location interaction more closely we used the regression approach described by Eberhart and Russel (1966) and a multivariate analysis approach (PLS-method) described by Aastveit and Martens (1986).

Experimental results

Table 2 presents the results of an analysis of variance. All the interesting effects were significant at the one per cent level. The variance components for the two-way interactions were rather small, however. For comparisons between lines this means that neither the two factor interactions nor the three factor interactions will dominate the variance for comparisons between lines. However, the variance components for interactions are usually larger than the residual variance shown in this series (e.g. Aastveit 1982). For this reason we may not ignore the interaction terms but keep in mind that interactions between varieties and environments may be relatively small in oats.

In order to study the genotype-location interaction more closely, the sum of squares was first split into an item for differences between regression coefficients (Table 2) and an item for deviation from linear regression. The F-values for both items were significant, but we found that the deviations from linear regression were rather small. The differences between linear regression coefficients took out 26.5 per cent of the total sum of squares for line-site interaction. Because of the relatively small effects of interaction, the regression model fits relatively well in this case. The λ_i values in Table 1 show some variation. Most of them are, however, relatively small, indicating that the responses of most of the genotypes to variable growing conditions measured by the average yield were fairly well described by linear regression. A few of the λ_i values were significant at the 5 per cent level. The regression as well as the deviation from linear regression methods, classified line number 3, 12, 18 and 23 as unstable, and 2, 13, 16 and 24 as stable. There was no negative correlation between grain yield and the regression coefficients.

The PLS method was applied for causal modelling of the relationship between biological and environmental variables. Only two factors appeared to be meaningful as judged by inspection of plots (Figure 1) and residuals (Table 3). The first and the second factor explained 33 and 16 per cent respectively of the sum of squares for genotype-sites interaction.

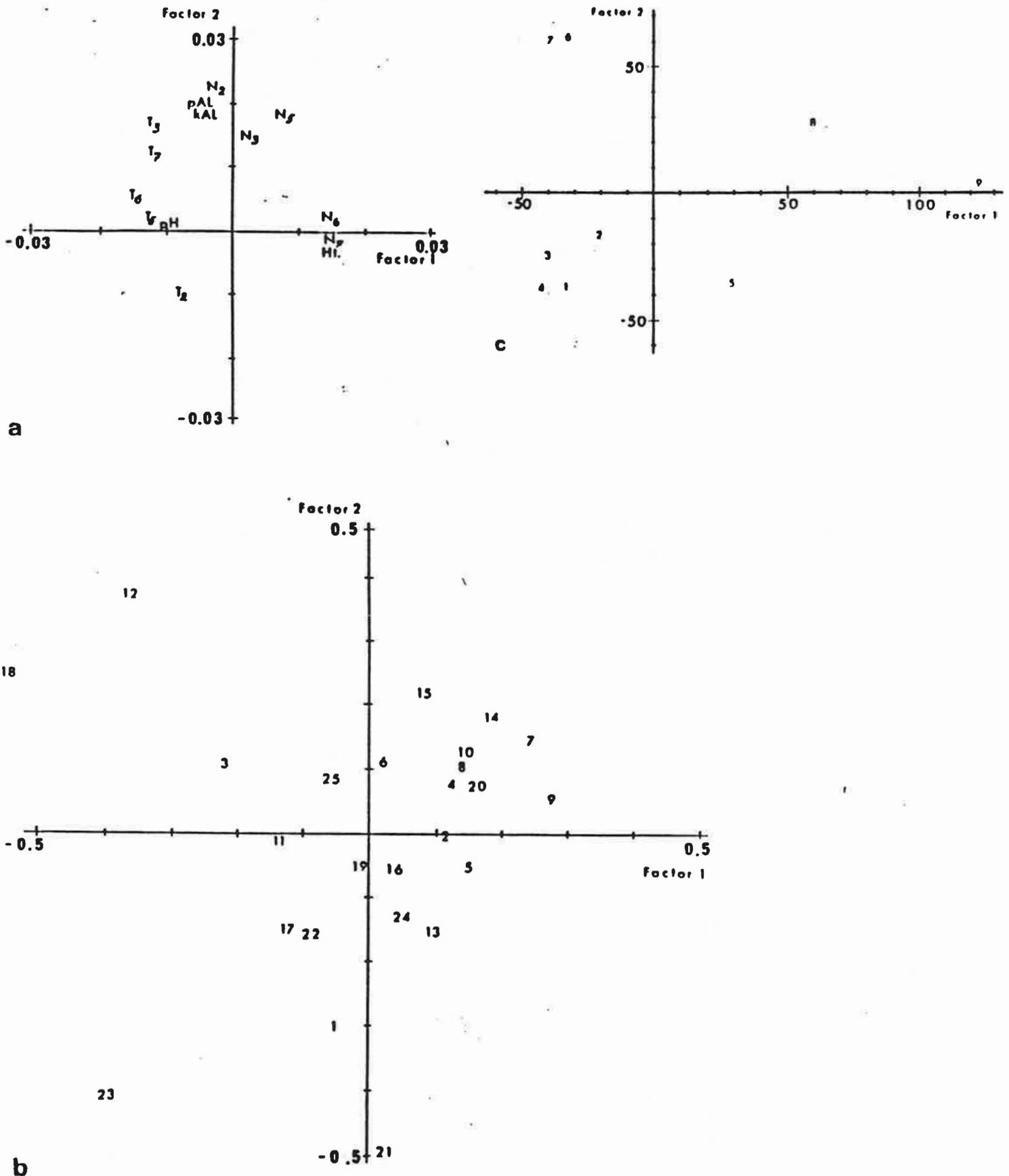


Fig. 1 a-c. a) Plot of the factor loadings for the environmental variables. b) Plot of the factor loadings for the lines due to the genotype \times site interaction. c) Plot of factor scores for locations due to the two factors of the PLS-analysis.

Table 1. Parentages and origin for 25 oat lines and cultivars included in the series of trials. Mean grain yields over years and locations and b_i = the regression coefficient and λ_i = deviation from the linear regression

Lines/ no.	Lines/ Cultivars	Parentage	Origin	Yield kg/daa	b_i	λ_i
5	Titus	Perle/Stjärn/Sol II	Svaløf AB	514	0.89	1.23
23	Puhti	Hannes/Rythi	Jokioinen	572	1.20	2.45*
17	Svea	Voll/Blixt/Titus	Svaløf AB	577	1.13	0.75
1	A9001	Mustang/Pol	Apelsvoll	569	0.95	1.75
2	A9004	----"----	----"----	580	0.94	0.17
4	A9018	Pol/Sang	----"----	572	0.90	0.46
6	A9028	--"---	----"----	538	0.91	0.89
8	A9052	Sv692013/Pol	----"----	533	0.95	1.45
9	A9055	Alfred/pol	----"----	594	0.87	0.79
11	A9058	Alfred/Sv692013	----"----	561	1.00	0.88
13	A9060	Alfred/Titus	----"----	559	0.92	0.42
25	A9065	Voll/Selma	Ap./Kv.h.	566	1.08	0.88
3	A0001	Mustang/Pol	Apelsvoll	584	1.16	2.21*
7	A0002	Pol/Sang	----"----	542	0.87	0.90
10	A0005	Alfred/Pol	----"----	561	0.96	0.98
12	A0006	Alfred/Sv692013	----"----	560	1.25	1.31
21	A0010	Tador/Gråkall	----"----	602	0.92	2.18*
14	A0015	Mustang/Pol	----"----	576	0.86	1.06
15	A0018	Weikus/Pol	----"----	572	0.96	1.14
16	Kapp	Gråkall/Tador	----"----	588	1.00	0.35
18	A0033	Alfred/Sv692013	----"----	548	1.26	2.52*
19	A0036	Voll/Selma	Ap.Kv.h.	593	1.01	1.64
20	A0040	Pol/Sang	Apelsvoll	582	0.95	1.34
22	A0059	--"---	----"----	599	1.07	1.05
24	Lena	Sang/Unisignum	----"----	590	0.97	0.60

* $0.05 < p < 0.01$

Table 2. Analysis of variance for grain yield

Source	PK	Mean square	F-value
Lines	24	35676.3	13.83***
Location	8	1796296.3	
Lines x loc	192	3787.6	1.47***
Year	3	1814910.3	
Lines x year	72	4196.9	1.63***
Lines x loc x year	576	2580.1	1.65***
Loc x year	24	315392.0	
Rep (loc. year)	35	23311.6	
Rest	865	1562.3	
Lines x loc	192	3787.6	
1. Regression	24	8037.4	
2. Dev. from req.	168	3180.5	

Table 3. PLS-regression of interaction to the climatic variables. The table shows the residual sum of squares for genotype-site interaction after inclusion of 0, 1, 2 and 3 factors

Factor	Interaction			Env.ment. var.				
	SS	DF	MS	SS	DF	MS	%	
0	727228	192	3787.6	100	112	112	1.0	100
1	490179	168	2917.7	77	67	98	0.68	68
2	369944	144	2569.1	68	38	84	0.46	46
3	307690	120	2564.168	68	18	70	0.26	26

Figure 1a shows that the first factor was dominated by temperature and rainfall during the time from ear emergence to harvest. Rainfall and temperature had opposite effect. The second factor was especially dominated by the temperature and rainfall during the time just before and after tillering. The soil phosphorus and potassium levels gave also important contributions to this factor.

Figure 1c shows that site No. 9 was unique relative to others. This site had a very large value of the first factor and was characterized by much rainfall and low temperature during the last growing period. Site No. 8 had some of the same distinctions, but the amount of the loading value was much lower. Sites No. 6 and 7 in the Oslofjord area were associated with positive direction of the second factor, while sites No. 1 to 5 to the North were associated with the negative direction.

The advantage of the PLS-model is the combined analysis of sites, genotypes and environmental effects. This is the basis for clustering of sites relative to both the genotype-site interaction and to the environmental variables (Figure 1c). In this figure, sites No. 1-5 may be classified as one cluster, No. 6 and 7 as another. We may therefore classify the South-East part of Norway as two different clusters of regions. The first region is the northern part of South-East Norway, and the second one the regions around the Oslofjord. The third region is the South-Western part of the country, while the fourth are the actual districts in Trøndelag.

In the factor loading the lines No. 12, 18, 21 and 23 deviated very much from the origin (Figure 1b). These lines were therefore classified as unstable. Variety No. 18 had a large negative value for factor 1. It gave high yield when temperature during the last part of the growing season was high and when rainfall was not too high. Lines No 12 and 18 were separated from line No. 23 by factor 2. While the former lines gave high yields when the precipitation around tillering was high, line No. 23 gave high yield when these factors were low. The fact that lines No. 12 and 18 are sister lines indicates that instability is genetically controlled.

The variance components for genotype-location interaction were close to zero in regions 1 and 2. Table 4 shows that the component for genotype-year interaction was zero for region 2, but highly significant from zero in the other regions.

Table 4. Estimates of the variance components in the different regions

Component	Region 1	Region 2	Region 3	Region 4
σ^2_S	6828.8**	165.9		
σ^2_{GS}	54.6	-30,0		
σ^2_E	6194.4**	2455.4	15936.7***	13628.8***
σ^2_{GE}	217.0**	-98.6	1128.5***	895.7***
σ^2_{GSE}	254.0*	602.6***		
σ^2_{SE}	2910.9***	1386.9		
σ^2_B	795.6***	1532.9***	592.4***	179.2**
σ^2	1960.2	910.2		

Discussion and conclusion

Analysis of variance of our experimental data has shown that genotype-year as well as genotype-location interaction were significant. However, the variance components for the two way interactions relative to the residual variance were rather small. This is in agreement with earlier studies in late maturing oat-lines (Aastveit 1953). Talbot (1984) did, however, show very low variance component for the genotype-year interactions, but not for the genotype-location interaction. It has been observed over years that oat varieties from the Nordic countries as well as from the Netherlands have been very well adapted to Norwegian growing conditions.

The PLS-method identified the same genotypes as the most stable or most unstable genotypes as did regression method. However, the ranking of the genotypes were not so easy to handle, since more than one component were needed to account for the interactions. The PLS method is in many ways similar to the principal component procedure, but it has the advantage that the genotypic reactions can be related to specific environmental factors. The PLS-method divided the cereal growing area in southern Norway into four regions.

In order to select for stability, our results indicate that variability experiments should be laid out at one location in each of the four regions identified. Selection for wide adaptation has been shown to be very efficient by successive selection for high yield of hybrid populations raised in two contrasting environments (location or season) (Oka 1975, Lu et. al 1976, Anderson 1980).

Some environmental factors seems to be more important than others for the explanation of genotype-location interaction. Temperature and rainfall, especially between heading and maturity had large influence. Soil phosphorus, soil potassium and sowing time had considerable effects on the interactions for the different characters.

Information on the environmental factors which contribute to genotype-environment interactions help the plant breeder to understand the nature of these interactions and in designing breeding procedures for developing stable cultivars which can better tolerate climatic and edafic variation. The weather and edafic variables used in this study represent only part of the environmental complex. With the inclusion of other environmental factors such as solar radiation and soil water availability, and with more precise observations on these factors in different periods of plant development, one may expect that a more sizable proportion of the genotype-environment interaction sum of squares could be accounted for.

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HOMOGENEITY OF OAT CULTIVARS WITH RESPECT TO OUTCROSSING

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Introduction

High genetic variability is the basis of the breeding process itself, whereas high genetic homogeneity is one of the fundamental demands on the resulting variety. Natural populations of self-pollinating species are known to maintain variability by outcrossing (Allard *et al.*, 1968; Imam and Allard, 1965). To what extent is the homogeneity of today's oat cultivars affected by outcrossing?

Materials and Methods

Field trials were conducted in 1984 at Kleinwald (France) and in 1984/85 at Augustenberg (FRG). The reproductive behaviour of white or yellow oat *Avena sativa* L. was determined with the cultivars 'Alfred', 'Borka', 'Erbgraf', 'Fabian', 'Flaemingsnova', 'Ponta', 'Selma' and 'Tiger'. The cultivars were randomly sown in two blocks as 3m six-row plots of 400 plants/m². The plots were surrounded two by two by a mixture of brown oat *Avena sativa* L. 'Sirene', naked oat *Avena nuda* L. 'Caesar' and biotypes of *Avena fatua* L. The ratio of the components was 1:1:0 at Kleinwald and 2:1:1 at Augustenberg. The mixture was sown as 300 plants/m². In all experiments, on five successive days 10 plants were randomly chosen in every plot for emasculation of 10 flowers per plant. The emasculated flowers were exposed to natural pollen dispersal, fertilized by flying pollen, harvested and sown next year in the field. The morphological characters of the F1 entries expressed the nature of the male parent as white, yellow, brown, naked or wild oat. To determine the variety of the white or yellow male parents, 14 florets per F1 plant were electrophoretically analysed. The amount of natural outcrossing was determined by electrophoresis with 300 florets randomly chosen in every plot.

The electrophoretical analysis was carried out with the prolamins. Every extract was subjected to IEF pH 5-8, PAGE pH 9,1 and PAGE pH 3,1. The IEF and the alkaline PAGE modified the methods of Ohms (1984). The acidic PAGE modified the standard reference method for identification of cereal cultivars (Anonymous, 1985).

Results and Discussion

The open flowering in oats is strongly dependant on climatic conditions (Bickelmann and Leist, 1986). These conditions were recorded on 3 days at Kleinwald in 1984, on 4 days at Augustenberg in 1984 and on 7 days in 1985. Seed set was 16% at Kleinwald and 21% at Augustenberg for the 8000 flowers emasculated per experiment. About half of the harvested karyopsis developed plants. Referring to the fertil karyopsis, seed set ranged from

9% to 16% for individual cultivars, without any significant varietal difference.

Comparing the ratio of cultivars and species in the field and their importance in pollinating emasculated flowers, significant differences occurred. At Kleinwald 'Sirene' represented 30% in the field and 27% of the pollinations. At Augustenberg this cultivar only took part in 16% of the pollinations, being half of its part in the field. 'Caesar' covered 30% of the area at Kleinwald and 15% at Augustenberg, but pollinated not more than 2-9% of the emasculated flowers. *A. fatua* occupied 15% of the area at Augustenberg and pollinated 9-13%. Concerning the pollinations by white or yellow oats, the intervarietal crossings came to about a quarter of all pollinations, but were exceeded by 39-51% of intravarietal crossings. Obviously the dimension of a field was not the main factor influencing the pollination capacity. Intraspecific crosses surpassed the interspecific crosses.

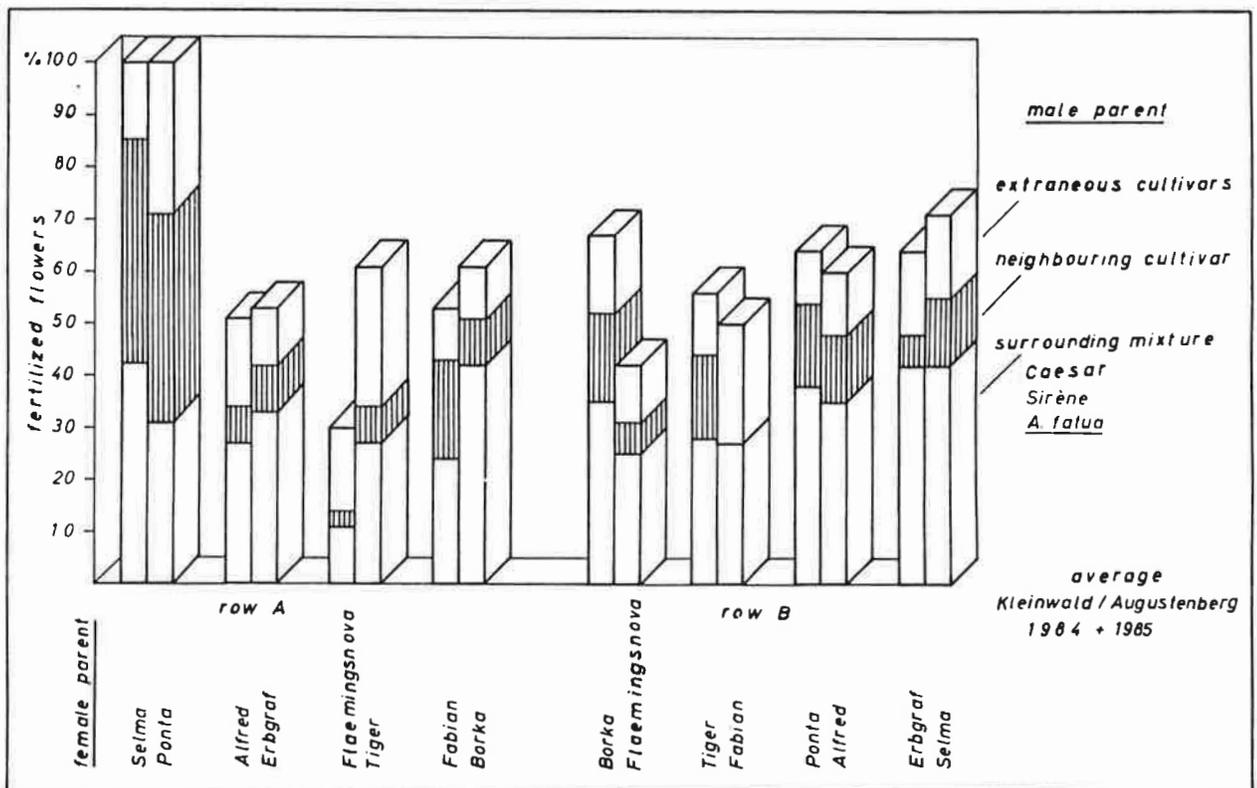


Fig. 1: The pollination of emasculated oat flowers (*A. sativa* L.) depending on the distance between the cultivars or species (*Avena* spp.) - at the average of Kleinwald and Augustenberg in 1984/85.

Depending on trial and plot, the emasculated flowers were pollinated to a different degree by cultivars and species (fig. 1). The components of the surrounding mixture pollinated 11-43%. The neighbouring cultivars accounted for 0-41% of the pollinations. 'Fabian' and 'Tiger' differed the most in the beginning of flowering. Therefore in row B the early flowering 'Fabian' was not pollinated by the late flowering 'Tiger'. Whereas 'Tiger' got some pollinations from late flowering 'Fabian'. The same difference between 'Flaemingsnova' and 'Tiger' gave

corresponding results in row A. The flowering period of 'Selma' and 'Ponta' agreed exactly and influenced the seed set. Though it should be noticed, that these cultivars and 'Borka' were not distinguishable by electrophoresis. Therefore the amount of pollinations by the neighbour might be overestimated in the case of 'Selma', 'Ponta' and 'Fabian' in row A as well as 'Flaemingsnova', 'Alfred' and 'Erbgraf' in row B. Pollinations by cultivars, not belonging to the surrounding mixture or to the neighbouring plot, randomly pollinated 8-37%. 29-70% of the pollinations resulted from intravarietal crosses. Especially for 'Flaemingsnova' the fraction of inbreeding was significantly high. The frequency of pollination mostly depended on the correspondence of the flowering periods, agreeing the best within a cultivar. The greater the distance between the cultivars, the more the frequency of pollination was influenced by chance. Genotypic effects might have been important in the case of 'Flaemingsnova'.

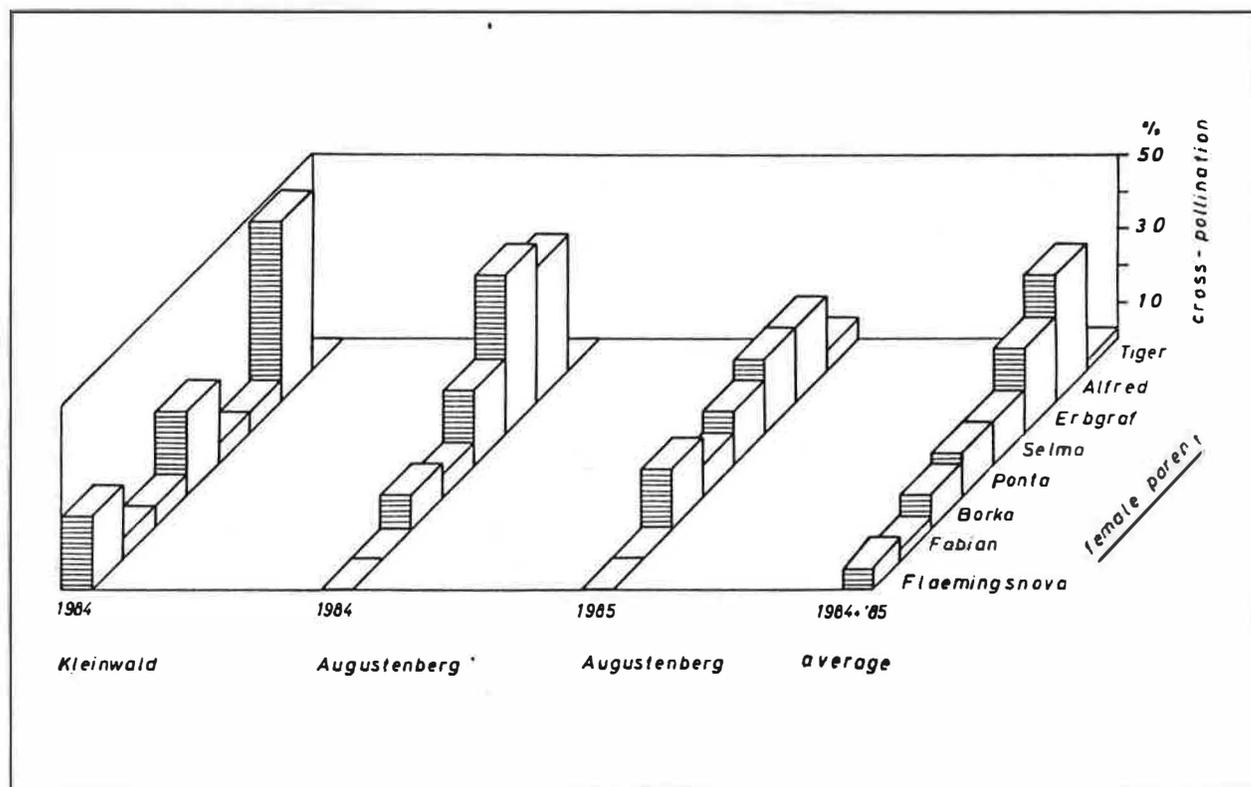


Fig. 2: Outcrossing in oat cultivars (*A. sativa* L.) in a field with great multiplicity of cultivars. The arrangement of the cultivars follows the beginning of flowering: 'Flaemingsnova'- 'Fabian' are early, 'Tiger' is late. The number of outcrossings per trial is set 100%.

In analysing the frequency of outcrossing in non-emasculated samples, clear varietal differences were found (fig. 2). 'Alfred' revealed significantly high frequencies of outcrossing in each trial. 'Erbgraf' produced adequate amounts of outcrossing at Augustenberg in 1984/85. It should be noticed that the frequencies of out-crossing might be underestimated for 'Borka', 'Selma' and 'Ponta' because of their electrophoretical identity. The degree of out-crossing was mainly determined by the date of

flowering. 'Alfred' and 'Erbgraf' were middle to late flowering and consequently experienced a great multiplicity of cultivars in the pollen swarm, increasing the opportunity of crossing. The early flowering 'Fabian' and 'Flaemingsnova' as well as the late flowering 'Tiger' rarely revealed outcrossing, because of the reduced multiplicity in the pollen swarm.

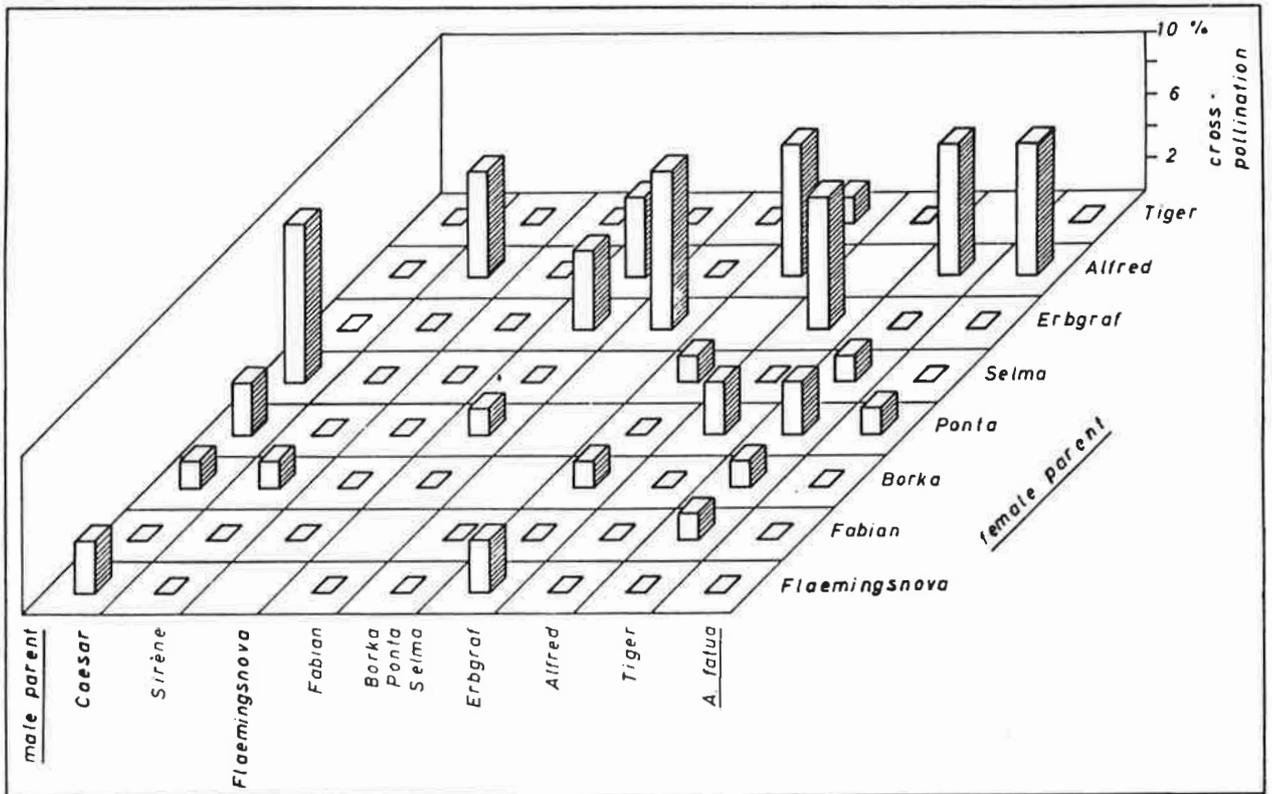


Fig. 3: The presentation of spontaneously occurring outcrossing in oat cultivars (*A. sativa* L.) - at the average of Kleinwald and Augustenberg in 1984/85. The arrangement of the cultivars follows the beginning of flowering: 'Caesar'-'Flaemingsnova' are early, 'Tiger' is late and *A. fatua* is early-late. The total number of outcrossing is set 100%.

The cultivars and species pollinated randomly and did not reveal significant differences in their importance as male parents. Corresponding to the experiment, 80 intervarietal and interspecific crossing combinations were possible (fig. 3). Analysing the samples of non-emasculated material, most of the combinations were missing, either they were not realized or were not represented in the sample. Outcrossing ranged from 8-9% for the most successful combinations, averaging 1.4% per plot and trial. *A. fatua* was the male parent in 10% of the crossings, this means an average of 0.2% per plot. The components of the surrounding mixture were less important in natural outcrossing than in pollination of emasculated flowers. The most successful combinations 'Erbgraf' × 'Selma', 'Erbgraf' × 'Alfred' and 'Alfred' × 'Erbgraf' profited from the neighbourhood of their plots and the agreement of their flowering periods. The overlapping of the flowering data favoured 'Selma' × 'Caesar', 'Alfred' × 'Tiger' and 'Alfred' × *A. fatua*.

Tab. 1: The frequency of outcrossing in oat cultivars (*A. sativa* L.) - depending on location and plot.

cultivar	frequency of outcrossing in % lower - upper approximate confidence limits					
	inter- varietal		intra- varietal		total	
	A	B	A	B	A	B
Kleinwald 1984						
Flaemingsnova	0-2,9	0-1,4	0-3,7	0-1,6	0-6,6	0-3,0
Fabian	0-1,4	0-0,5	0-0,9	0-0,4	0-2,4	0-0,9
Borka	0-1,4	0-1,4	0-1,0	0-0,9	0-2,4	0-2,3
Ponta	0-3,5	0-1,4	0-2,1	0-1,2	0-5,6	0-2,6
Selma	0-1,4	0-1,7	0-1,2	0-1,2	0-2,6	0-2,9
Erbgraf	0-2,5	0-1,4	0-1,8	0-1,1	0-4,3	0-2,5
Alfred	0-4,7	0-3,5	0-4,5	0-1,7	0-8,2	0-5,2
Tiger	0-0,7	0-0,7	0-0,6	0-0,4	0-1,3	0-1,1
Augustenberg 1984						
Flaemingsnova	0-1,1	0-1,1	0-1,8	0-2,0	0-2,9	0-3,1
Fabian	0-0,5	0-0,5	0-0,5	0-0,6	0-1,0	0-1,1
Borka	0-1,4	0-1,4	0-1,1	0-1,5	0-2,5	0-2,9
Ponta	0-1,7	0-1,4	0-1,2	0-1,3	0-2,9	0-2,7
Selma	0-3,5	0-1,7	0-3,4	0-1,2	0-6,9	0-2,9
Erbgraf	0-4,7	0-2,9	0-4,0	0-1,9	0-8,7	0-4,8
Alfred	0-4,7	0-2,2	0-3,4	0-1,3	0-8,1	0-3,5
Tiger	0-0,7	0-0,7	0-0,4	0-0,6	0-1,1	0-1,3
Augustenberg 1985						
Flaemingsnova	0-1,1	0-1,1	0-0,4	0-1,0	0-1,5	0-2,1
Fabian	0-0,5	0-0,5	0-0,7	0-0,6	0-1,2	0-1,1
Borka	0-1,4	0-2,2	0-1,4	0-1,1	0-2,8	0-3,3
Ponta	0-1,4	0-1,4	0-1,6	0-0,7	0-3,0	0-2,1
Selma	0-1,4	0-2,2	0-0,9	0-0,7	0-2,3	0-2,9
Erbgraf	0-2,9	0-1,4	0-1,4	0-1,0	0-4,3	0-2,4
Alfred	0-3,5	0-3,3	0-2,2	0-1,7	0-5,7	0-5,0
Tiger	0-1,4	0-0,7	0-0,4	0-0,4	0-1,8	0-1,1
level of probability $p = 0,05\%$						

The intravarietal crossings were not detectable by electrophoresis. Therefore these frequencies were estimated, taking into account the relations of the emasculation experiment (tab. 1). The frequencies of intervarietal and interspecific outcrossing did not exceed the upper confidence limits of 0,5-4,7% for individual cultivars and plots. The amount of intravarietal crossing was estimated with upper confidence limits of 0,4-4,5%. Summing up these results, the spontaneously occurring outcrossings were equal to or less than 1,1-8,7%.

Conclusions

Studies of the emasculation experiment lead to much the same conclusions as studies of natural populations, namely that the amount of outcrossing is affected by the climatic conditions influencing the open flowering, the agreement of the flowering periods, the local distance, the direction of the wind and the genotype of crossing parents. According to the very protective German seed legislative, the potential for crossing has to be limited. The distance between fields for seed propagation should be 100 m minimum. In the nursery an early isolation of promising lines should guarantee the attainment of homogeneity.

The experimental conditions make it reasonable to assume that the amount of spontaneously occurring intervarietal and inter-specific crossing is equivalent to that of intravarietal crossing. The main characters of a cultivar, selected for during the breeding process, are clearly changed by intervarietal or inter-specific crossing. Contrary to this, intravarietal crosses only evoke aberrations from varietal characters if they were heterozygous. Intravarietal crossings may exhibit plants non-typical for the variety as fatuoids if the variety comprises hidden heterozygosity or hidden aneuploidy. The evidence of outcrossing depends on the character detectable and selected. To preserve the varietal homogeneity even in the case of intravarietal crossing carefully bred cultivars are essential, especially when mutagenic events or interspecific crosses occur at the beginning of the breeding process. Intravarietal crossing may be excluded by breeding for absolute cleistogamy.

The results reviewed here, indicate that the amount of outcrossing maintains a dynamic recombination system and possibly a system of adaptation and adaptability in successful cultivars.

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INTERNATIONAL TRADE IN OATS

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Oats are grown in some fifty-three countries around the world, comprising seven in Africa, North Central America three, Europe twenty-four, Asia nine, South America seven, Oceania two, and the Soviet Union. For the period 1985/87, global oat production is estimated to have averaged 48.4 million tonnes, compared with 42.5 MT in 1979/81.

Most of the world's oats are consumed within countries of origin, the approximate production apportionment for 1985/87 being; the Soviet Union, 46 per cent, Europe, 27 per cent, North Central America, 19 per cent, Oceania 3.3 per cent, South America, 1.7, Asia 1.5 and Africa half a per cent.

About three per cent of global oats output enters world trade, compared with wheat, (19.4), corn, (14.2), barley, (9.6), grain sorghum, (17.3). For the period 1982/87, six countries accounted for 85 per cent of exports, while eight countries were responsible for 73 per cent of imports.

In this decade, Finland, Sweden and France have substantially advanced exports, Australia and Canada have remained virtually static, while Argentina and the United States have lost ground. Soviet purchases have fluctuated widely, while the United States has become the world's leading importer.

The United States of America

From 1985/86 production of 7.5 MT output declined to 5.6 MT in 1986/87 and 5.4 MT in 1987/88, respectively. The United States commenced to import oats in 1982 and these have risen to an annual average level of around half a million tonnes. This represents about 5 per cent of overall US supply and have been purchased from Sweden, Finland, Canada and, more recently, Argentina.

Oats are included in Government feed grain programmes, however grower participation has not been significant; 14 to 37 per cent during 1982/86. Reasons cited include heavy on-farm use, lack of economic incentives for participation and a shift to barley. Declining US oat production is not a recent phenomenon, but in fact has been exhibited in trends over several decades. Quality oat imports are required for the racehorse industry and dietary changes, especially in young urban households. Fibre, at present accounting for a rising 15 per cent of the market, is now breakfast fare.

Breakfast cereals have replaced the traditional first meal of the day, which used to comprise rolled bacon, eggs, pancakes, maple syrup, waffles and oatmeal. Concern over cholesterol and carbohydrates has been overtaken by cancer prevention foodstuffs. This "great leap forward" by-passed the European café au lait and croissants tradition.

Australia

Oats rank third in cereal production, after wheat and barley. About 1.85 million hectares are under cultivation, of which 54 per cent is for grain and the balance being for hay, green feed

and silage. Eighty-five per cent of the grain is fed to livestock and 14 per cent of oat grain is exported, (mainly unmilled), with rolled oat exports less than one per cent. Principal overseas markets are Japan, South America, Europe, and occasionally, the Soviet Union.

Feed Application

In common with other countries, oats provide a highly satisfactory base of metabolism energy for sheep, cattle and goats. Oats are also appropriate for horses, as the fibrous part of oats allow for bulky feed. Traditionally oats have not been utilised in pig and poultry rations, as the non ruminant animals experience difficulty absorbing most of the fibre in oats.

"Australia rides on the sheep's back", although it has fallen off several times over the last two decades. With the return to natural fibres, Australian wool prices have soared in 1988. This is putting pressure on domestic oat prices, despite current good seasonal conditions, which are not the norm usually. Oats continue to occupy a key role in farmer strategies.

Food Usage

Consumption of oats as porridge rose steadily in Australia in the early part of this century and this trend continued through the Depression years prior to World War Two.

"Ready to eat" breakfast foods displaced oats in the 1950's and 1960's, despite the introduction of "instant oats". In the 1980's, oatmeal and rolled oats are experiencing a comeback, together with increasing consumption of muesli foods and multigrain bread which includes oats.

Australian consumers are becoming more aware of "more fibre, less fat", to reduce the incidence of heart disease and cancer. Nutritional benefits of oats are becoming more appreciated and accepted. There is also increasing concern regarding the quality of refined and processed foods and the nutritional value of "unnatural vitamins and mineral supplements".

Europe

Oats are grown widely in both Eastern and Western Europe, while the Soviet Union is a major producer in its own right. Production has been declining steadily in this region. In the period 1979/81 Europe accounted for 33.8 per cent of world output. By 1986, this had fallen to 27.3 and an estimated 25.5 per cent in 1987.

Within the European Community (EC12), oats are a "free grain", in so far as oats are not specifically included in the Common Agricultural Policy price regime. Oat growers do not receive an assured price, as compared with wheat, barley and corn. Oat prices are usually geared to feed barley prices and research has been focussed on wheat, barley and corn to the detriment of oats.

Shortfalls in the United Kingdom, Belgium/Luxemburg, Denmark, Italy and the Netherlands necessitate imports from other EC 12 members, with occasional shipments from Scandinavia.

Prices

In this decade cereal production has outpaced consumption, at prevailing levels of utilisation, resulting in increasing stockpiles. Prices became depressed as international trade declined for wheat and coarse grains.

Exporting countries, such as Australia and Canada, whose governments provide minimal support to their growers, were caught in the fallout from the trade war between the European Community and the United States, both of whom subsidise exports.

International prices for certain cereals, including wheat (milling), durum wheat, rice and oats started to rise over 1986/87. The first three cereals reacted to adverse weather influences, which may also had a marginal impact on oat prices. While oat prices advanced to a record plateau, they subsequently retreated, but still remain firm.

In the international arena, cheap feed wheat offers have undermined other coarse grains, especially feed barley and corn. However the current drought, which has been affecting the 1988 crop has sent cereal and soybean prices soaring on US Grain Exchanges.

GLOBAL OATS TRADE BY MAJOR COUNTRIESPER CENT

<u>EXPORTERS</u>	<u>AVERAGE MARKET SHARE</u>		
	<u>COUNTRY</u>	<u>1982/87</u>	<u>1980/81</u>
Sweden	23.4	26.1	13.0
France	17.3	19.7	11.1
Australia	16.3	11.4	20.9
Finland	12.0	0.0	3.4
Canada	11.0	5.1	9.6
Argentina	5.0	7.6	12.2
USA	2.7	12.2	14.5
Other	12.3	17.9	15.3

Source: FAO, USDA

PER CENT

<u>IMPORTERS</u>	<u>AVERAGE MARKET SHARE</u>		
	<u>COUNTRY</u>	<u>1982/87</u>	<u>1980/81</u>
USA	31.4	2.0	1.4
Germany	11.2	19.8	26.8
USSR	10.0	0.0	9.4
Switzerland	8.5	11.3	10.5
Japan	7.5	11.4	11.1
Italy	5.8	8.1	9.7
Belgium/Luxemburg	4.5	4.9	4.5
Netherlands	4.3	2.9	3.8
Others	16.8	39.6	22.8

Source : FAO, USDA

RECOVERY OF HAPLOID OATS FOLLOWING APPLICATION OF MAIZE POLLEN TO EMASCULATED OAT FLORETS

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 USDA-ARS and University of Minnesota

Four haploid plants of cultivated oats (*Avena sativa* L.) were recovered by embryo rescue following pollination of approximately 600 emasculated oat florets with maize (*Zea mays* L.) pollen. Interspecies hybrid zygote formation followed by elimination of maize chromosomes during initial cell divisions presumably occurred. This explanation is based on an analogy to the situation in wheat (*Triticum aestivum* L.) by maize hybridizations described by Laurie and Bennett (*Can. J. Genet. Cytol.* 28:313, 1986). Each of the four oat haploids was from a different cultivar - 'Stout', 'Starter', 'Steele', and 'Black Mesdag' - and each involved a different source of maize pollen - 2 inbreds, 1 hybrid, and 1 open-pollinating variety.

Haploid embryos rescued 12 days post-pollination were less than 1 mm in length compared to embryos about 3 mm in length in self-pollinated controls. Development in the embryos was apparently reduced because there was little or no accompanying endosperm development. The medium used for embryo rescue in these initial efforts was Murashige and Skoog medium containing 7% sucrose and the amino acids of Norstog (*In Vitro* 8:307, 1973). Cytological examination of root tip cells revealed the oat haploid chromosome number of 21 in each of the recovered plants.

Modifications of various aspects of the technique including genotypes, embryo rescue medium, and growth conditions of donor plants are being investigated to improve the efficiency of haploid plant recovery. Oat haploids from this technique will be useful for producing aneuploid stocks, for initiation of tissue cultures for direct selection of recessive traits, and for producing pure breeding doubled haploid lines for genetic and breeding experiments.

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Oat Breeding at the Crop Development Centre, University of Saskatchewan, Saskatoon, Canada - B.G. Rossnagel and R.S. Bhatti.

Despite restriction to approximately 1/4 scientific man year, an effective breeding program has been developed. A modified pedigree/single seed descent procedure is utilized. Crosses (10-15) are made during winter at Texas A & M University, with the F1 grown at Saskatoon that summer. F2 populations of 2,000 spaced plants are field grown at Saskatoon the next summer, with 300-400 panicle selections taken. Two to four grains/ panicle are sent to New Zealand as a space planted F3 winter increase. Single panicles/plant are harvested, returned to Saskatoon, bulk threshed and screened for plumpness. Two thousand grains then form a space planted F4 nursery at Saskatoon. Panicle selections (200-400) are taken, threshed, visually screened for seed quality (plumpness, % hull, size and uniformity) and advanced to F5 hill plots. Hill plots are evaluated for maturity, height and adaptation, hand harvested, visually screened for grain quality and advanced to unreplicated F6 yield trials, (10-50 genotypes per population).

F6 yield trials are grown at a single location with highly selective technical screening for grain quality. The best 30-50 of the 300-400 F6 genotypes are advanced to a four location yield trial the following season. The resultant best 5-10 genotypes are advanced to regional and national trials.

This simple program, combining repeated strong selection for grain quality and field performance has lead to the rapid development of genotypes of superior quality and yield, as represented by the cultivar Calibre released in 1982. To further speed the procedure a second generation of winter increase is being considered.

HAY YIELD OF OT207 DERIVED SEMIDWARF OATS

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Western Australian Department of Agriculture

The Canadian semidwarf oat OT207 has become an important parent in the high-rainfall breeding programme of Western Australia. Progeny from crosses with this line have proved to have exceptional straw strength and resistance to grain shedding; and to have very high grain yields. Farmers in Western Australia prefer dual purpose oats suitable for grain or hay production, and many had expressed doubts about the suitability of semidwarf oats for hay production.

Trials over two seasons have compared hay yields of semidwarf and tall oat lines from the breeding programme with accepted hay cultivars. The semidwarf lines exhibited a wide range of yield potential, from very low yielding lines to two very high yielding lines which are being considered for registration and release as hay oats. Digestibility and protein content were determined in the trials and the semidwarf oats had hay quality comparable with accepted hay cultivars, some showing very good digestibility.

MOLECULAR CHARACTERIZATION OF OAT SEED GLOBULINS

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The major storage protein in oat seeds is an 11S globulin. This protein accounts for about 70% of the seed protein, while the prolamine, avenin, accounts for only 5%-10% of the total. To better understand the structure of the oat globulin and the mechanisms responsible for the high ratio of globulin to prolamine synthesis, we have isolated and characterized cDNA and genomic clones corresponding to this protein. From the DNA sequence of these clones we have deduced several structural features of the protein that are responsible for its unique physical characteristics. The precursor for the oat globulin contains a signal peptide of 24 amino acids followed by an acidic polypeptide of 293 amino acids and a basic polypeptide of 201 amino acids. Near the C-terminus of the acidic polypeptide are 4 to 5 repeats of a glutamine-rich octapeptide. These octapeptides appear to be located on the surface of the molecule and are responsible for the reduced solubility of the oat protein relative to similar globulins in legume seeds. Comparison with 11S globulins in legumes shows about 30-40% homology; the protein is about 70% homologous with the glutelin protein in rice. The gene encoding the oat globulin contains three introns similar to 11S globulin genes in legumes.

We have used immunocytochemical techniques to localize the globulin in developing oat endosperm. The globulin is deposited in vacuoles that are extensions of rough endoplasmic reticulum (RER) cisternae. Interestingly, the globulin is deposited around aggregates of prolamine protein. Aggregates of the prolamine form directly within the RER and are subsequently transported into the vacuole where they become embedded globulin.

OAT CULTIVAR IDENTIFICATION BY ELECTROPHORESIS OF SEED PROTEINS

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Reliable and fast methods of oat cultivar identification are needed in the seed trade and will become even more important in the future if special purpose cultivars are developed. We extracted 25-mg samples of oat flour or single seeds of United States oat varieties with 25% chloroethanol, separated the extracted proteins on 7.5% acrylamide gels at pH 3.1 and stained with them Coomassie brilliant blue R250. Of 34 cultivars analyzed, 12 had unique electrophoretic patterns and each of the others was included in one of five groups of varieties whose members shared common patterns. Single seeds of several cultivars were extracted and individually analyzed to determine whether biotypes exist within the cultivars. This acidic gel method is more reliable than SDS-PAGE and the extraction technique is simpler than previously used sequential extraction methods. Other techniques, such as electrophoretic analysis of esterase isozymes, have been tested for their abilities to differentiate cultivars whose chloroethanol-soluble protein electrophoregrams are identical.

ABSTRACT - Resistance to biotic stresses

INFLUENCE OF HOST VIRUS CONTENT ON THE ACQUISITION AND TRANSMISSION OF BARLEY YELLOW DWARF VIRUS. A.M.N. Pereira, R.M. Lister, and D.J. Barbara. Dept. Botany and Plant Pathology, Purdue Univ., W. Lafayette, Indiana 47907, USA

In some cases tolerance to barley yellow dwarf virus (BYDV) has been associated with relatively reduced virus productivity. We have examined the possibility that such reduced virus titer could reduce BYDV spread by reducing virus transmission. Cereal plants (oats, wheat and barley) showed wide variations in BYDV content (as assessed by ELISA) among different leaves of the same age on different plants. Selected individual leaves were compared as virus sources for the acquisition and transmission of BYDV isolates (P-PAV, MAV and RPV) by specific (efficient) or non-specific (inefficient) vectors. Overall, there was no convincing evidence that differences in virus acquisition efficiency were correlated with differences in virus content. Of 31 experiments testing various combinations of host, virus, vector, and acquisition feeding time, 23 showed no such correlations and seven showed poor correlations. By contrast, when aphids fed through membranes on purified virus preparations, correlation between virus concentration and virus acquisition was evident for both efficient and inefficient vectors. Also, aphids apparently acquired virus more efficiently by feeding on virus preparations than by feeding on individual leaves containing the same overall virus concentration. The combined results suggest that total BYDV content is not the primary factor affecting virus acquisition from plants by vectors, but that acquisition is probably strongly influenced by other factors, especially uneven distribution of virus within the leaf.

