Achievements and impact of the Collaborative Oat Research Enterprise (CORE)

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ABSTRACT

The Collaborative Oat Research Enterprise (CORE) was initiated in 2009 and ran until approximately 2014. It consisted of a set of coordinated projects, funded investigators, and collaborators who were united by an over-arching goal of developing modern tools for genomics and molecular breeding in oat. Principle outcomes of the CORE included: (1) sets of experimental germplasm, (2) a comprehensive cDNA library and sequence resource, (3) a SNP genotyping array, (4) genotyping-by-sequencing methods, (5) genotype/phenotype data housed in a relational database, (6) a complete consensus linkage map, and (7) a foundational study on population structure, linkage disequilibrium, and adaptation in cultivated oat. Here, we present the results of an impact assessment, which includes a survey sent to 130 scientists in the oat community. Of the 56 survey respondents, 15 were principle CORE investigators, 21 were non-funded collaborators, and 20 were not involved with CORE. A majority (37) of respondents considered that CORE results were essential and/or had been used substantially in oat research, while 29 respondents considered that the results were essential and/or would be used substantially in oat breeding. Respondents also evaluated the impact of each individual CORE outcome on their own research. Most responses ranged between “indirect benefit” to “essential”, with the consensus map showing the highest proportion of “essential” ratings. Nevertheless, there were between two and ten respondents per question who gave responses of “I don’t know” or “no benefit”. An examination of text-based responses to “lessons learned” and “recommendations” suggested that there were a small number of researchers who felt excluded from the CORE project, or who considered that communication could have been improved. These and other lessons may provide guidance to future large multi-institutional research enterprises. We also assessed the impact of CORE through 33 key citations, and through a tabulation of 30 new research projects dependent on CORE results. From this, we conclude that CORE has had a major impact in enabling and encouraging ongoing research, and in building a strong and vibrant oat research community.

Introduction

The Collaborative Oat Research Enterprise (CORE) was the largest coordinated research effort in oat to date. This enterprise brought together more than 30 investigators to develop platforms for oat genomics, germplasm panels, phenotypic evaluations, and association analyses that could be applied globally to ongoing research and improvement of oat. While it is the consensus of most authors that CORE was a resounding success, every large enterprise is destined to encounter problems or to produce unexpected outcomes and lessons, and CORE was no exception. Large projects like CORE should be evaluated upon completion: not only to assess their impact and uptake, but also to publicize and promote further uptake, and to recommend future work. The objectives of this report are, therefore, to (1) provide an overview of the organization and original goals of CORE, (2) describe the tangible outcomes of CORE, (3) evaluate the ongoing impact of these outcomes, (4) describe lessons learned, and (5) recommend ongoing work in basic and applied oat genomics. The authors of this work include direct participants in the CORE project, as well as those who have been indirect collaborators or early adopters of results from the CORE. We are not an exhaustive list of CORE participants, but most of the authors participated in a survey of CORE impact, and co-developed an interpretation of this survey which is reported in this paper.

History, organization, funding, and overall goals of CORE

The CORE began life in 2009 as the “Big Avena SNP Strategy” (BASS): a project led by Eric Jackson and funded by General Mills, Inc. to produce a cDNA sequence resource from which single nucleotide polymorphism (SNP) markers could be discovered and further projects could be developed. It was recognized that this was a ‘seed project’, and it was the intention then to seek additional funding and to build additional objectives with the over-arching goal of creating a world-class platform for genomics and molecular breeding in oat. Prior to CORE, a successful project in diversity array technology (DArT) had established the first high-throughput marker platform in oat (Tinker *et al*. 2009), which was experiencing strong uptake. However, the CORE project sought to improve on this work in the following ways: to develop a SNP-based technology that could be anchored to candidate gene sequences, to increase marker density and develop routine, public genotyping methods, to develop the first high-density consensus linkage map, to develop a standard set of representative germplasm that was extensively genotyped and phenotyped, and to analyze these data to provide QTL inferences for molecular breeding. Research proposals oriented around the above goals were presented to public and private funding partners, who responded enthusiastically by funding a set of projects that were linked through leadership and deliverables into what became the CORE. Although the funding and project ecosystem was considerably more complex than this, the funding packages were approximately structured such that the United States Department of Agriculture and Food Initiative (USDA-AFRI) program funded a deeper cDNA resource from additional germplasm, the development of SNP genotyping arrays, and their application in a worldwide diversity panel, while the North American Millers Association (NAMA) provided funds for assembling and genotyping a large population of breeder’s germplasm, and for phenotyping this germplasm in key environments. Recognizing the need for additional phenotyping in Canadian environments, the Prairie Oat Growers Association (POGA), with matching funds from Agriculture and

Agri-Food Canada (AAFC), provided funding for phenotyping the germplasm in Canadian environments and for assaying key quality traits. An additional set of funds from the Canadian Genomics Research and Development Initiative (GRDI) provided funding to develop and apply a genotyping-by-sequencing (GBS) approach that would achieve a substantially increased marker density beyond that provided by the SNP arrays.

Despite garnering a budget of more than $3 million USD to fund more than 15 research teams, the scope of CORE and the need for globally-representative germplasm and test-sites required the non-funded participation of many additional collaborators. Generally, the invitation to participate in the CORE was open to any researcher who expressed an interest and brought tangible contributions to the table. Although no formal record of CORE membership was kept, an estimated 20 additional collaborating teams were added over the duration of the CORE project. Inevitably, this produced a gradient of CORE engagement from key investigators through to collaborators who weren’t quite sure if they were members. So, while the intention was to be inclusive, the unstructured nature of CORE membership may (in hind-sight) have caused some confusion and un-fulfilled expectations.

With this complex set of inter-linked goals, a diverse set of funding partners, and a large set of investigators and collaborators, the CORE presented challenges in leadership, project-delivery, and expectation-management. Nevertheless, the roles in key CORE deliveries were clearly-defined, and a formidable set of milestones was achieved. For those who may not appreciate the magnitude of these challenges, we mention a few notable activities below.

Key CORE investigators attended a rigorous set of project meetings and workshops (described below) to plan and coordinate the work. The assembly of diverse and representative germplasm panels was accomplished through engagement with breeders and consensus building. The purification and distribution of seeds, the planning and conducting of field tests, the coordination of quality assays, and the collection and curation of data required many people who spent many days of dedicated attention to detail. The discovery and validation of SNPs in the hexaploid oat genome represented new, uncharted territory, but this challenge, too, was overcome by iteratively testing a variety of sequence assembly and SNP selection algorithms, and through the progressive validation of pilot assays.

Brief history of the CORE workshops:

- 2009, March 4-6: Minneapolis MN, USA (kickoff meeting, germplasm selection)
- 2009, Sept. 14-18: Boston MA, USA (first sequencing results, planning SNP discovery)
- 2010, Feb. 2-4: Albany CA, USA (Planning first pilot SNP array)
- 2010, April 18-20: Baton Rouge LA, USA (general CORE meeting at AOWC)
- 2011, April 15-17: Dallas TX, USA (general meeting, visualizing molecular breeding)
- 2012, March 1-3: Kannapolis NC, USA (planning final SNP array and genotyping strategy)
- 2013, March 6-9: Ottawa ON, Canada (Final CORE project meeting, future plans)

Key Outcomes of CORE

Most outcomes of the CORE project have been published, and most data have been deposited in public data repositories. Here we summarize a key set of seven CORE deliverables followed by brief elaborations. These deliverables were presented in the same order to survey recipients (see later).

Outcome 1. Germplasm panels

Defined germplasm panels were a key component of the CORE project, and the distribution and testing of these panels spawned many additional projects. Furthermore, the ability of breeders to grow and observe a diverse set of germplasm from international colleagues resulted in many new breeding opportunities, and likely contributed to a major expansion of oat genetic diversity. Three key diversity panels were assembled, with final numbers (after quality control) presented below. The worldwide diversity panel (also called the "AFRI" panel) contained 109 accessions. This panel, and a smaller subset of 20 lines, was used in SNP validation, with the intention that the resulting SNPs would be applicable in global germplasm. The other two panels contained breeder-nominated lines which represented modern breeding germplasm from North American and Nordic spring oat programs (433 lines) and a mixture of germplasm from southern USA and UK winter oat breeding programs (140 lines). Further to this, the CORE project utilized and genotyped 12 bi-parental mapping populations contributed by collaborators.

Outcome 2. The cDNA sequence resource

The cDNA libraries and resulting sequence resource contained an estimated representation of more than 30,000 expressed gene sequences from oat. These libraries were made from pools of RNA from four different tissues (leaf, root, inflorescence, and immature seed) from twenty diverse oat lines (Oliver *et al*. 2011b; Oliver *et al*. 2013). The cDNA sequence resource was used to discover SNPs in the later parts of the project, but has also been used for other purposes, including gene discovery and further marker development. While the original intention was to publish an annotated analysis of the cDNA resource, the potential impact of such a publication has fallen. Future plans may include depositing this resource in a public database, but, currently, the resource is distributed by request for use in any non-commercial application.

Outcome 3. Illumina SNP array

The discovery of true SNPs that behave as diploid genetic markers was a special challenge in hexaploid oat, and no recipe for success existed prior to the CORE project. Thus, plans were made for a series of pilot SNP arrays to test and evaluate procedures for SNP identification. The first successful efforts at SNP validation by the CORE project represented a major achievement that provided guidance for SNP discovery in other polyploids (Oliver *et al*. 2011b). Following this, the first pilot SNP array, containing 1536 potential SNPs, was used to develop the first version of the CORE consensus map (Oliver *et al*. 2013). Two more pilot arrays were produced and tested, and the resulting work allowed the development of a final, publicly available 6K SNP array, described by Tinker *et al*. (2014). This publication included extensive annotation of the cDNA sequences from which the SNP assays were developed.

Outcome 4. Genotyping by sequencing (GBS) methods

When the CORE project was planned, the intention was to build upon the DArT technique to develop a sequence-based assay. At the time, other GBS methods were not widely known. After the publication of a successful 2-enzyme GBS system in wheat (Poland *et al.* 2012), the decision was made to collaborate with Jesse Poland in the application of similar GBS methods to oat. The assay proved to be highly successful in oat, although we encountered challenges because bioinformatics pipelines were not yet mature. Our resulting GBS foundation study in oat (Huang *et al.* 2014) was based on a subset of CORE mapping populations and a set 300 diversity lines that included the CORE world diversity panel. This work focused on testing and combining two different bioinformatics pipelines, and on thoroughly evaluating the resulting SNPs. Later, we developed a novel GBS pipeline which has been used in ongoing work in oat (Tinker *et al.* 2016).

Outcome 5. Primary genotype/phenotype data

The SNP and GBS genotyping methods have been applied to all three CORE diversity panels as well as to 12 mapping populations. In addition, the diversity panels have been grown and evaluated in 35 trials for up to 40 different traits. These data have been extensively curated, and represent the foundation on which remaining CORE deliverables are built. Since only a fraction of the primary data has been mined by the CORE project, the publication of this primary data will encourage further outcomes in the oat community beyond the formal CORE publications. Thus, a follow-up to the CORE project has involved the identification of a public database system, and the staffing of a dedicated oat curator to manage data from CORE and from other public oat projects. All key genotype and phenotype data from CORE can now be found in the T3/oat database, and we recommend starting on the following page, where these data are summarized: https://triticeaetoolbox.org/oat/toronto.php. Furthermore, we direct the interested reader to a series of Oat Newsletter reports by Saied *et al.* (http://oatnews.org/node/505) which provide information and tutorials on the T3/oat database. We also note that further CORE publications are in preparation or under review, so users of the CORE data should not publish integrative results from these data without consulting those identified in the data statement in the T3/oat link above.

Outcome 6. Oat consensus linkage maps

The first consensus linkage map developed by the CORE project was based on six mapping populations genotyped using the first pilot SNP array (Oliver *et al.* 2013). Importantly, this work pioneered a system of assigning linkage groups to physical chromosomes using monosomic hybrid analysis. With the publication of the final SNP array (Tinker *et al.* 2014) and genotyping by sequencing methods (Huang *et al.* 2014), and with an additional six populations available for map integration, a refined consensus linkage map was developed (Chaffin *et al.* 2016). This map integrated more than 7000 additional markers into a common framework of 21 chromosomes, and resolved several issues with chromosome assignment.

Outcome 7. Foundation study on linkage disequilibrium, population structure, and flowering time

The genotyped and phenotyped CORE diversity populations provide many opportunities for QTL discovery through association mapping, and for integration of useful alleles into other germplasm. However, a key pre-requisite for association mapping is the existence of systematic pattern of linkage disequilibrium (LD) that can be statistically separated from other causes of marker-trait association, which may result from population structure. The CORE foundation study by Esvelt Klos *et al.* (2016) was intended to evaluate LD and population structure in oat, to test association analysis using a model trait (flowering time) related to adaptation, and to provide recommendations for association analysis of other traits in the CORE populations.

The impact of CORE based on an anonymous online survey

Survey methods

Potential survey participants were identified from recent mailing lists in the oat community including those from the International Oat Conference, the American Oat Workers, and the Oat Newsletter. A subset of 130 invited participants were then selected based on the following criteria. Most participants were selected because they worked in a field related to genetics or breeding, but some participants from other fields were added because they had a broad knowledge of the oat community. We invited only one participant per research team, favoring those who had principle-investigator status, except when a team member had strong or unique engagement with the oat community. The list included all principle investigators who were directly affiliated with the CORE project. Several research managers and representatives from private companies with significant internal research programs were also included. A list of invited participants is available by request. All potential participants were sent an anonymous online survey which was developed in Google Docs. Although the survey closed on Nov. 18, 2016, the survey has been re-opened indefinitely in case readers which to examine it and/or contribute additional responses after reading this paper: https://docs.google.com/a/elfinwood.com/forms/d/e/1FAIpQLSeTFlmiQWWulPiFVDW58lUeKSpUCM2ZJhKx2qAD2XaJGN7hdQ/viewform?c=0&w=1

The first survey question asked respondents to identify the meaning of the CORE acronym. Since the acronym was not defined in the survey, it was intended to eliminate robots or internet trolls who may have stumbled on the survey without reading the email invitation. Since the email invitation contained other instructions, as well as a preliminary draft of this manuscript to provide context, participants were asked to verify that they had read this email. Participants were then asked to identify their association with CORE, and to describe their area of work using drop-down selections. Then they were presented with a list of the seven CORE outcomes. They were asked to rank each outcome, as well as the overall CORE project, based on its impact on their own work. Answers were selected from drop-down menus that required one-and-only-one of the following selections per outcome:

1. - No benefit to my work
2. - Benefits my work indirectly
3. - I intend to use these results
4. - I have used these results
5. - Essential to my work
6. - I don't know

Next, participants were also asked to rank overall CORE outcomes based on their perceived impact on the global oat research community and on oat breeding, with similar pre-defined responses. Finally, participants were given an opportunity to provide free-form comments on the following questions: (1) please list any problems, concerns, criticisms, or lessons-learned that you would like to highlight, in relation to the CORE project, (2) please list any recommendations for further research to build on CORE results, and (3) please list any other comments you may have.

While the above online survey results were collected anonymously, all participants who took the survey were asked to send a separate email to two neutral survey observers (Tyler Tiede and Sam Snyder; authors on this paper) who were appointed by industry stakeholders at PepsiCo Global Research and Grain Millers, Inc., respectively. These emails were not linked to individual survey responses, but served to identify participants who took the survey, and to provide an additional opportunity to send specific indicators of impact, including publications and new research projects.

Profile of survey respondents

A total of 56 participants completed the anonymous online survey between the dates of November 8 and November 18, 2016. This number includes responses from two participants from China that were entered manually, because ‘Google Forms’ were blocked in their country. It does not include one response that was deleted because the respondent failed to identify the meaning of the CORE acronym and provided exclusively “I don’t know” answers. All of the remaining 56 respondents identified their participation by a separate email to the survey observers.

Of the 56 valid respondents, 36 (64%) identified themselves as either CORE investigators or CORE collaborators, while only one respondent had not previously heard of the CORE project (Figure 1A). This suggests that researchers who were part of, or aware of, the CORE project were more willing to respond to the survey than others. However, it may also reflect a broad awareness of CORE in the oat community, and the fact that those who were not aware of CORE were also not known to those who ran this survey. The survey respondents were also biased toward oat breeders and researchers in fields related to genomics (Figure 1B). This bias was intentional, as reflected in the invitations that were sent.

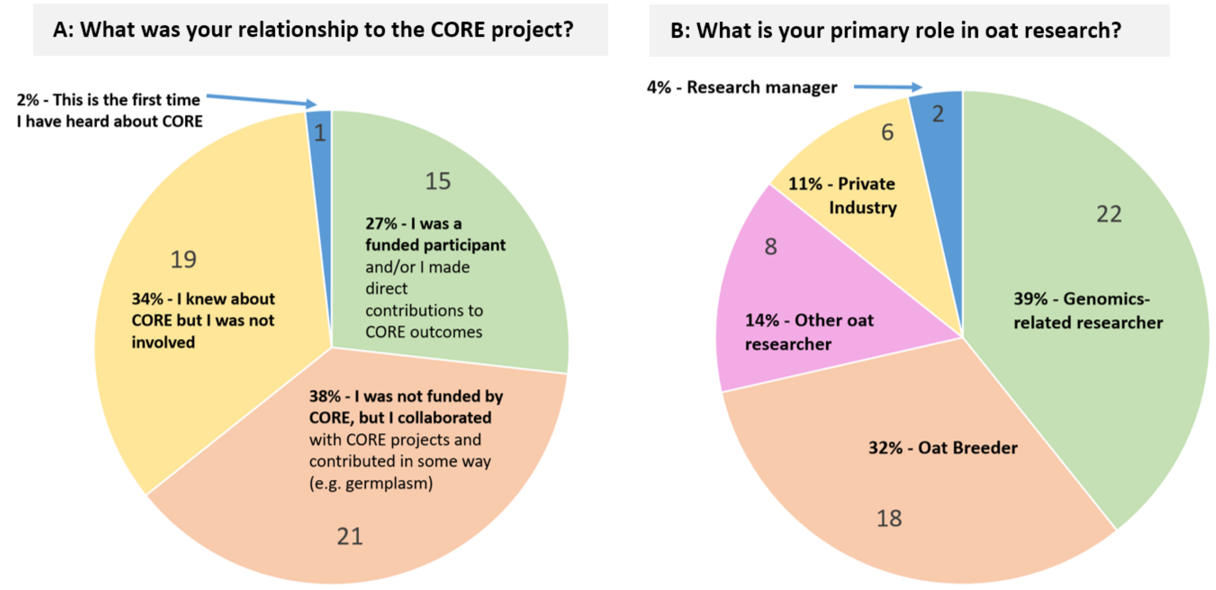
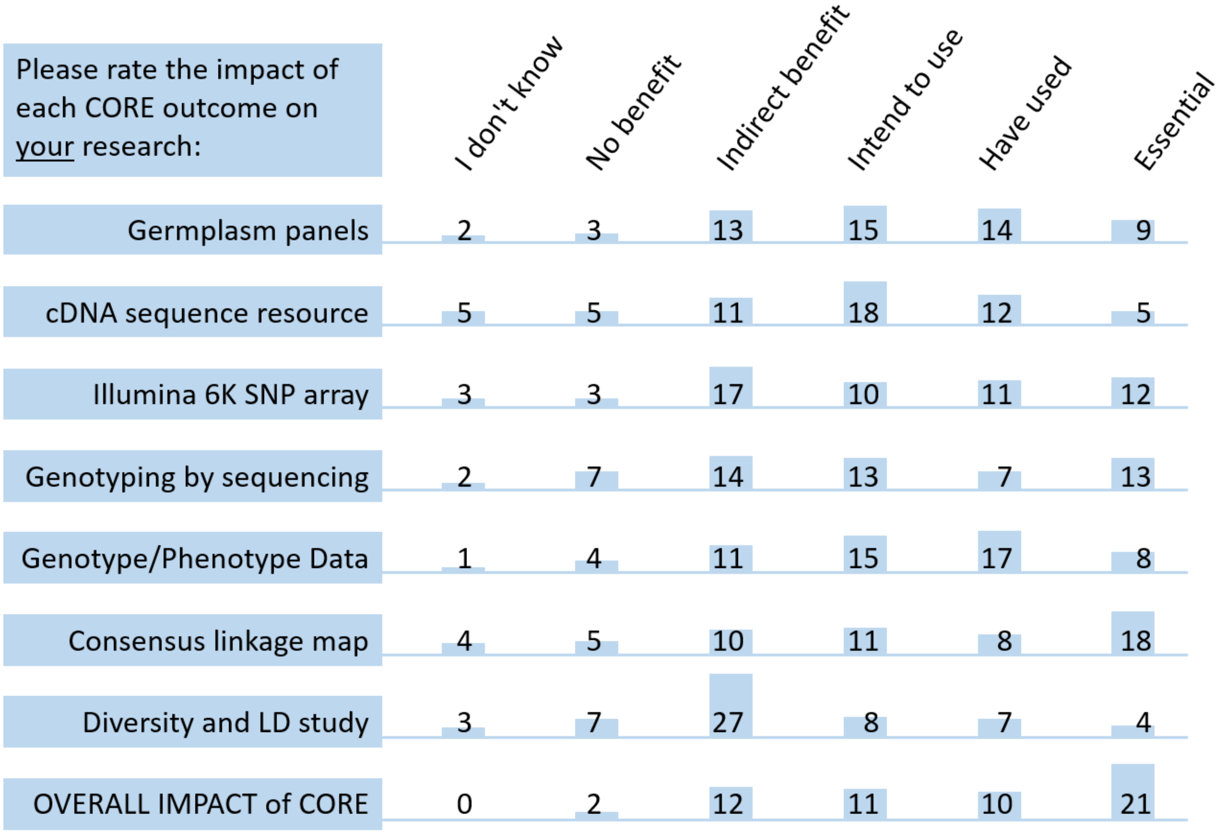


Figure 1. Distribution of 56 survey respondents based on their relation to the CORE project and their primary role in oat research. Questions are indicated at the top of panels A and B. Valid answers are shown in each pie slice, together with the number and percentage of respondents selecting each answer.

Impact of CORE outcomes on individual researchers

Of the 56 respondents, more than 46 (82%) consistently ranked the impact of all outcomes on their own work as either “indirect benefit”, “intend to use”, “have used”, or “essential”, with an average of 49 (88%) making these selections when averaged across questions (Figure 2). To examine the bias caused by respondents who collaborated with CORE, we produced a parallel analysis based only on the 20 respondents who identified as not being part of CORE (Supplementary table 1). While this subset of respondents showed some different trends, there was still an average of 17 (84%) of these respondents who identified impact as “indirect benefit” or higher when averaged across questions. Looking only at the overall impact of CORE, 21 of 56 (38%) of all respondents considered it essential, while 6 of 20 (30%) of non-CORE researchers considered it essential. In both the full analysis (Figure 2) as well as the subset (Supplementary table 1), the individual outcome with the highest number of “essential” ratings was the consensus linkage map. This may reflect the fact that the first consensus map represented one of the earliest CORE publications (Oliver *et al*. 2013), but it may also reflect the importance of the map in supporting a wide variety of different research needs. Supplementary tables 2 and 3 provide the breakdown of responses from 18 breeders and 22 genomics researchers, respectively. These breakdowns clearly show that more of the outcomes were essential to genomics researchers than to oat breeders, while the latter group perceived more of a delayed or indirect benefit.



Please rate the impact of each CORE outcome on <u>your</u> research:	I don't know	No benefit	Indirect benefit	Intend to use	Have used	Essential
Germplasm panels	2	3	13	15	14	9
cDNA sequence resource	5	5	11	18	12	5
Illumina 6K SNP array	3	3	17	10	11	12
Genotyping by sequencing	2	7	14	13	7	13
Genotype/Phenotype Data	1	4	11	15	17	8
Consensus linkage map	4	5	10	11	8	18
Diversity and LD study	3	7	27	8	7	4
OVERALL IMPACT of CORE	0	2	12	11	10	21

Figure 2. Distribution of 56 survey respondents based on their ratings (from I don't know to essential, shown on top) related to seven specific outcomes and one overall outcome (shown on left). Numbers and bar sizes indicate the number times a given rating was selected for the outcome to the left.

Perceived overall impact of CORE on research and breeding

In parallel with the above analysis, we examined responses to two questions designed to rate overall impact on either global oat research or global oat breeding, as perceived by each respondent (Figure 3). These responses reflected a substantially higher perceived overall impact than the average impact on survey respondents. For example, 27 (48%) of respondents perceived that CORE was essential for global oat research while 21 (38%) considered it was essential for their own research. While this may seem contradictory, this reflects the fact that a person can perceive something as essential even if they know it will not be used by everyone. In Figure 3, it is also apparent that most respondents consider that CORE has a higher direct impact on oat research in general than it does on oat breeding, even though the wording of the responses were adjusted (*e.g.*, has been used *vs*. will be used) to account for the reality that many breeding applications are still in the future. Nevertheless, only four respondents to each question selected the “don’t know” or “little benefit” categories. Based on some comments (discussed below), we suspect that a small number of these respondents could have been voicing an unhappiness regarding their experience with CORE, possibly related to inclusiveness or communications.

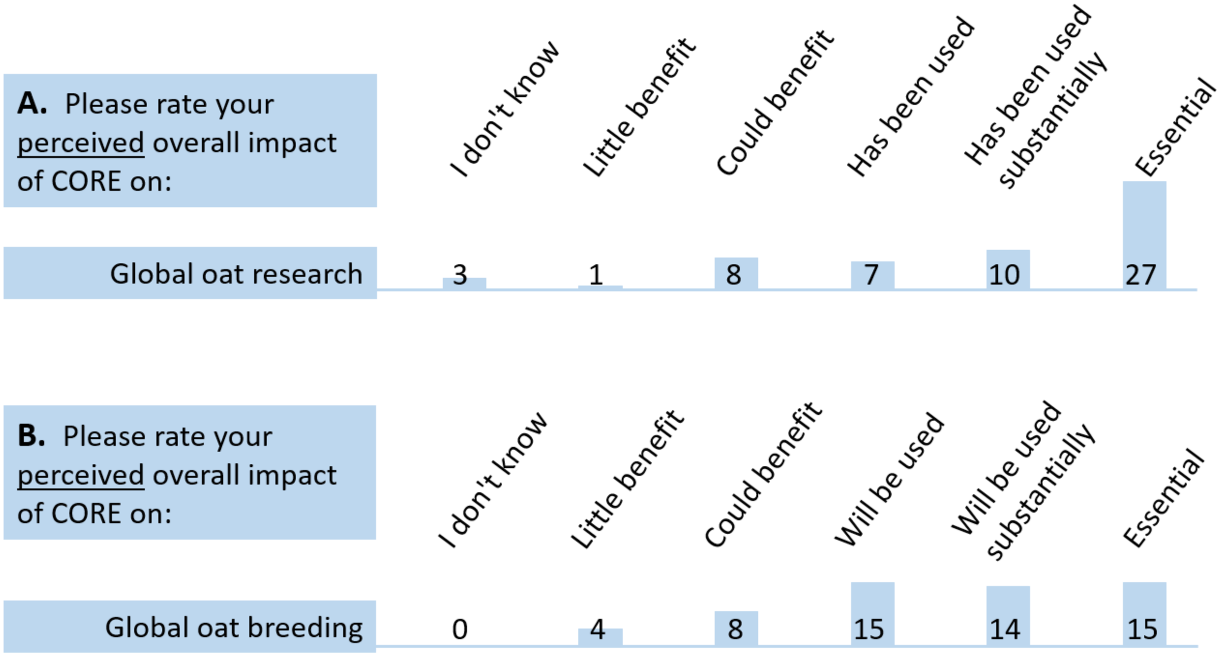


Figure 3. Distribution of 56 survey respondents based on their ratings (from I don't know to essential, shown on top) of their perceived impact of the overall CORE project on global oat research (panel A) or oat breeding (panel B). Numbers and bar sizes indicate the number times a given rating was selected.

Impact of CORE on new publications

Survey respondents were given the opportunity to list any papers that they had written or contributed to that were directly dependent on results from the CORE project. This list of publications was supplemented by research using Google Scholar. We then excluded citations that did not relate to oat research, review articles, and citations where related CORE outcomes were not used in either the methods or some critical element of interpretation (*e.g.*, comparative mapping). For example, there were many papers citing work by Oliver *et al.* (2011b) and Huang *et al.* (2014), but most citations related to work in other species where these references were part of a review or interpretation of literature. Conference presentations, posters, and newsletter articles were also excluded. While these are important impacts, their analysis goes beyond the scope of this paper. A summary of the remaining 33 key papers that have used CORE results in the development of oat research is presented in Table 1. Manuscripts at the bottom of the table were identified by respondents as being in mature stages of preparation or publication. Given that many parts of the CORE project were only published in the last year, we feel that this list represents a substantial uptake of CORE outcomes in the literature, which will expand rapidly in the next few years.

Table 1. List of publications describing the development of oat research with critical dependence on CORE outcomes. Since CORE outcomes are also interdependent, CORE papers are listed at the top of the table and indicated by an asterisk.

Publication	Description	CORE outcomes	CORE Citations
*Oliver *et al.* (2011b)	CORE SNP discovery paper (first)	cDNA, Germplasm	(predates other CORE publications)
*Oliver *et al.* (2013)	CORE consensus map (first)	SNP, Germplasm	Oliver *et al.* (2011b)
*Huang *et al.* (2014)	CORE GBS analysis	Germplasm	Oliver *et al.* (2013)
*Tinker *et al.* (2014)	CORE 6K SNP assay	cDNA, SNP, Germplasm	Oliver *et al.* (2011b) Oliver *et al.* (2013)
*Chaffin *et al.* (2016)	CORE consensus map (new)	SNP, GBS, Germplasm	Oliver *et al.* (2013) Tinker *et al.* (2014) Huang *et al.* (2014)
*(Esvelt Klos *et al.* 2016)	CORE population structure and LD	SNP, GBS, Germplasm, Data	Oliver *et al.* (2013) Tinker *et al.* (2014) Huang *et al.* (2014) Chaffin *et al.* (2016)
Oliver *et al.* (2011a)	Mapping in tetraploid *Avena*	Map, SNP	Oliver *et al.* (2011b)
Gnanesh *et al.* (2013)	Crown rust resistance gene *Pc91*	Map	Oliver *et al.* (2013)
Gutierrez-Gonzalez *et al.* (2013)	The hexaploid oat seed transcriptome	cDNA, Map, SNP	Oliver *et al.* (2011b) Oliver *et al.* (2013)
He *et al.* (2013)	QTL affecting *Fusarium* resistance in oat	Map	Oliver *et al.* (2013)
Babiker *et al.* (2014)	Mapping oat rust resistance	Map, SNP	Oliver *et al.* (2011b) Oliver *et al.* (2013)
Herrmann *et al.* (2014)	QTL for quality and agronomic traits	Map	Oliver *et al.* (2013)
Hsam *et al.* (2014)	Resistance to powdery mildew in oat	Map	Oliver *et al.* (2013)
Lin *et al.* (2014)	Adult resistance to crown rust in oat	Map, SNP, GBS	Oliver *et al.* (2013) Tinker *et al.* (2014) Huang *et al.* (2014)
Gnanesh *et al.* (2015)	Seedling crown rust resistance gene in oat	Map, SNP, GBS	Oliver *et al.* (2013) Tinker *et al.* (2014) Huang *et al.* (2014)

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Montilla-Bascón *et al.* (2015)	Rust and mildew resistance in oat	Map	Oliver *et al.* (2013)
Schneider *et al.* (2015)	Aluminum tolerance in hexaploid oat	Map, SNP	Oliver *et al.* (2013) Tinker *et al.* (2014)
Fominaya *et al.* (2016)	Genome analysis in *Avena*	Map	Chaffin *et al.* (2016)
Foresman *et al.* (2016)	Mapping barley yellow dwarf resistance	Map, SNP, GBS	Oliver *et al.* (2011b) Oliver *et al.* (2013) Huang *et al.* (2014) Tinker *et al.* (2014)
Gutierrez-Gonzalez and Garvin (2016)	Vitamin E biosynthesis genes in oat	Map	Oliver *et al.* (2013)
Loarce *et al.* (2016)	Genes expressed for partial rust resistance	Map	Oliver *et al.* (2013)
Pellizzaro *et al.* (2016)	Markers linked to multiflorous trait	Map, SNP	Oliver *et al.* (2013) Tinker *et al.* (2014)
Tinker *et al.* (2016)	Haplotag GBS software	GBS	Huang *et al.* (2014)
Tumino *et al.* (2016)	Mapping frost tolerance in oat	Map, SNP	Tinker *et al.* (2014) Chaffin *et al.* (2016)
Winkler *et al.* (2016)	Genetic diversity of oat landraces	Map, SNP	Tinker *et al.* (2014) Chaffin *et al.* (2016)
Yan *et al.* (2016)	Analysis of *Avena* wild relatives	Map, GBS	Huang *et al.* (2014) Chaffin *et al.* (2016)
Esvelt Klos *et al.* (under review)	Association mapping of oat rust resistance	SNP, GBS, Map, Germplasm, Data	Oliver *et al.* (2013) Tinker *et al.* (2014) Huang *et al.* (2014) Chaffin *et al.* (2016)
Bjørnstad *et al.* (under review)	Genetic variation and associations involving Fusarium head blight and deoxynivalenol accumulation in cultivated oat (*Avena sativa* L.)	SNP, GBS, Map, Germplasm, Data	Oliver *et al.* (2013) Tinker *et al.* (2014) Huang *et al.* (2014) Chaffin *et al.* (2016)
Howarth *et al.* (in preparation)	Association mapping of mildew resistance in oats	Map, SNP, GBS, germplasm data	Oliver *et al.* (2013) Tinker *et al.* (2014) Huang *et al.* (2014) Chaffin *et al.* (2016)

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Publication	Description	CORE outcomes	CORE Citations
Wise *et al.* (in review)	Tissue distribution of avenanthramides in oat	Map	Chaffin *et al.* (2016)
Ceplitis *et al.* (in preparation)	Two manuscripts, topics not disclosed	Map, SNP	Tinker *et al.* (2014) Huang *et al.* (2014) Chaffin *et al.* (2016)
Dumlupinar (in preparation)	Genotyping oat landraces from Turkey	Map, SNP	Tinker *et al.* (2014) Huang *et al.* (2014) Chaffin *et al.* (2016)
Peng *et al.* (in submission)	Markers linked to dwarfing gene	Map, SNP, GBS	Tinker *et al.* (2014) Huang *et al.* (2014) Chaffin *et al.* (2016)

Impact of CORE on new research initiatives

Survey respondents were given an opportunity to indicate whether they had applied for or received funding for any new research initiatives linked to results from the CORE project. Respondents identified a total of 30 such projects (Table 2). While some respondents identified the amount and duration of funding, this information was not consistently provided and is, therefore, not included. Since there was no way for us to access information about projects beyond those represented in the survey, and because fewer than half of the survey respondents answered this additional question, we consider this list of projects to be very incomplete. Nevertheless, the number and diversity of new projects that bear some dependence on CORE is remarkable and inspiring. It is impossible to say how many projects would exist without the work of CORE, but it is unlikely that any of them could have depended on a pre-existing oat consensus map, a SNP array, or any of the other CORE outcomes. Furthermore, we consider that the impact of CORE on new work in the oat community goes beyond these tangible outcomes. Many of the research teams who are conducting new research were brought together into trusting collaborative relationships through their associations with the CORE project. The scope and ambitious magnitude of CORE probably inspired new teams to think beyond the current limitations of oat genomics. And finally, CORE and its results have given confidence to talented new oat researchers that their ambitions won't be limited by the lack of a modern genomics platform in oat.

Table 2. List of 27 research projects (funded or pending) that were identified by survey respondents as being dependent on or influenced by outcomes from CORE. Most surnames can be found in the list of authors and do not necessarily represent the project leads.

Surname	Description	Status
Azar	Marker application in private industry	Funded
Caffe-Treml	Accelerating genetic improvement for oat milling and nutritional quality	Funded
Ceplitis	Renewal of oat breeding program	Funded
Dumlupinar	Association mapping in oat landraces	Funded
Fu	Characterization of wild oat germplasm	Funded
Howarth	Generation of oat varieties with enhanced resistance to crown rust and mildew	Completed
Howarth	Analysis of the genetic and environmental factors influencing grain quality in oats	Funded
Howarth	Identification of *Fusarium* resistance within UK oat breeding lines	Funded
Huang	Genetic architecture of forage traits	Pending
Jannink/Sorrells	Industry collaboration in molecular breeding	Funded
Jannink	Transcriptomics of oat seed composition	Pending
Jellen	NSF project to sequence hexaploid oat	Funded
Langdon	Tools and resources for oat breeding	Funded
Langdon	Enhanced breeding of oats for human health and nutrition	Funded
Langdon	BBSRC Partnering award, and BBSRC Sparking Impact workshop in Brussels	Funded
Langdon	Oat adaptation based on exome analysis	Pending
Mitchell Fetch	Molecular breeding and genomic selection	Pending
Paczos Grzeda	Linkage and association mapping of oat	Funded
Paczos Grzeda	Molecular profiling of polish cultivars and breeding lines	Completed
Peng	The origin of naked oat	Funded
Peng	Phylogeny of the hexaploid *Avena* species	Funded
Peng	GWAS of some important characters in *Avena*	Funded
Prats	Resistance to biotic and abiotic stress	Funded
Singh	Transposon-Mediated Activation Tagging in oat	Funded
Tinker	Accessing Adaptive Ancestral *Avena* Alleles	Funded
Tinker	Next generation genomics for oat improvement	Completed
Tinker	Oat improvement in the Canadian Field Crops Research Alliance	Funded

Table 2. List of 27 research projects (funded or pending) that were identified by survey respondents as being dependent on or influenced by outcomes from CORE. Most surnames can be found in the list of authors and do not necessarily represent the project leads.

Surname	Description	Status
Vogelgsang	Investigating the potential of Swiss grown oats for human consumption	Pending
Zwer	Sodicity tolerant oat varieties	Funded
Zwer	Root lesion, root knot, and stem nematodes resistance in oat	Funded

Lessons learned, recommendations, and other comments

In a final set of three optional questions, survey respondents were invited to identify any problems or lessons learned in relation to the CORE project, to suggest ongoing work, or to provide any additional comments as they wished. Table 3 shows a complete summary of responses received for each of these three questions. A generalized interpretation of these comments was made by grouping these comments under the heading “interpretation”. Under the “lessons learned” question, 30 comments were received, eight of which were of the “most things were OK” nature (classified as “general/positive”). Although the comments were diverse, thirteen of the “lessons” comments were interpreted as a plea for better communications. Individual comments suggested that communication is important both within the project and within the broader oat community. Some of these comments referenced problems encountered by CORE that may have been related to communication, including a perception that CORE was a “members only club”, and some delays in project delivery that may have been caused by changes or uncertainty in leadership. A final set of nine comments from this question were interpreted as “ongoing work is needed”. These included comments suggesting that the momentum of CORE had slowed, or that more effort was required to generate uptake and utilization of results.

Under the “ongoing recommendations” question, 33 comments were received. Seven of these comments gave recommendations related to data management, integration, and analysis. These included improving and ensuring continuity of database tools such as T3/Oat and GrainGenes, or mining such databases to integrate data, to find more SNPS, or to learn more about GxE interactions. Seven comments related to engaging breeders and industry stakeholders to find practical applications and capture downstream value from the CORE results. Five comments gave recommendations for increased attention to phenotypes, either to address specific traits or to develop a deeper picture of GxE interactions. Six comments gave recommendations for further development of technologies, including genome sequencing, exome capture, and mutant populations. Two comments related to improving or reducing the cost of genotyping methods to facilitate uptake in breeding programs. Two comments specifically addressed the need for improved communication. One comment specifically addressed the need to attract new researchers to oat by ensuring an up-to-date genomics platform that is competitive with wheat, corn, and barley. The three remaining comments under this question were general and/or encouraging.

Under the “other comments” question, only 16 additional comments were received. Twelve of these were classified as “general/positive” comments of an encouraging nature, while four gave additional recommendations for ongoing work, including genome sequencing, applications in breeding, and database development.

Discussion and conclusions

CORE had a timely vision, concrete goals, capable investigators, strong industry support, and generous funding. Generally, the survey responses, new projects, and manuscript citations reported in this paper have validated that the CORE outcomes have had the intended high impact on oat research and breeding. Not only did CORE provide necessary tools, but it also increased the momentum and connectivity of the oat community, and brought a stronger and more direct dialog between industry, breeders, and the public oat research community. However, it is unlikely that any enterprise on the scale of CORE could operate without setbacks, or without producing lessons and recommendations. CORE attempted to be inclusive, but universal inclusion was not feasible, accidental exclusion probably happened, and limits to inclusiveness may not have been transparent. These factors may have compounded the perception of isolation by anyone who was not included in the CORE. Today, a large project such as CORE can take advantage of new communication tools in the oat community, including the revitalized Oat Newsletter (oatnews.org) and Oat Global (oatglobal.org), both of which promise to provide a stronger virtual network among oat workers and to bridge the time between major oat conferences. Major new initiatives such as the Oat Rust Initiative should communicate frequently through these venues, and should clarify ways in which new members could contribute. We note that the T3/Oat project has published frequent updates in the Oat Newsletter (Saied *et al.* 2016: http://oatnews.org/node/505) and we encourage other projects to do the same. Many other lessons and recommendations from the CORE project relate to communication as well. The need for internal communications within a project cannot be satisfied by an increased frequency of email. Today, there are excellent project management tools, methods to survey participants, and a better awareness of the need for project accountability and contingency plans.

Among the recommendations for new research directions that should follow CORE, the largest category of survey responses related to information management and integration. The development of T3/Oat by the T3 project team (Blake *et al.* 2016) and staffing of an oat curator at Cornell University was an initial response to that need, but this survey may reflect a need for stronger emphasis and continuity in this area. The second largest category of recommendations was related to the need to engage stakeholders and breeders in finding practical applications. We agree that this should be an ongoing focus of the community and of any new oat projects. The third category of recommendations related to phenotyping. Although CORE invested heavily in phenotyping, we agree on the importance of this area, especially in regard to developing tools for molecular breeding, and we recommend that future projects should place greater emphasis on planning and standardization of phenotypic data. Many other recommendations, including further sequencing and genomics, already have substantial traction in the community, as reflected in the list of new projects in Table 2.

In conclusion, we hope that this paper will serve multiple needs in the oat community: that it will draw attention to the work that was done and to new resources that are available, that it will provide information to stakeholders on the value of the research that they funded, that it will provide information and direction regarding new opportunities, and, finally, that it will provide lessons and recommendations to guide new research enterprises.

Table 3. Complete list of text-based comments received for three optional survey questions. Responses have been categorized and grouped by interpretive criteria shown in the second column.

Question*	Interpretation	Comment from survey respondent
Lessons learned	General / positive	The importance of open sharing in oat research was decisive.
		Oat researchers can use the CORE results more convenient.
		The CORE project was accomplished through a great team work. There were some technical issues during OPA development, but they were ironed out eventually. The SNP marker source contributed to the success of many of the downstream applications.
		My impression is that the project promised to much to the oat industry funders based on conversations that I have had. I think the progress from CORE was impressive. The advances in markers alone were substantial and made genetic analysis of traits in oat possible. Based on this improvement alone, I would say the project was a success.
		No criticism
		Uniform acceptance and cooperation
		at the beginning there was a communication problem but Nick Tinker was able to solved it
		hard to know how to avoid some personal/personality conflicts that arose, but I think the project was a huge success
	Need increased communication etc.	A more formalized (and funded) system of communications, with in-person meetings, would have benefitted this work and improved the timeliness of results.
		I do not have enough familiarity with the project and its impact in the research / breeding community to comment in any detail here. One concern would be a general one, that sequence data and gene characterization could be deployed later on to place IP restrictions on germplasm as they have in other crop species. The free exchange of material for research and

		breeding is a great benefit of working with oats.
		I just know a little about the CORE project, so I could not give any comment now.
		It would be beneficial and valuable if CORE present their achievements and plans on the platform available to interested researchers and breeders.
		I am not directly engaged in breeding or research but if we are to develop the genetic potential of oats it is critical that there is collaboration and partnerships in strategic research and importantly there is regular and open communication of research
		Need to have data sheets for phenotyping in a common format and more communication re phenotyping in particular. Importance of quality control for both phenotyping and genotyping data as well as seed production. Project funding ended before data analysis
		Seems to be very much a 'Members Only' club.
		First heard specifics of CORE at IOC in Beijing 2012
		Lack of communication with stakeholders on the applied side.
		Need to ensure full democratization and utilization
		Industry should be informed more regularly of the work being done
		Relationship management and stakeholders engagement could have been more effective.
		CORE was impeccably managed at first, but some deliverables and the publication plan suffered in timeliness because there was not a clear contingency plan when Don Obert and Eric Jackson left their USDA positions.
	Ongoing work is needed	On-going support to further the genomic research to the next level
		For a broader usage of marker in applied breeding programmes costs for genotyping need to be reduced
		CORE has adapted state of the art molecular breeding technologies to oats. But global problems of oat breeding are not related to the short term introduction of such technologies due to underfinancing of the oat breeding sector at all. CORE will contribute to understanding the genetic basics of the oat crop only.
		Provided the oat research community with a huge amount of phenotypic and genotypic information and helped get oat molecular marker information closer to other crop species. There was a lot of momentum during the project, but it seems to have slowed down since then.

		inadequate investment in oat research, particularly in oat genomics, is obvious. This would be more critical, given the cultivated oat is polyploidy and has a large genome, explaining the lack of big progress in oat genomic research. The current CORE project has some achievement, but many technical issues may have hindered the development of many molecular tools that could be applied to oat breeding, among which issues are polyploid and gene and chromosomal duplication. For example, we may not know for certain which oat chromosomes are and their origins, left the rest with the identification of genes of agro importance. One major critique is that the CORE effort over the several years seemed to be not well thought, behaving like trying this tool first to see what we can do next, without a clear understanding of their limits and advantages.
		I'd like to see more research efforts concerning the correlation genotype versus phenotype.
		I believe there are results that will be utilized in oat research, and in my breeding program....but I need to find real-world applications that can possibly enhance or substitute for currently-utilized breeding tools.
		CORE project provides essential information for activities such as genomic selection, but employing the information in a practical breeding program in a manner that will improve breeding efficiency is still challenging.
		Not enough oat workers! Particularly in USA
Ongoing recommendations	Data management / integration / analysis	Integrate markers and maps with genomic data
		[...split...] ongoing funding for T3 database and/or sustainable integration into Graingenes
		Continued identification of useful markers, especially those for multigene traits, or for those that are highly affected by environment. Also research/training in ways to develop high through-put systems. Development of ways to handle the huge data sets.
		Suggest compile a list of papers arising from this work
		[...split...] Essential to keep maintaining and updating T3-oat database and keeping all data open access. Updated consensus map.
		Additional SNP discovery to bring the number of mapped variants to a level comparable with other cereals. Validation and effect estimation of QTL identified in CORE mapping efforts. Integration of the consensus linkage map, physical map and genome sequence
		More detail about the context of experiments in which

		phenotypic data were collected could help users to interpret the data (e.g. for a given trial, what were the weather conditions and field management like) and use it with better precision.
	Engage stakeholders / practical solutions	Future research based on the outcomes of CORE should be much more directed to the solution of more practically important problems of oat breeding.
		Need to include oat breeders.
		[...split...] All research must deliver impact not just in a scientific field but to a wider society
		Private breeding material should be included, from all breeding programs
		Breeding programs could engage as critical/peer partners to enable easier/faster impact in breeding globally.
		Look for direct applications within global oat breeding efforts and commercialization
		[...split...] Increased involvement of stakeholders (growers, collection centres, millers, marketing etc.)
	Phenotyping / traits	Research on the correlation between genotype and phenotype plus the interaction with environment is needed. [...split...]
		Fund post docs to get more phenotype info and for genotyping in Canadian labs
		[...split...] Continued world-wide collaboration and multi environment trials- The environment affects many traits as much as genotype. Development of common genotyping platforms and resources available world-wide.
		[...split...] More research could be focused on traits of agronomic importance to oat breeding in elite breeding lines using advanced genomic approaches such as exome capture and RNA-seq profiling. Extension to characterize oat germplasm in genebanks would also be fruitful.
		Continue to fund genetic research with emphasis on traits that are of top priority: beta-glucan content, rust resistance, lodging resistance, etc.
	Sequencing and genomics	New higher-density SNP array, genome sequencing, re-sequencing [...split...]
		The hexaploid oat reference sequence will be available soon, the consensus map may be updated and marker information may be expanded by developing oat POPSEQ integrating ESTs, oat SNPs and GBS marker data.
		Mutant populations
		Exome advanced analysis.
		Develop a complete genome sequence (diploid, tetraploid

		and hexaploid)
		[…split…] Given the current investment level, the research should focus on specific workable and achievable projects with well-thought experimental designs to develop some basic genomic tools.
	Genotyping / molecular breeding	Utilize the data in genomic selection
		Cost reductions for genotyping could promote usage of mas in breeding. Further alternative services to DArT sequencing could be helpful to reduce costs.
	Better communication	Higher level of collaborative communication.
		Meetings of the CORE group is essential to keep all informed of progress and potential use of the research information.
	Engage new researchers	We must attract new researchers and scientists to oats on the basis of prospecting the as yet untapped genetic potential. We compete with with corn, soy, cotton wheat and barley so we need outreach programmes to ensure that oats are on the research menus of institutes. […split…] We need a continual new generation of young researchers.
	General / positive	Thanks for all grateful efforts
		I just know a little about the CORE project, so I could not give any comment now.
		CORE was an excellent project and it should continue taking advantage of the new molecular technologies and with germplasm from different regions of the world
Other Comments		Thank you to all involved for making this incredible project happen and keeping it open to all to make use of.
		Overall, I would rate CORE a success with some commendable deliverables, given the biological complexity of oat genome, the limited investment in oat genomic research, and the poor oat research support.
		I really appreciate the activities related to CORE and support further activities. It is important to have experience and knowledge related to modern biotech methods available in oats too. Nevertheless, I don't expect any concrete results out of CORE related projects to solve the big problems in oat breeding via these methods in the near future.
		Oat breeding research is in a better place thanks to CORE.
		As a oat researcher in genomics my studies took great advantage of the availability of the 6K SNP array and the consensus map recently published by Chaffin *et al.* (2016). I hope a first draft of the hexaploid oat genome

		will be soon available, so that also (re-)sequencing will became a feasible option.
		It is a great work
		It has been a wonderful resource to tap into for development of molecular markers in oat pre-breeding
		It is very important to continue all efforts to enhance oat position on the market and in science generally.
		Thanks to funders and organisers for providing excellent resources and encouraging collaboration across so many programmes
		this was an ambitious project, and generated a lot of beneficial information
		Thanks to Nick Tinker for driving this forward.
		Many thanks are due to the excellent coordinators of this project!!
	Ongoing work is needed	A complete reference sequence of one or more oats could accelerate mapping.
		oat sequence data base should be maintained
		Suggest a list of cultivars used and geographical source. I believe I provided NZ cultivars to a Swedish? breeder for this CORE work, but did not know specifically about CORE until the Beijing OIC 2012
		We need to enhance the application of the research results to oat breeding.

*Complete questions were: (1) "Please list any problems, concerns, criticisms, or lessons-learned that you would like to highlight, in relation to the CORE project." (= Lessons Learned). (2) "Please list any recommendations for further research to build on CORE results." (=Ongoing Recommendations). (3) Please list any other comments you may have." (=Other Comments). Some survey responses that contained comments related to more than one category were split (indicated by "[…split…]").

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Supplementary Table 1. Distribution of a subset of 20 respondents who were not involved with CORE. See parallel presentation in Figure 2 for the distribution of all 56 respondents.

Responses	I don't know	No benefit	Benefits indirectly	I intend to use	I have used	Essential
CORE germplasm panels	1	1	5	8	5	0
CORE cDNA sequence resource	2	4	3	9	1	1
CORE Illumina 6K SNP array	1	2	6	5	4	2
genotyping by sequencing methods	1	3	5	5	1	5
primary data: genotypes and phenotypes	1	2	4	9	2	2
oat consensus linkage maps	1	3	3	6	1	6
LD and population structure	1	2	12	2	2	1
OVERALL IMPACT of CORE	0	1	4	7	2	6

Supplementary Table 2. Distribution of 22 genomics-related researchers (see Figure 2).

Responses	I don't know	No benefit	Benefits indirectly	I intend to use	I have used	Essential
CORE germplasm panels	0	0	4	5	6	7
CORE cDNA sequence resource	1	0	1	8	7	5
CORE Illumina 6K SNP array	0	0	7	3	5	7
genotyping by sequencing methods	0	0	3	5	3	11
primary data: genotypes and phenotypes	0	0	2	4	9	7
oat consensus linkage maps	0	0	2	4	3	13
LD and population structure	0	1	11	3	4	3
OVERALL IMPACT of CORE	0	0	2	5	5	12

Supplementary Table 3. Distribution of 18 oat breeders (see Figure 2).

Responses	I don't know	No benefit	Benefits indirectly	I intend to use	I have used	Essential
CORE germplasm panels	1	0	3	10	3	1
CORE cDNA sequence resource	2	1	3	8	4	0
CORE Illumina 6K SNP array	1	0	5	6	3	3
genotyping by sequencing methods	1	2	4	8	2	1
primary data: genotypes and phenotypes	1	1	2	9	4	1
oat consensus linkage maps	1	1	4	5	4	3
LD and population structure	1	1	10	4	1	1
OVERALL IMPACT of CORE	0	0	3	5	5	5