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From Bench to Bountiful Harvests: A Road Map for the Next Decade of *Arabidopsis* Research [OA]

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In the face of an increasing world population and climate instability, the demands for food and fuel will continue to rise. Plant science will be crucial to help meet these exponentially increasing requirements for food and fuel supplies. Fundamental plant research will play a major role in providing key advances in our understanding of basic plant processes that can then flow into practical advances through knowledge sharing and collaborations. The model plant *Arabidopsis thaliana* has played a major role in our understanding of plant biology, and the *Arabidopsis* community has developed many tools and resources to continue building on this knowledge. Drawing from previous experience of internationally coordinated projects, The international *Arabidopsis* community, represented by the Multinational Arabidopsis Steering Committee (MASC), has drawn up a road map for the next decade of *Arabidopsis* research to inform scientists and decision makers on the future foci of *Arabidopsis* research within the wider plant science landscape. This article provides a summary of the MASC road map.

INTRODUCTION: GLOBAL CHALLENGES AND THE SMALL PLANT WITH BIG IDEAS

Humans depend on plants for almost every aspect of life, from the food we eat to the medicine we rely on. However, this interdependent relationship is being stretched to its limits as a result of an ever-increasing world population and the effects of climate instability. The world population is estimated to increase from the current 7 billion to 9 billion by 2050 (Ronald, 2011), and emerging economies with wealthier populations will require increasing amounts of fuel to run vehicles, operate factories, and produce consumer goods at a pace that until recently only occurred in a few countries. Expanding our knowledge of plant processes will therefore be crucial to meet the pressing need for food, feed, fuel, and shelter and to mitigate the negative effects of climate change

(Weckwerth, 2011a). This is a very exciting time for the international plant science community, because recognition and public awareness of the importance of plant research to our future has increased significantly in the past few years. This presents the community with both opportunity and challenge. To help solve these difficult global problems, we must increase our commitment to the fundamental research that provides key advances in understanding while simultaneously guaranteeing that this augments practical advances through efficient knowledge sharing and beneficial collaborations.

Arabidopsis thaliana is a member of the Brassicaceae family, which includes mustard, cabbage, and oilseed rape. Its small size, rapid generation time, small genome, and ability to generate a large amount of seed by self-pollination have contributed to making *Arabidopsis* the reference plant for plant biology. Significant investments in *Arabidopsis* research during past decades have led to the generation of a fully

annotated genome (Arabidopsis Genome Initiative, 2000), myriad tools and resources, and a flourishing international community of researchers. *Arabidopsis* is the most studied flowering plant and a reference organism for all biology; in 2011 alone, 3768 peer-reviewed journal articles were published on *Arabidopsis* (based on a PubMed search on March 12, 2012). This compares very favorably to the 3637 and 2267 articles published on rice (*Oryza sativa*) and maize (*Zea mays*), respectively. By focusing on a single tractable system, the international community has made dramatic advances in our understanding of plants and basic biology, including the identification of the major plant hormone receptors (Dharmasiri et al., 2005a; Dharmasiri et al., 2005b; Kepinski and Leyser, 2005; Ueguchi-Tanaka et al., 2005; Chini et al., 2007; Thines et al., 2007; Melotto et al., 2008; Ma et al., 2009; Park et al., 2009), the elucidation of florigen (Corbesier et al., 2007; Tamaki et al., 2007), and the identification

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of small RNAs (Hamilton and Baulcombe, 1999; Baulcombe, 2004). In parallel, the resources required for systems approaches in *Arabidopsis* have developed at an unforeseen speed: from genome-wide mutagenesis, genotyping of hundreds of accessions, epigenomics, transcriptomics, proteomics, protein interactions, metabolomics, to genome-scale metabolic reconstruction and computational modeling. *Arabidopsis* serves as a unique plant model that will inform at-

tempts to establish similar platforms for crop and ecological research (Figure 1) (Fiehn et al., 2000; Alonso et al., 2003; Heazlewood et al., 2008; Lister et al., 2008; Weckwerth et al., 2008; Poolman et al., 2009; Hancock et al., 2011). As a result of this outstanding progress, the *Arabidopsis* research community is now ideally placed to help address current and future global challenges.

As many major projects and funding programs involving *Arabidopsis* research

came to a close in 2010, the international *Arabidopsis* community, represented by the Multinational Arabidopsis Steering Committee (MASC), have drawn up a new road map for *Arabidopsis* research, entitled "From Bench to Bountiful Harvests," that will be made available in full in the annual MASC report (Multinational Arabidopsis Steering Committee, 2012). The purpose of the road map is to inform scientists, funding bodies, and decisions makers on
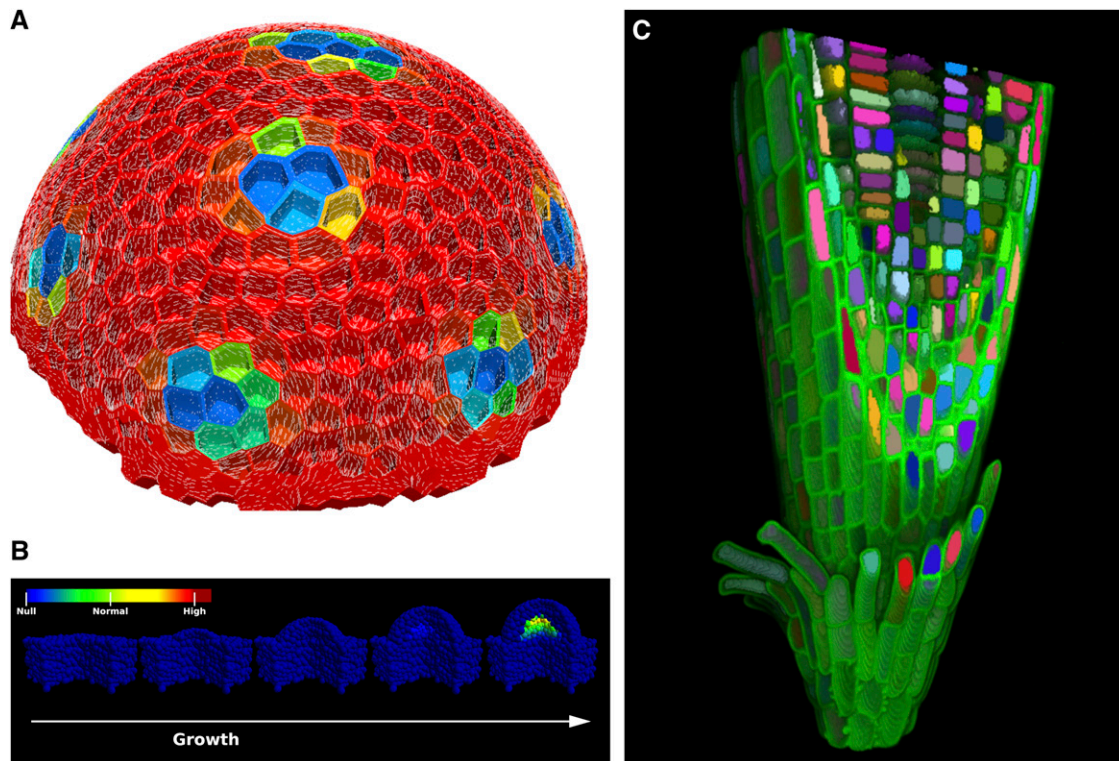

Figure 1. *Arabidopsis* Serves as a Unique Plant Model for Predictive Modeling Approaches That Will Inform Attempts to Establish Similar Platforms for Crop and Ecological Research.

(A) Virtual Shoot Apical Meristem (SAM). Example of a model of the *Arabidopsis* SAM combining biochemical and mechanical interactions. Auxin transport model is simulated on the three-dimensional (3D) cellular template of the L1 layer of meristem. Resulting peaks of auxin are visualized as a color map from red (low) to blue (high). High auxin concentration is assumed to loosen the walls of the cells, which is simulated in a Finite Element model as lowering the elastic modulus of those walls. This leads to the pattern of the maximal principal stress direction (pictured as thin white lines) circumventing the auxin maxima, which coincide with microtubule organization during primordia formation. (*Image courtesy of Henrik Jönsson*, *Lund University*, *Sweden and Elliot Meyerowitz*, *The Sainsbury Laboratory University of Cambridge*, *United Kingdom*.)
(B) SAM signaling model displaying possible WUSCHEL activation by tissue geometry modifications. From left to right, a bulge grows on top of a flat tissue section. The geometrical changes are sufficient to activate the expression of WUSCHEL important for a functional shoot meristem. (*Image courtesy of Henrik Jönsson*, *Lund University*, *Sweden and Elliot Meyerowitz*, *The Sainsbury Laboratory University of Cambridge*, *United Kingdom*.)
(C) Virtual root. 3D visualization of an *Arabidopsis* root apex produced using automated image analysis and visualization techniques. Automated image analysis techniques are used to extract the 3D geometry from confocal microscope images of an *Arabidopsis* root apex. The extracted geometry can then be used in modeling applications to provide a foundation for realistic 3D models. (*Image courtesy of the Centre for Plant Integrative Biology*, *University of Nottingham*, *United Kingdom*.)

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the future foci of *Arabidopsis* research. Drawing from several reports, discussions, and recommendations that have emerged in recent years, including the more recent "2020 European Vision for Plant Science" (Beynon et al., 2008) and "An International Model for the Future of Plant Science" (Dennis et al., 2011), the road map details the future direction of an internationally coordinated plan for *Arabidopsis* research within the wider plant science landscape.

Here we provide a summary of the road map, in which we seek to inform the wider scientific community of the research objectives and goals that are to be pursued by the international *Arabidopsis* community over the next 10 years. For *Arabidopsis* scientists, it provides an international framework for their research in the absence of a dedicated funding program. We hope this will be useful not only to *Arabidopsis* scientists but also to the rest of the plant science community and beyond.

THE NEXT 10 YEARS: FROM BENCH TO FIELDS

In the past 20 years, *Arabidopsis* and plant biology research have largely focused on a reductionist approach to answering biological questions by studying a single gene or limited group of genes in specific pathways or processes. Although this approach has been and will continue to be tremendously successful, plant research is moving into a new era in which studies of complex biological organization and processes will consider all the relevant molecular constituents. This type of holistic approach has revealed that biological processes are much more complex than previously believed; the simple linear relationship between a gene and its biological output (i.e., the relationship between a genotype and phenotype) is no longer adequate. Mutations do not always generate distinct phenotypes, and a phenotype is often dependent on environmental conditions. A major challenge for the future is therefore to understand this complexity so that genomic sequences can be linked to physiological outcomes. This will provide the fundamental knowledge base required for agricultural

improvement, to generate the vast array of plant-based products, and for efforts to improve our environment.

The new decadal vision for international *Arabidopsis* research, "From Bench to Bountiful Harvests," has been proposed by MASC in an effort to understand the fundamental processes of plant biology in sufficient detail to accurately predict both outputs of the system and the effect of perturbations. By obtaining in-depth knowledge of how the genome is translated into a continuum of processes, from the single molecule to cells and tissues, the whole plant, plant populations, and fields of plants, it will be possible to build in silico models with the predictive power needed to drive plant science forward (Weckwerth 2011a).

To achieve this vision, the road map outlines the following five objectives (Figure 2).

1. Build a Predictive Model of an *Arabidopsis* Plant from Its Molecular Parts

Functional genome annotation of *Arabidopsis* has been a major concern of the *Arabidopsis* and wider plant science communities over the past decade. This has led to one of the most comprehensively annotated genomes available. Consequently, the *Arabidopsis* genome provides one of the richest resources for the establishment of predictive models. For example, recently the first steps toward a genome-scale metabolic reconstruction were undertaken (Poolman et al., 2009; de Oliveira Dal'Molin et al., 2010). These first drafts of predictive metabolic models are fragmentary and require refinement. However, they provide the backbone for continuous improvement of a genome-scale understanding of metabolism and physiology (Weckwerth, 2011b). The inventory of metabolites, proteins, and transcripts in *Arabidopsis* are described qualitatively and to some extent quantitatively, but the dynamic interactions between the plant and the environment that lead to specific phenotypes and phenotypic plasticity are poorly understood, and only rare examples exist (Atwell et al., 2010). In the next decade, the road map therefore proposes not only large-scale molecular studies in

Arabidopsis, but more importantly linkage of these data with modeling and predictive approaches. This implies a strong focus on the integration of different types of experimental and environmental data with the metabolic reconstructions of *Arabidopsis* to build computational models with predictive value. Only by integrating all the available information will it be possible to build models that enhance our understanding of these interactions, enabling us to make accurate predictions and exploit this knowledge to optimize plant growth. Accurate and quantifiable data obtained at many levels (including transcripts, methylation patterns, chromatin patterns, comparative genomics, proteomics, metabolomics, protein interactions, protein location, and temporal data) will be required. The data will then need to be translated into functional networks at various scales linked to mathematical models compared across thousands of accessions and associated with meteorological and geographical information. Although this is an ambitious goal, work to integrate these different types of data has begun (Hancock et al., 2011).

2. Build the International Arabidopsis Informatics Consortium, an International Informatics and Data Infrastructure

The recent explosion in data means that careful consideration of data management, data analysis, and data access will be key to the success of plant science and biology in general. Bioinformatics is therefore a key component of the road map. An internationally coordinated data infrastructure to collect, store, visualize, and interpret the diverse array of biological and theoretical data will be required. To address these issues, the *Arabidopsis* community has recently proposed the initiation of the International Arabidopsis Informatics Consortium (IAIC). The IAIC will consist of a globally distributed system of data and resources that would be managed by a single international consortium capable of leveraging expertise and funding on a global scale (International Arabidopsis Informatics Consortium, 2010). A model for the establishment
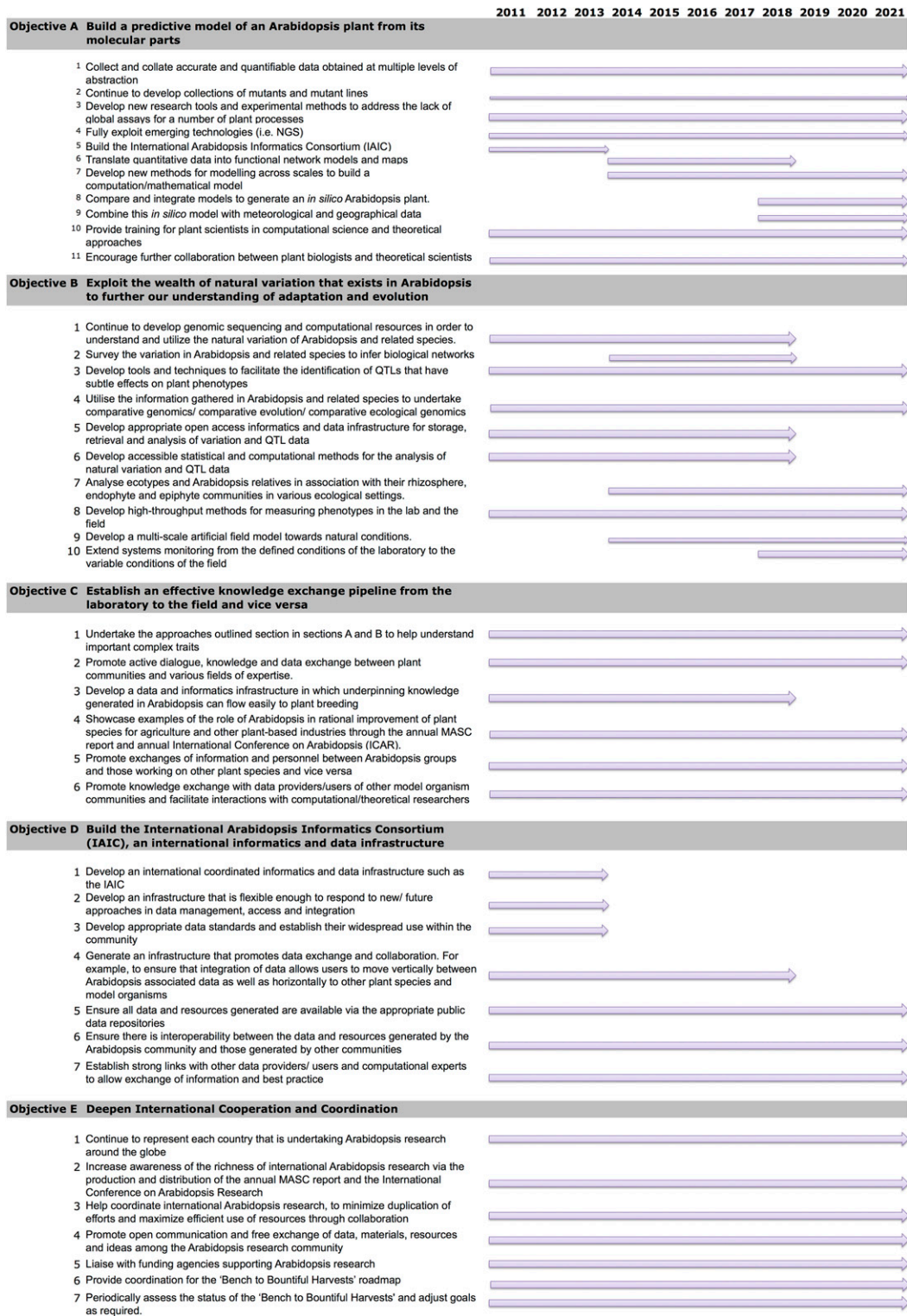
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	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021	

Objective A Build a predictive model of an Arabidopsis plant from its molecular parts

1. Collect and collate accurate and quantifiable data obtained at multiple levels of abstraction
2. Continue to develop collections of mutants and mutant lines
3. Develop new research tools and experimental methods to address the lack of global assays for a number of plant processes
4. Fully exploit emerging technologies (i.e. NGS)
5. Build the International Arabidopsis Informatics Consortium (IAIC)
6. Translate quantitative data into functional network models and maps
7. Develop new methods for modelling across scales to build a computation/mathematical model
8. Compare and integrate models to generate an *in silico* Arabidopsis plant.
9. Combine this *in silico* model with meteorological and geographical data
10. Provide training for plant scientists in computational science and theoretical approaches
11. Encourage further collaboration between plant biologists and theoretical scientists

Objective B Exploit the wealth of natural variation that exists in Arabidopsis to further our understanding of adaptation and evolution

1. Continue to develop genomic sequencing and computational resources in order to understand and utilize the natural variation of Arabidopsis and related species.
2. Survey the variation in Arabidopsis and related species to infer biological networks
3. Develop tools and techniques to facilitate the identification of QTLs that have subtle effects on plant phenotypes
4. Utilise the information gathered in Arabidopsis and related species to undertake comparative genomics/ comparative evolution/ comparative ecological genomics
5. Develop appropriate open access informatics and data infrastructure for storage, retrieval and analysis of variation and QTL data
6. Develop accessible statistical and computational methods for the analysis of natural variation and QTL data
7. Analyse ecotypes and Arabidopsis relatives in association with their rhizosphere, endophyte and epiphyte communities in various ecological settings.
8. Develop high-throughput methods for measuring phenotypes in the lab and the field
9. Develop a multi-scale artificial field model towards natural conditions.
10. Extend systems monitoring from the defined conditions of the laboratory to the variable conditions of the field

Objective C Establish an effective knowledge exchange pipeline from the laboratory to the field and vice versa

1. Undertake the approaches outlined section in sections A and B to help understand important complex traits
2. Promote active dialogue, knowledge and data exchange between plant communities and various fields of expertise.
3. Develop a data and informatics infrastructure in which underpinning knowledge generated in Arabidopsis can flow easily to plant breeding
4. Showcase examples of the role of Arabidopsis in rational improvement of plant species for agriculture and other plant-based industries through the annual MASC report and annual International Conference on Arabidopsis (ICAR).
5. Promote exchanges of information and personnel between Arabidopsis groups and those working on other plant species and vice versa
6. Promote knowledge exchange with data providers/users of other model organism communities and facilitate interactions with computational/theoretical researchers

Objective D Build the International Arabidopsis Informatics Consortium (IAIC), an international informatics and data infrastructure

1. Develop an international coordinated informatics and data infrastructure such as the IAIC
2. Develop an infrastructure that is flexible enough to respond to new/ future approaches in data management, access and integration
3. Develop appropriate data standards and establish their widespread use within the community
4. Generate an infrastructure that promotes data exchange and collaboration. For example, to ensure that integration of data allows users to move vertically between Arabidopsis associated data as well as horizontally to other plant species and model organisms
5. Ensure all data and resources generated are available via the appropriate public data repositories
6. Ensure there is interoperability between the data and resources generated by the Arabidopsis community and those generated by other communities
7. Establish strong links with other data providers/ users and computational experts to allow exchange of information and best practice

Objective E Deepen International Cooperation and Coordination

1. Continue to represent each country that is undertaking Arabidopsis research around the globe
2. Increase awareness of the richness of international Arabidopsis research via the production and distribution of the annual MASC report and the International Conference on Arabidopsis Research
3. Help coordinate international Arabidopsis research, to minimize duplication of efforts and maximize efficient use of resources through collaboration
4. Promote open communication and free exchange of data, materials, resources and ideas among the Arabidopsis research community
5. Liaise with funding agencies supporting Arabidopsis research
6. Provide coordination for the 'Bench to Bountiful Harvests' roadmap
7. Periodically assess the status of the 'Bench to Bountiful Harvests' and adjust goals as required.

Figure 2. Timeline of the Objectives and Goals of the "Bench to Bountiful Harvests" MASC Road Map.

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of this new Arabidopsis Information Portal (AIP) is proposed in this issue (International Arabidopsis Informatics Consortium, 2012). Key data, tools, and resources, such as the databases for genomic and key molecular stocks, the gold standard genome, and annotation and curation of functional data, will provide the core of the information platform on to which many different international modules, including those driven by the MASC subcommittees, can be added. Good examples of integrated and user-friendly structures that could function as modules of the AIP included the MASCP-Gator (http://www.masc-proteomics.org/mascp/index.php/Gator)——a Web interface integrating world-wide distributed proteomics databases and providing *Arabidopsis* researchers with first hints regarding functional interpretation of proteins (Joshi et al., 2011). A similar structure for a metabolomics Web interface is currently in development, driven by the international MASC metabolomics subcommittee.

The construction and implementation of the AIP as described by the IAIC offers the opportunity to establish *Arabidopsis* not only as the primary plant for predictive modeling, but also to serve as a mechanism for enhancing collaboration with other model systems (such as yeast, worm, and mouse), for interaction and comparisons with other plants species, and to visualize the importance of plant sciences for our society.

3. Exploit the Wealth of Natural Variation That Exists in *Arabidopsis* to Further Our Understanding of Adaptation and Evolution

In another approach to understand how genotype relates to phenotype, new technologies, such as Next Generation Sequencing and phenotyping platforms, will be exploited to study *Arabidopsis* natural variation and develop an efficient method to predict phenotype from genotype information. Linking the phenotypic variations that can be observed in nature to the underlying genotypic variation will enable us to exploit this variation to engineer beneficial traits into plants (Atwell et al., 2010). For example,

a genome-wide association study by Filiault and Maloof (2012) assessed the shade avoidance response across a range of *Arabidopsis* accessions and revealed that this trait is controlled by several small to moderate effect loci, which include those involved in auxin biosynthesis and signaling as well as gibberellin biosynthesis and signaling. The results of this study provide a platform to understand the molecular nature of this physical response, which is of great relevance to commercially cultivated crops, where high planting densities can trigger the shade avoidance response and decrease yield.

The wealth of genomic and genetic information available in *Arabidopsis* (Atwell et al., 2010) provides a means to address fundamental questions of quantitative genetics, such as biomass production, water and nitrogen use efficiency, or drought resistance, that become too expensive to study in crops initially, because of labor costs and field space requirements. However, the information obtained through primary studies in *Arabidopsis* will need to feed into and be linked up with the activities of crop researchers and international consortia (see objective 4 and 5).

4. Establish an Effective Knowledge Exchange Pipeline from the Laboratory to the Field and Vice Versa

By establishing an efficient two-way knowledge exchange pipeline between *Arabidopsis* scientists and other plant scientists, fundamental advances generated by basic research will flow into practical programs, such as the breeding of plants of agricultural and commercial importance. The unprecedented genome-scale technologies combined with theoretical and computational approaches are allowing research to be conducted in previously intractable plant species, and this is predicted to increase exponentially during the next decade. At the same time, the wealth of data and resources accrued in *Arabidopsis* is an essential resource for plant scientists working on the development of tools and techniques in other species. By establishing an efficient two-way information exchange, and by

responding to the requests and needs from the field, *Arabidopsis* research can deliver cutting-edge technologies and underpinning knowledge that can then be translated and adapted to other plant species.

To facilitate this information exchange, we will plan to partner with groups focused on key crop species, such as the International Rice Research Institute, the International Research Initiative for Wheat Improvement, the International Maize and Wheat Improvement Center, and other centers of the Consultative Group on International Agricultural Research, to organize workshops at the annual International Conference on Arabidopsis Research (ICAR). We expect these workshops to focus on key traits and issues, such as water use efficiency, disease resistance, and the sustainable intensification of agriculture. The workshops will build on and learn from current efforts, such as the workshop between the International Plant Proteomics Organization and the MASC proteomics subcommittee that will be held this year at the ICAR 2012 in Vienna. The International Plant Proteomics Organization was recently founded to extend proteomics studies from model systems to applied systems and to amplify the interest in applied research in agriculturally important plant systems (http://www.inppo.com/). We hope that these proposed workshops will help to foster communication across the plant science sector, with the aim of understanding and outlining where the *Arabidopsis* community can best place its efforts to help crop researchers provide answers to global problems. Similar workshops could also be organized at other meetings, such as the American Society of Plant Biology and European Plant Science Organization (EPSO) meetings as well as the International Congress of Plant Molecular Biology.

5. Deepen International Cooperation and Coordination

The challenges that plant biologists must address over the next decade are too large for any single country to address alone. International coordination of research and investment is critical for the future success of plant science research. The *Arabidopsis* community has a long tradition of international

collaboration. This was amply illustrated by the efficient data and resource sharing that occurred during the sequencing of the *Arabidopsis* genome (Arabidopsis Genome Initiative, 2000) and in the Multinational Coordinated *Arabidopsis thaliana* Functional Genomics Project (Multinational Arabidopsis Steering Committee, 2010, 2011). In each of these initiatives, MASC helped to ensure success by promoting coordination among the international community. More recently, MASC has been central to the establishment of the IAIC, which aims to facilitate the construction of a single core informatics resource for *Arabidopsis* (International Arabidopsis Informatics Consortium, 2010).

Originally established in 1990 to promote international cooperation and assist in the free exchange of ideas and information, MASC has continued to provide a unifying voice for the international community in subsequent decades. In the current period of financial uncertainty, an internationally coordinated research plan is more important than ever to leverage national investments, prevent duplication of effort, and synergize the outcomes assisting decision makers and funding agencies as they develop priorities.

In addition, we plan to promote international communication and coordination outside the *Arabidopsis* community with organizations such as Global Plant Council (GPC) and EPSO. EPSO is an independent academic organization that represents more than 226 research institutes, departments, and universities from 30 countries in Europe and beyond. EPSO's mission is to improve the effect and visibility of plant science in Europe (http://www.epsoweb. org/). The GPC was recently formed representing 23 plant societies from around the world and aims to "brings plant scientists together to work synergistically toward solving the pressing problems facing humankind" (http://www.globalplantcouncil. org/index.htm). To initiate a dialog between MASC, EPSO, and the GPC, and to determine how the *Arabidopsis* community might best help the EPSO and GPC achieve their goals, we will invite their representatives to attend the annual MASC meetings at the ICAR. This commu-

nication, alongside the activities of objective 4, will foster a better understanding among *Arabidopsis* researchers of global problems in agriculture and help to ensure that the goals of MASC are aligned with those of the wider plant science sector.

CONCLUSION

Arabidopsis research played a central role in enabling the revolutionary changes that occurred in plant biology during the past 20 years. In the decade after the publication of the *Arabidopsis* genome, publically available shared genomic tools, resources (http://www.Arabidopsis.org; http://Arabidopsis.info), and collections of genome-wide insertion mutations (Alonso et al., 2003) have allowed researchers to make major advances in plant and general biology. This vast toolbox, in addition to the inherent strengths that led to its initial adoption as a reference system, make it likely that *Arabidopsis* will continue to be the plant species in which novel forms of data are first accrued and exploited and in which new techniques are tested and perfected. Moreover, functional genome annotation is still lagging behind the speed of genome sequencing. Here, *Arabidopsis* serves as a primary model system for continuous genome annotation improvement and comparative genome annotation exploiting natural genetic variation. Eventually, the catalog of functionally characterized genes in *Arabidopsis* accessions will serve as a template for newly sequenced plant species and translational research in crop species.

Research in commercially important species, such as wheat, is beginning to blossom, but technological challenges remain. It is therefore of fundamental importance that *Arabidopsis* research continue to provide fundamental understanding of basic plant biology. *Arabidopsis* research has also made surprising contributions in some very unexpected areas. For example, despite not being a halophyte, a clever screen for salt hypersensitivity in *Arabidopsis* (Zhu, 2000) provided key information on a signaling pathway that is central to salt tolerance and sodium homeostasis in *Arabidopsis*, crops,

and halophytes (Li et al., 2006; Remans et al., 2006; Xu et al., 2006; Amtmann et al., 2008; Ho et al., 2009; Weinl and Kudla, 2009). There are many other examples of how *Arabidopsis* research has affected surprising areas of plant and animal biology (Multinational Arabidopsis Steering Committee, 2010, 2011). It will therefore be essential that *Arabidopsis*, along with a small number of other key plant species, continue to be used for focused studies of plant biology.

The next decade will present many challenges for plant science, including the sustainable production of food and energy. By fulfilling the objectives of the road map, we can build on the success of the past and continue to make rapid progress toward meeting these challenges. An in-depth understanding of the interaction of plant processes that were traditionally studied in isolation will be obtained. Computational models with predictive value will be generated. A deeper understanding of the interaction between plant and environment will be obtained through the integration of climatological and environmental data with experimental data, enabling the development of predictive models. The road map will help to build and maintain a cohesive and productive *Arabidopsis* community by providing vision and goals for the next 10 years. By doing so, the *Arabidopsis* research community will continue to provide the fundamental advances in understanding that will be needed to meet future global challenges.

AUTHOR CONTRIBUTIONS

All authors contributed to writing the article.

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