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Published in:

Plant Biotechnology Journal

DOI:

[10.1111/pbi.12467](https://doi.org/10.1111/pbi.12467)

Publication date:

2016

Citation for published version (APA):

Abberton, M. T., Batley, J., bentley, A., Bryant, J., cai, H., Cockram, J., Costa de Oliveira, A., Cseke, L., Dempewolf, H., de Pace, C., Edwards, D., Gepts, P., Greenland, A., Hall, A., Henry, R., Hori, K., Howe, G. T., Hughes, S., Humphreys, M., ... Yano, M. (2016). Global agricultural intensification during climate change: a role for genomics. *Plant Biotechnology Journal*, 14(4), 1095-1098. <https://doi.org/10.1111/pbi.12467>

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Review article

Global agricultural intensification during climate change: a role for genomics

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Received 25 May 2015;

revised 23 July 2015;

accepted 6 August 2015.

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Summary

Agriculture is now facing the 'perfect storm' of climate change, increasing costs of fertilizer and rising food demands from a larger and wealthier human population. These factors point to a global food deficit unless the efficiency and resilience of crop production is increased. The intensification of agriculture has focused on improving production under optimized conditions, with significant agronomic inputs. Furthermore, the intensive cultivation of a limited number of crops has drastically narrowed the number of plant species humans rely on. A new agricultural paradigm is required, reducing dependence on high inputs and increasing crop diversity, yield stability and environmental resilience. Genomics offers unprecedented opportunities to increase crop yield, quality and stability of production through advanced breeding strategies, enhancing the resilience of major crops to climate variability, and increasing the productivity and range of minor crops to diversify the food supply. Here we review the state of the art of genomic-assisted breeding for the most important staples that

Please cite this article as: Abberton, M., Batley, J., Bentley, A., Bryant, J., Cai, H., Cockram, J., Costa de Oliveira, A., Cseke, L.J., Dempewolf, H., De Pace, C., Edwards, D., Gepts, P., Greenland, A., Hall, A.E., Henry, R., Hori, K., Howe, G.T., Hughes, S., Humphreys, M., Lightfoot, D., Marshall, A., Mayes, S., Nguyen, H.T., Ogonnaya, F.C., Ortiz, R., Paterson, A.H., Tuberosa, R., Valliyodan, B., Varshney, R.K. and Yano, M. (2015) Global agricultural intensification during climate change: a role for genomics. *Plant Biotechnol. J.*, doi: 10.1111/pbi.12467

Keywords: climate change, food security, sustainability.

feed the world, and how to use and adapt such genomic tools to accelerate development of both major and minor crops with desired traits that enhance adaptation to, or mitigate the effects of climate change.

Introduction

The failure to maintain global food production in line with population growth is evidenced by increasing food prices and greater global food insecurity (FAO, 2014). Continued failure to maintain increases in food production will lead to further increases in food prices in developed countries, as well as social unrest and famine in developing countries. Predicting future food shortages is a challenge due to the variable nature of the climate. Fisher *et al.* predict that yield increases of major crops of 1.1–1.3% per year are required to feed the world in 2050 (Fischer *et al.*, 2014). Global climate change will make it difficult to achieve these yield increases in some regions. In addition, Hisas predicted that there will be a global deficit of major crops by 2020 (Hisas, 2011). The main causes of yield loss include extreme temperatures; altered rainfall patterns, which lead to droughts and floods; and other extreme weather events, the frequency of which are expected to increase due to the changing climate. Crop pathogens and pests may also change their geographical distribution, with predicted increases in severity due to changes in rainfall, increasing temperatures and CO₂ concentrations. Novel plant breeding approaches are required to mitigate some of the worst scenarios of climate change while ensuring the maintenance of consistent crop production.

The three key steps in agricultural history – domestication, displacement of native crops by major commercial crops together with genetically limited introductions of non-native species and the intensification of agricultural production during and since the Green Revolution – each represent potential bottlenecks which have reduced crop genetic and trait diversity. Domestication has often been a haphazard affair with some regions, such as Europe, domesticating relatively few species, while other regions have been responsible for many of the major crops now grown (Meyer *et al.*, 2012). Host plant disease resistance and dwarfing genes were introduced during the Green Revolution, together with an increased use of irrigation and artificial nitrogen fertilizer, further genetic improvement to utilize the increased resources, and highly tailored management of biotic and abiotic stresses (Khush, 2001; Pingali, 2012). These advances have led to significant increases in production of the major staples over the last century across most of the world (Fischer *et al.*, 2009), driven primarily by conventional plant breeding coupled with intensification and simplification of production systems (Duvick, 2005).

Crop breeding has largely been driven by selection for yield and adaptation to specific agro-climatic regions. However, selection under such 'ideal', high-input environments is likely to have led to the loss of some genes for efficiency or adaptation to stress; particularly, if such genes have minor deleterious effects when present in nonstressed or high-input environments. Moreover, not all agroecological practices are compatible with the Green Revolution cultivars – for example, most modern semi-dwarf (*sd1*) rice cultivars perform poorly under the rain-fed ecosystems of Asia and Africa that occupy ~30% of world rice lands, where drought, submergence, low soil fertility and other abiotic stresses are commonplace (Paterson and Li, 2011). Progress is being made

in breeding submergence tolerant rice, however, with contributions by molecular breeding (Singh *et al.*, 2013).

The requirement to increase food production under new climatic and agronomic constraints presents three potential challenges: (i) to modify our selection criteria to focus on efficiency or adaptation/tolerance to stress(es) in addition to total yield, (ii) to determine whether such efficiency/stress-tolerance alleles are still present and exploitable in our elite material and wider breeding germplasm and (iii) to develop new and to expand the use of current minor crops, particularly where they offer better nutrition, environmental sustainability and/or resilience while requiring lower inputs than current major crop species. The altered agricultural paradigm away from high inputs towards stability and environmental resilience of yields, alongside decreasing inputs, is a daunting challenge. However, this challenge can be addressed through the accelerated application of genomic tools.

Genomic-based breeding

A genomic-based breeding strategy for new cultivars should start by defining the stress(es) that are expected to more severely affect crop production and productivity under a certain climate change scenario. As the impact of climate change will be different for diverse crops and environments, tailored solutions may need to be applied. Data from multi-environment testing provide an opportunity for modelling stress impacts on crops and target populations. Plant breeders, crop physiologists and genebank curators will search for morphological and physiological traits in available germplasm that could enhance crop adaptation under such climatic variability. In this regard, crop physiology may help define ideotypes to be pursued for enhancing such adaptation. In the future, crops need to be more heat tolerant, with greater water and nutrient use efficiency, both to counter the effects of climate change and to mitigate the impact of crop production on the causes of climate change.

Understanding genetic diversity in a species at the DNA sequence level permits the identification of agronomically valuable genes and associated molecular genetic markers while providing a means to select for these genes in breeding programs. The main driver of the current genomic revolution is the advance of next-generation DNA sequencing (NGS) technology, which has recently broken the boundary of the \$1000 human genome. This technology is revolutionizing crop breeding as fast as it has revolutionized medicine. It not only enables the sequencing of diverse crop genomes but also facilitates the association of genomic diversity with agronomic traits, providing the foundation for genomic-assisted breeding. Sequencing technology continues to advance and it is likely that within a few years, all major crops will have benefitted from sequence-based genomic improvement.

An understanding of gene networks and the identification of the sequence or epigenetic variation that underlies agricultural traits conferring environmental resilience would revolutionize our ability to truly breed for new ideotypes. These could be suited to particular environments and include the appropriate combination of stress-tolerance genes for desirable traits, even for performance under environmental volatility itself. Genomics, in

association with phenotypic information, can provide breeders with the knowledge they need to make more rapid selections and apply advanced breeding strategies to produce climate-resilient crops. Genetic mapping and quantitative trait loci (QTL) analysis, association genetics (AG) studies and genomic selection (GS) approaches have recently had an impact on the development of new crop varieties. AG and GS were previously hampered by the lack of very high marker density coverage of the genome. However, the development of massively parallel NGS methods has made the characterization of very large numbers of markers possible (Edwards *et al.*, 2013).

Over millions of years, new genes have evolved and been shuffled and selected in a wide range of environments to produce the diversity we see in wild species. In contrast, the selection and domestication of crops by humans is relatively recent, having occurred over the last 10 000 years or less. Currently, breeders of most major crops are reshuffling relatively few alleles to produce enhanced combinations that provide increased yield and other attractive agronomic characteristics (Gepts, 2004). Genomics offers the potential to greatly increase the diversity of alleles available to breeders through the mining of allied gene pools and the genomes of crop wild relatives. Scientists have recently issued a strong call for action and major investments into better characterizing the wealth of genetic resources that lies conserved in the world's genebanks (McCouch, 2013). The Diversity Seek initiative consortium aims to facilitate access to diverse germplasm and associated data. This germplasm, together with genomics tools, enables the rapid identification and selection of the rare novel beneficial alleles and their controlled incorporation into crop germplasm. As we enter the age of genomic-based crop improvement, this technology will be used to help safeguard our future through increased food security.

The application of genomics for crop improvement varies between crops and also between the major breeding companies and smaller domestic or specialist crop breeders. With the continued rapid advances in genome technologies, the application of genomics to identify and transfer valuable agronomic genes from allied gene pools and crop relatives to elite crops will increase in pace and assist in meeting the challenge of continued global food production.

Broadening the crop base

The current economic models for plant breeding have resulted in major investment and subsequent advances for a limited number of major crops, with little if any benefit for minor or orphan crops. The increased application of genomics coupled with the need to diversify the sources of our food supply will likely see this situation change. Substantial investment is now required for relatively minor gains in major crops. In contrast, our increased knowledge of crop genomics, together with reducing costs, is expected to facilitate the rapid improvement of minor crops and even the adaptation of nontraditional crop species for human consumption. A greater understanding of both the genomics and physiology of diverse plant species will be required if we are to increase diversity of both major and minor crops. The integration of new frontiers in crop modelling, genome biology and phenotyping technologies increases the potential for narrowing the genotype–phenotype divide and will contribute towards crop improvement through ‘plant breeding by design’ (Fridman and Zamir, 2012; Yin *et al.*, 2004).

Diversification of agriculture, both in terms of crops grown and the agricultural system itself (e.g. intercropping), could significantly improve agricultural resilience, but the application of genomics to a far broader range of crops is also required to harness the full potential of many of these species, as well as for the staple crops which will continue to represent the main focus of breeding research. Knowledge-intensive crop breeding approaches and translational genomics will contribute to develop climate-proof, genetically enhanced seed-embedded technology – which in synergy with sustainable agro-ecosystem management, eco-efficient crop husbandry and sound postharvest handling will assist feeding the world in this century of climate change.

Future genomic-based crop improvement might be generalized as advancing the productivity frontier, continuing and strengthening efforts to improve crop productivity and quality under generally favourable conditions, as well as intrinsic defences against pests, maximizing the amount and quality of food that can be produced from limited arable land. Particularly, large incremental returns on investment may be realized in crops that have received relatively limited prior attention, but which may be of great importance in parts of the world where development challenges are the greatest and market failure is most acute. In widely grown crops with long histories of improvement, large investments may be required to realize small incremental gains, but such gains will be leveraged quickly across large production areas.

Conclusions

A second Green Revolution, driven largely by eliminating production constraints, may integrate activities towards advancing the productivity frontier and transforming production systems. Genomic tools provide an infrastructure to lay bare the secrets of the genetic potential of plants to respond to a range of environments. Much foundational work remains to be done – and translating this information into climate resilient crops will require additional large investments. As agricultural initiatives can take 15–30 years to yield maximal returns (Alston, 2000), the required investments need to be made now. By working together, leading crop genome researchers can help safeguard future food supplies.

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4 Michael Abberton et al.

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