

²Key Laboratory of Industrial Biotechnology, Ministry of Education, Jiangnan University, Wuxi 214122, China

³National Engineering Laboratory for Cereal Fermentation Technology, Jiangnan University, Wuxi 214122, China

*Correspondence: mingli@jiangnan.edu.cn (L. Liu).

<https://doi.org/10.1016/j.tplants.2017.12.008>

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Spotlight

Fast-Forwarding Genetic Gain

Huihui Li,^{1,2} Awais Rasheed,^{1,2,*} Lee T. Hickey,³ and Zhonghu He^{1,2,*}

‘Speed breeding’ enables scientists to exploit gene bank accessions and mutant collections for an unparalleled rapid gene discovery and gene deployment. Combining

speed breeding and other leading-edge plant breeding technologies with strategic global partnerships, has the potential to achieve the genetic gain targets required to deliver our future crops.

Rapid Breeding Cycles: Reaping the Low Hanging Fruit of Increasing Genetic Gain

Modern crop breeding and advances in management practices have contributed substantially to the annual gain of 0.8–1.2% in crop productivity. Nevertheless, this current rate of improvement is not sufficient to keep up with food and biofuel demands for the projected global population in 2050 (the 2050 challenge) [1]. Achieving linear progress to aim for 2% genetic gain is a huge challenge when crop yields have plateaued in some regions, due to the narrow genetic base and lack of potential to increase harvest index within elite breeding stocks. Sustained yield increases will also be hampered by extreme weather and the occurrence of more aggressive strains of pests and pathogens. In essence, genetic gain in a crop breeding program is determined by the following equation:

$$\Delta G = i h \sigma_A / L, \quad [1]$$

where i is the selection intensity, h is the square root of the heritability in the narrow sense, σ_A is the square root of the additive genetic variance, and L is the length of breeding cycle interval or generation. While tweaking selection accuracy and intensity can lead to minor improvements in genetic gain, the introduction of new favorable alleles through rapid breeding cycles seems to be one possible scenario to substantially boost the rate of gain and could help achieve the ‘2050 challenge’. If we plot duration of growth cycle in a population, the extreme phenotypes for short growth periods exist in almost every crop species, for instance Mini-Maize (*Zea mays*) and ‘Apogee’ wheat (*Triticum*

aestivum). Such extreme phenotypes are useful as ‘model’ variants to understand the plant biology, because they significantly reduce the project timeline. However, the recent development of ‘speed breeding’ uses extended photoperiods and controlled temperature regimes to achieve rapid generation cycling in fully enclosed growth rooms or glasshouses for large-scale application in crop breeding programs. This provides a highly flexible platform to achieve rapid generation advancement, irrespective of genetic background, where up to four to seven generations per year can be achieved in six crop species including wheat, durum wheat (*Triticum turgidum*), barley (*Hordeum vulgare*), chickpea (*Cicer arietinum*), pea (*Pisum sativum*), and canola (*Brassica napus*) [2]. A similar approach could be adapted to reduce vegetative growth in maize and rice (*Oryza sativa*) where short days are required to trigger the reproductive phase. This holds significant promise, not only to rapidly develop populations for genetic studies, but also for introgression of favorable alleles into elite germplasm for crop improvement.

Harnessing Diversity in Gene Banks to Boost Additive Genetic Variation

The vast number of valuable germplasm collections in gene banks is a source of genetic variation to potentially raise genetic gain. However, there are two major constraints: (i) time and resources required to precisely characterize the accessions at large scale, and (ii) identifying and transferring the useful alleles into adapted germplasm. An integrated approach using a combination of speed breeding and genomic selection could fast-track gene bank mining. Realistically, only a small fraction of the accessions can be phenotyped, yet genotyping of gene banks is becoming a routine activity in the post-genomics era and could enable prediction of traits for larger numbers of

accessions in the gene banks [3]. Such useful variants can be rapidly backcrossed using speed breeding, which has several advantages over double haploid technology, including phenotyping-on-the-go, which allows selection during development of inbred lines [2]. An extension to this approach could be the use of gene bank passport data to extract the long-term climate data (e.g., rain fall, temperature, soil PH, frost, aridity index) from the Geographic Information System (GIS) collection sites. These environmental data can be used as a proxy for tolerance to biotic and abiotic stresses, and could lead to discovery of favorable alleles/haplotypes that are valuable for crop improvement [4]. In this way, the efficiency of prebreeding and research could be improved, thus accelerating the deployment of climate-smart cultivars.

Novel Breeding Strategies using Genomic Selection and Multiplex Genome Editing

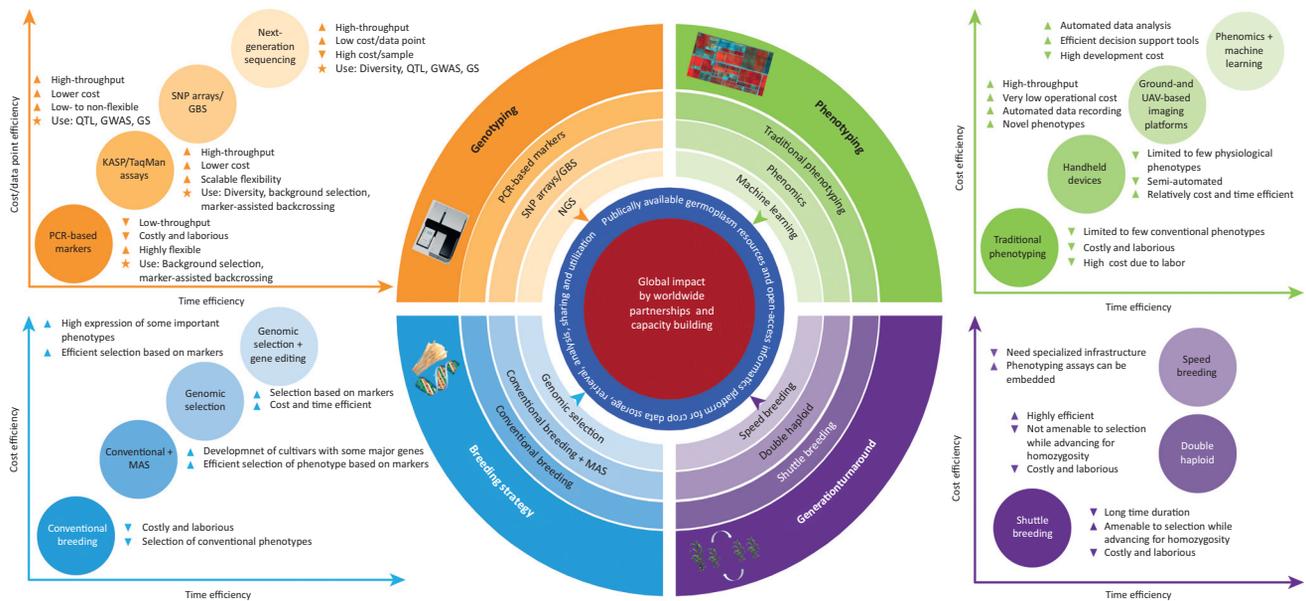
Genomic selection has emerged as one of the most promising breeding strategies to increase genetic gain and its advantages over traditional practices have been demonstrated for major crops [4]. More recently, genomic selection has also proven a useful tool to accelerate genetic gain for heterosis breeding [5]. Several low-cost and high-throughput SNP chips and NGS (next generation sequencing)-based platforms have made it possible to genotype large breeding populations for genomic selection [6]. Genomic selection can be fine-tuned by incorporating high throughput phenotyping for yield-associated physiological traits, markers for well-characterized major genes, and parametric and nonparametric statistical and computational models [4]. Remarkably, there has been a three-million-fold increase in sequencing throughput since 1975 and a million-fold decrease in cost over a decade, which has led to huge progress in sequencing crop species [7]. Efforts are now focused on whole-

genome sequencing of members of a gene-pool (pan-genome) to increase our understanding of the genetics underlying crop adaptability [6]. Such insight could enable the adoption of several approaches already implemented in livestock genomics. For example, haplotypes consisting of two or more SNPs with strong linkage-disequilibrium are multi-allelic in nature and are more informative than bi-allelic SNP markers. Highly conserved haplotypes selected by plant breeders during modern breeding could be replaced by more beneficial haplotypes from genetic resources. Furthermore, gene-editing could play an important role for fine tuning expression of key genes and reducing linkage drag. It is now possible to create new alleles or inactivate/activate homoeo-alleles of a gene with major effect on phenotype. The CRISPR-Cas9 tool, allowing multiplex gene editing, has become more high-throughput and is considered a non-GMO approach in some countries [8]. DNA synthesis platforms have evolved significantly with one-billion-fold increase in oligo-nucleotide synthesis and the promising success of gene-editing have prompted a realistic discussion of writing and radically re-writing complex genomes [9]. Such advocacy for large-scale genome re-writing is motivated by experiments on simple bacterial organisms, which have shown that re-engineering the genome of particular bacterial strains could render the bacteria less susceptible to viruses and more efficient at producing a biomolecule of interest [10].

Integrated Approaches and International Partnerships

If applied in isolation, a tool or technology will unlikely accelerate the rate of genetic gain in crop breeding. However, the successful integration of several technologies has the potential to break stagnant yield barriers in various crops (Figure 1). For instance, high-throughput hyperspectral phenomics for yield-associated

physiological traits [11] could be used to discover haplotypes that are different from haplotypes of conventional phenotypes (plant height, flowering time, grain yield per se, etc.) that have been selected by plant breeders. The fast-track replacement of historically fixed haplotypes with new beneficial haplotypes of yield-associated traits could potentially make room to further improve the harvest index in crop plants. Integration of 'speed breeding' with aforementioned approaches could help achieve the 2050 genetic gain targets for the four Fs (food, feed, fiber, and fuel). The catalyst is the globally coordinated network for the development of unified standards and common monitoring protocols integrating genomics with phenotypic data, including eco-geographic information, all with open-access terms for the availability of physical (e.g., germplasm and infrastructure) and information resources to the scientific community [12]. One example is the Excellence in Breeding (EiB; <http://excellenceinbreeding.org/>) platform, under which the CGIAR (Consortium of International Agricultural Research Centers) is aligning its overall bioinformatics across modern breeding technologies. These types of initiatives will help to modernize breeding programs, particularly those in developing countries, by embracing new technology and innovation. The tools, services, knowledge, resources, and peer interactions facilitated by the EiB, will allow breeders a transition into the digital era, including storage, retrieval, analysis, sharing, interpretation, and utilization of electronic data. This will enable breeders to adopt best practices, use new tools, and integrate breeding approaches, saving time in developing new higher yielding cultivars, of better quality, and more resilient to weather extremes and local stress environments. However, the enthusiasm over the role of genomics and other breeding tools must not overlook the yield gap between developed and developing



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Figure 1. The Integrated Strategies Leading to a Common Decision Support Tool to Accelerate Genetic Gain Within the Context of New Technologies. The features of individual aspects, such as genotyping, phenotyping, generation turnaround, and breeding strategy are described in biplots, along with key advantages (denoted as Δ) and disadvantages (denoted as ∇). The low color intensity indicates the higher possibility of technologies to integrate with other technologies.

countries (largely due to the lack of farm mechanization) and the significant contributions from agronomy and management to raise yield on farms in developing countries by up to 30%.

Acknowledgments

We are grateful to Drs. Mark E. Sorrells and Ed Buckler (Cornell University, USA) and Rajeev Varshney (ICRISAT, India) for useful suggestions. We acknowledge financial support from the National Key Research and Development Program of China (2016YFE0108600, 2016YFD0100303) and the National Natural Science Foundation of China (31550110212, 31471174). The authors also give thanks to the Australian Research Council for an Early Career Discovery Research Award (Project No. DE170101296) to LTH.

¹Institute of Crop Sciences, Chinese Academy of Agricultural Sciences (CAAS), 12 Zhongguancun South Street, Beijing 100081, China

²International Maize and Wheat Improvement Centre (CIMMYT), c/o CAAS, 12 Zhongguancun South Street, Beijing 100081, China

³Queensland Alliance for Agriculture and Food Innovation, The University of Queensland, St Lucia, Queensland, 4072, Australia

*Correspondence:

a.rasheed@cgjar.org (A. Rasheed) and z.he@cgjar.org (Z. He).

<https://doi.org/10.1016/j.tplants.2018.01.007>

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