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Innovations continuously enhance crop breeding and demand new strategic planning

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ABSTRACT

Food security relies on continuous supplies of improved products from plant breeding and their assimilation into agriculture. Extraordinary innovations in the life sciences have brought plant breeding into a new phase of opportunity. These include the means to discover, manage and select better versus poorer versions of genes and the ability to change gene sequences in situ by gene editing. Genomics is also revealing the thousands of different microbes in all plants and the roles that their genomes play in determining crop traits that can be further improved by addition of the right microbes. Assimilation of such innovations into breeding strategies can have major impacts on rates of breeding gain but to achieve this will require comprehensive strategic leadership, planning and investments by scientists, leading global agencies and all governments based on appreciation of (i) the continuous streams of innovations underpinning crop improvement and (ii) the necessities for more rapid crop improvements everywhere to help avert otherwise inevitable catastrophes.

1. Introduction

The annual rate of gain of production in farmers' fields has slowed for major cereal crops in recent years (Fisher and Edmeades, 2010; Fisher et al., 2009). This has added to the global food security concerns. World food production must increase substantially to avoid catastrophies and the breeding of new crop varieties must play its part (Tilman et al., 2011). This puts a huge responsibility on plant breeders. What limits faster rates of gain via plant breeding? The many constraints include deployment of new genetic variation from the crop or another species; the ability to make commercially improved genotypes much faster and cheaper; the ability to recognize superior genotypes more easily; the organization of plant breeding resources and the movement of germplasm efficiently around the world; better cost input versus output ratios and preferences of consumers.

Plant breeding is based on bringing together different sets of chromosomes and the reassortment of genes into different combinations during gamete formation. The best combinations can then be selected amongst the offspring in relevant environments. The processes involve the constituents of all chromosomes comprising a huge number of the informational units created and selected during evolution, domestication and modern breeding. Therefore it is necessary to have complete genome sequences, or their proxy, of large numbers of strains of every crop to both interpret what has been going on in plant breeding and selection and to design/select preferred forms of plants. Fortunately, there have been remarkable innovations over the past 40 years in genomics, coming from huge investments across the life sciences, that enable new understanding of what chromosomal information determines plant properties.

The application of genome sequencing to plants has also revealed the presence of thousands of bacterial and fungal strains that live inside plants as endophytes. These discoveries are radically changing our views on what a plant is and how its properties are determined. Finally, breakthroughs in changing individual gene sequences in chromosomes to preferred designs have emerged that have extraordinary potential in plant breeding when preferred forms of genes are known (National Academy, 2016). Consequently, a new nexus between genomics, genetics and breeding technologies has arrived that promises increased efficiency in crop improvement for future food security. This is therefore a special era in the history of plant breeding and reminds us that the future will not be like the past or the present. However, the evolving opportunities demand new investment and planning in breeding, regulations, consumer awareness and politics to avoid failure, disappointment and unnecessary controversy.

This paper draws attention to some of the major current and future innovations in plant improvement and key global challenges for deploying them. Comprehensive innovation-driven, strategic planning and leadership by international bodies and governments will be essential for the innovations to play their part in achieving increased food production.

2. Innovations bringing together genomics and breeding, 1975–2015

Innovations from conception to full deployment can sometimes take several decades. To illustrate one forty-year path of innovations

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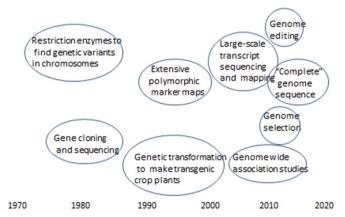


Fig. 1. Initial adoptions of genomics-based technologies into plant breeding over the past 40 years. The technologies that were assimilated into leading plant breeding programs are positioned in time approximately as they were initially adopted. This does not mean that they have been widely adopted. Costs as well as other factors have commonly resulted in slow rates of adoption by most plant breeding organizations.

that has finally come to have major impact on applied plant breeding I use the development of genomics-based breeding in wheat from the 1970s to the present, (Fig. 1). Many diverse innovations had to be integrated. Studies into the isolated DNAs that comprise plant genomes started extensively in the 1970s (e.g. Rimpau et al., 1978). This time can be considered the beginnings of crop plant genomics. The innovations that resulted in being able to clone DNA matured in the late 1970s (Gerlach and Bedbrook, 1979; Bedbrook et al., 1980) and launched the search to clone plant genes and so identify their DNA sequences. By the early 1980s, copies of plant genes had been sequenced and published (e.g Forde et al., 1981; Smith et al., 1983). Many scientists were motivated to start defining plant genes in the belief that it would help plant breeding but the way this would happen was not clear. It was obvious that it would be possible to define genetic variation in DNA but not how this could be used directly by breeders at scale..

Large numbers of polymorphisms in DNA sequences between different plants revealed by treatments with restriction enzymes, or differences in the lengths of tandemly organised DNA sequences due to variation in numbers of copies of repetitive units (microsatellite DNAs) were gradually discovered from the late 1970s and mapped extensively using segregating populations during the early-mid 1990s (Röder et al., 1998; Somers et al., 2004). Geneticists used molecular marker maps from the 1990s but breeders only for specialist uses where known polymorphisms were associated with known phenotypes. Disease resistances, encoded by single, mapped alleles, were ideal candidates to be selected in breeding programs based on genetically linked DNA polymorphisms (Li et al., 2015). It took high throughput, acceptably cheap methods to assay large numbers of polymorphisms to bring use of whole genome mapping and the discovery of better alleles into a broad-based breeding context. By 2007 Monsanto had reported that marker assisted breeding had become their conventional norm and increased the mean performance of progeny compared to conventional breeding methodologies (Eathington et al., 2007; Mammadov et al., 2012). Then genome-wide association studies (GWAS) between segregating markers associated with better alleles and phenotypes could be made and documented for elite populations (Huang and Han, 2014; Sukumaran et al., 2015). From this "Genomic Selection", i.e. the selection of plants based on the markers (better alleles) for all chromosome segments found to be co-inherited with a trait in segregating populations, promises to be a huge step forward in efficiency when applied appropriately in known populations (Heslot et al., 2012). It will enable breeders to select seeds that have desired traits without growing the whole plant. Thus what breeders evaluate in the field will be enriched for key traits and so land, time and money will

not be wasted growing plants to be thrown away. More resources can then be spent on finding even better traits. This should significantly reduce a previous large problem when handling many genetically complex traits.

Finally, a more-or-less complete DNA sequence from a hexaploid wheat accession has been produced using advanced sequencing and bioinformatics (Brenchly et al., 2012; Mayer et al., 2014). This reference sequence is a landmark that will, in time, make an enormous difference to wheat breeding, especially when variants found in a range of individuals are mapped upon it (Huang et al., 2013) and knowledge of the diversity in defined chromosomal segments is understood.

In summary, it has taken some 40 years of innovations from defining the first DNA markers to the routine application of DNA polymorphisms for selection of genetically complex traits (Eathington et al., 2007; Fig. 1). This is not only because enough markers were unavailable until recently but mainly because methods were too expensive and statistically uncertain to apply routinely in breeding programs by applied breeders. While huge cost reductions have occurred in recent years, cost/low investment is still a major reason why marker assisted breeding is not widely used in small breeding programs. To achieve the recent reductions in costs and allow applications at the required scale it has taken many millions of dollars, many entrepreneurs and small startup companies with an eye to profitability from the human genetics/medical world to provide the means of using genomics for applied plant breeding. In fact, nearly all the landmark innovations that have created what we know as plant genomics have been based on innovations outside plant sciences and agriculture. This will continue. Thus it should be recognized that future developments in applied plant breeding will be dependent on discoveries and investments elsewhere, especially in medical sciences. Given that these will surely emerge in the richer countries we should look at projections of funding and innovation strategies in the medical and IT worlds to see the future opportunities for plant breeding based on high throughput genetic and genomic analysis beyond those noted in Fig. 1. The frontiers are in an exciting, very different and powerful position compared with ten years ago. Also, the innovations in genomics are being complemented by innovations in the means of measuring traits and the performance of plants in fields by drones equipped with cameras able to detect different properties of plants (Pieruschka and Poorter, 2012).

3. Innovations in trait improvement by crop genome editing

A "holy grail" for breeders has long been the wish to be able to replace alleles (specific variant forms of a gene) in situ with better alleles for specific traits. The need to do this remains and will be increased by the need to adjust existing crops where increasing temperature, drought, cold, new insects and diseases occur due to climate change (Jaggard, Qi and Ober, 2010). If advances in genomics coupled with phenotyping are giving us the means of identifying better alleles, how can the alleles be assembled more effectively? Where favourable alleles are known, this has been routinely achieved by backcrossing but this process is lengthy and still suffers from deleterious alleles linked to the favourable genes that cannot be easily separated by recombination. In the last few years the challenge of modifying defined genes to alternative alleles in situ has leapt ahead with the developments of truly ground-breaking technologies that have changed plant science and breeding opportunities (Kumar and Jain, 2014; Voytas, 2013; Ran, 2014). There are various versions but all are based on deliberate cleavage of chromosomes at specific target sites and then modification of the DNA during repair of the broken sites. The different techniques all enable gene-specific "editing". The changes are made in cells from which whole plants are regenerated, as in the initial steps of making transgenic plants.

The preferred method of cleaving DNA and modifying a gene sequence is now the CRISPR/cas9 system emanating from Clustered

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