Opinion

Accelerating plant breeding

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The growing demand for food with limited arable land available necessitates that the yield of major food crops continues to increase over time. Advances in marker technology, predictive statistics, and breeding methodology have allowed for continued increases in crop performance through genetic improvement. However, one major bottleneck is the generation time of plants, which is biologically limited and has not been improved since the introduction of doubled haploid technology. In this opinion article, we propose to implement *in vitro* nurseries, which could substantially shorten generation time through rapid cycles of meiosis and mitosis. This could prove a useful tool for speeding up future breeding programs with the aim of sustainable food production.

Keeping up with demand

Crop production has steadily increased over time and it has been suggested that 50% of the progress is attributable to advances in crop management and breeding [1,2]. For example, the three major crops in the US, maize (*Zea mays*), wheat (*Triticum* spp.), and soybean (*Glycine max*), show positive linear increases in average yield from 1930 to 2012 [3] (Figure 1). However, changes in climatic patterns, land, and water availability now provide additional challenges for plant breeders and geneticists to ensure yield stability in varying environments [4]. To meet the projected increase of global demand for food, feed, and fiber (100% by 2050 [5]), the linear progress seen in Figure 1 will need to be increased. To increase the rate of genetic improvement (see Glossary), the efficiency, reliability, and speed of genetic improvement must be increased. In this opinion article, we propose an idea benefitting the speed of genetic improvement through the implementation of rapid generation cycling by the use of the *in vitro* nursery. Through rapid cycles of meiosis and mitosis conducted in tissue culture, generation times of crop species can be decreased allowing more opportunities for recombination and selection in a given unit of time.

The breeder's equation

Five modifiable components are used to estimate genetic gain (Box 1): additive genetic and phenotypic variance (which can be combined as narrow sense heritability), selection intensity, parental control, and time [6–9]. Choice of germplasm for formation of segregating populations affects additive variation (genetic variation that can be transmitted to the next generation), whereas choice and management of selection environments affects phenotypic variance. A combination of these components affects selection efficiency. Selection intensity, corresponding to percentage of individuals advanced after a cycle of selection, can be easily modified. The aforementioned factors can be optimized through knowledge of the germplasm and the use of predictive tools. The most critical remaining factor to maximize genetic gain is time. The number of generations per year is biologically limited. The most extreme cases are short generation times (six/year) in *Arabidopsis* (*Arabidopsis thaliana*) versus long generation times in tree species (multiple years/generation). Advances in cycle time have been limited, except for the use of off-season nurseries and doubled haploid technology.

Glossary

Backcross: a breeding methodology where a gene or few genes (e.g., resistance to a disease) usually contained within a wild or less than acceptable line are transferred to high performing lines by crossing the two lines and then repeatedly crossing the progeny back to the high performing parent while selecting for the gene or few genes of interest. The objective is to produce progeny that are as genetically similar to the high performing parent as possible while containing the gene or few genes desired from the less than acceptable parent.

BC4 line: backcross 4 line; lines which are derived after four generations of backcrossing.

Full-sib recurrent selection: a method of genotypic recurrent selection where individuals are evaluated for performance by paired plant cross pollinations which generates a set of full-sib (i.e., two shared parents) families which are tested in replicated trials to generate data for selection. Requires two seasons per cycle.

Genetic improvement/gain: the change in mean performance of a population that occurs as the result of the selection and recombination of superior performing individuals in a population.

Half-sib recurrent selection: a method of genotypic recurrent selection where individuals are evaluated for performance by cross pollination with a tester which generates a set of half-sib (i.e., one shared parent) families which are tested in replicated trials to generate data for selection. Requires one to three seasons per cycle depending on the specific method used.

Introgression: a relatively small portion of the genome of an unadapted individual, which is transferred through conventional crossing to adapted germplasm for evaluation of its utility for genetic improvement.

Linkage drag: the undesirable transfer of unwanted genes along with the gene/locus of interest due to physical linkage causing a decrease in performance of the progeny.

MABC: marker assisted backcross; a variation of the backcross breeding methodology where molecular markers are used to select for the trait of interest, and if desired for maximum recovery of the desired parent genome.

Self-incompatibility: the inability of a plant with functional male and female gametes to produce a zygote through self-fertilization.

Selfed progeny recurrent selection: a method of genotypic recurrent selection where individuals are evaluated for performance by development of selfed families (i.e., $F_{2:3}$, $F_{3:4}$, $F_{4:5}$, etc.), which are tested in replicated trials to generate data for selection. Requires 3+ seasons per cycle depending on how advanced the generation of self-pollination is (i.e., more time is required for $F_{4:5}$ than $F_{2:3}$).

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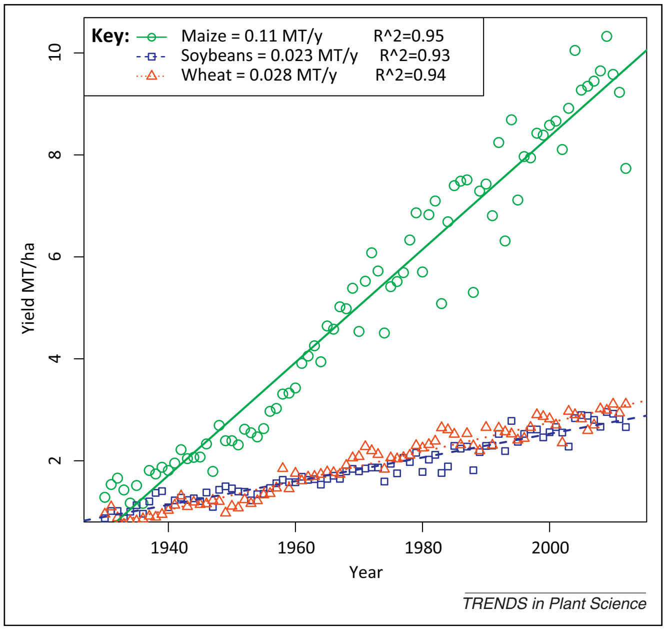

Figure 1. Yield gains of major US crops. Average yield per year in metric tons/ha (MT/ha) for each of the three major US crops (maize, wheat, and soybean) from 1930 to 2012 [3]. Each crop shows a linear increasing trend over time with maize having the highest annual gain of 0.11 MT/year followed by wheat at 0.028 MT/year and soybeans at 0.023 MT/year for average grain yield. This increase in mean yield per hectare needs to be increased to meet the demands of a growing human population.

Speeding up

Off-season nurseries, popularized by the pioneering plant breeder Norman Borlaug among others, can help to reduce the time needed to release new cultivars, for example, the time for producing a new wheat cultivar was shortened from 10–12 to 5–6 years [10]. For pure line and hybrid crop breeding, the ability to generate homozygous and homogeneous lines is another time constraint. However, by using doubled haploids (DHs) in different crop species, homozygous and homogeneous lines have been produced in two rather than five or more generations, and was the last major breakthrough to reduce cycle time [11–13]. The most popular being the maize DH system using the *R1-nj* color marker [14]. However, the different steps of the DH process (Figure 2) have biological and genotypic limitations. The success rates for haploid induction [11,15–17], adaptation to tissue culture (in the case of anther culture) [18], and doubling [19] have all been shown to be genotype-dependent in different crop species. Breeders using DHs will unintentionally practice recurrent selection for loci increasing success rates of the DH process [20], which might constrain genetic variation in breeding populations, at least for respective genome regions.

The *in vitro* nursery

Currently, the most efficient way to produce homozygous and homogeneous lines is through a combination of off-season nurseries (generations per year) and DH technology (homozygosity per generation). We propose the concept of an *in vitro* nursery, where new genotypes are formed by *in vitro* production of gametes and their subsequent fusion. Here, generation time is limited by how quickly somatic cells can form new gametes and how quickly these gametes can be fused.

Box 1. Genetic gain: the breeder's equation

The objective of plant breeding is the identification and development of superior individuals and families. The mean performance of breeding populations is increased through selection of individual plants with higher than average performance. This change in mean performance of the breeding population can be expressed as genetic gain in different forms, depending on the situation [6].

Genetic gain per cycle:

$$G_c = kch^2\sigma_P \qquad \text{[I]}$$

$$G_c = \frac{kc\sigma_A^2}{\sigma_P} \quad \text{where } h^2 = \frac{\sigma_A^2}{\sigma_P^2} \qquad \text{[II]}$$

As seen in Equation I in the case of one cycle of selection, k is the selection differential expressed in standard deviation units, representing the percentage of individuals selected and advanced to the next generation. The degree of parental control (i.e., genetic control of males, females, both sexes) is quantified in c. Narrow sense heritability (h^2) is a measure of what proportion of phenotypic variance (σ_P^2) can be explained by additive genetic variance (σ_A^2). Equation II can be derived by substituting σ_A^2/σ_P^2 for heritability. The additive genetic variance is the component of the genetic variance that is transmitted to the progeny (except in polyploids where some dominance variance is transmitted and in clonal breeding, where all genetic variance is transmitted).

Different selection schemes (e.g., half-sib, full-sib, selfed families) require different numbers of seasons to complete a full selection cycle. For comparison of alternative breeding schemes, the calculation of genetic gain per year is more informative than gain per cycle. This is achieved by dividing Equation II by the number of years (y) required per cycle.

Genetic gain per year:

$$G_y = \frac{kc\sigma_A^2}{y\sigma_P} \qquad \text{[III]}$$

Equation III can be expanded further for specific situations, when different environments and replications are used and to quantify variance that is contained within and among families in the selection scheme. These expansions are beyond the scope of this article; the reader is referred to [6] for an in-depth discussion of the different forms of the genetic gain equations.

By modifying the components in Equation III, breeders are able to maximize genetic gain. Some components are simpler to manipulate than others. This article focuses on the management of time (expressed as y) as a method to maximize genetic gain.

The general progression of the *in vitro* nursery is outlined in Figure 3. Tissue is extracted from the basal leaf section of selected genotypes and converted into an *in vitro* cell culture and induced to mitotically divide through application of growth regulators such as 2,4-D [21], which can be maintained in minimal space requirements in a laboratory setting with each cell callus occupying approximately 4 mm^2 [22]. Genotypes of interest are subsequently isolated and single somatic cells are induced to undergo meiosis for generation of new gametes. These gametes are subsequently fused to generate new genotypes in a similar way to the *in vivo* unification of pollen and egg cells. However, in contrast to the *in vivo* system, where the breeder would need to wait until seed maturity and the flowering of progeny to produce the next generation, fused diploid cells could immediately be induced to undergo meiosis within the *in vitro* system, and produce gametes for new crosses, or for artificial genome doubling to produce a new homogeneous/homozygous cell line [23]. Several techniques exist for fusion of plant gametes *in vitro*: electrically induced fusion, chemically induced fusion, and calcium induced fusion [24,25]. Successful fusion of plant

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