

Getting the 'MOST' out of crop improvement

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Unraveling the function of genes affecting agronomic traits is accelerating due to progress in DNA sequencing and other high-throughput genomic approaches. Characterized genes can be exploited by plant breeders by using either marker-aided selection (MAS) or transgenic procedures. Here, we propose a third 'outlet', 'molecular strengthening' (MOST), as alternative option for exploiting detailed molecular understanding of trait expression, which is comparable to the pharmaceutical treatment of human diseases. MOST treatments can be used to enhance yield stability. Alternatively, they can be used to control traits temporally, such as flowering time to facilitate crosses for plant breeders. We also discuss the essence for developing MOST treatments, their prospects, and limitations.

Understanding of the molecular basis of traits is accumulating

The amount of sequences deposited in GenBank (<ftp://ftp.ncbi.nih.gov/genbank/gbrel.txt>) increased from 11 billion to 165 billion base pairs from 2000 to 2014. Due to progress in high-throughput sequencing approaches (next- and third-generation sequencing [1,2]), resequencing of well-characterized species has become affordable [3,4], as well as *de novo* sequencing of species without reference genomes [5,6]. Even for polyploid species, major breakthroughs have been reported [7]. Resulting DNA sequence information can be converted into effective molecular marker applications [8,9] to generate genetic and physical maps, thus facilitating mapping of agronomic traits [10,11]. Alternatively, sequencing can be used directly for genome-wide association studies (GWAS; see **Glossary**) [12,13] or candidate gene-based association studies [14,15] to identify genes and intragenic polymorphisms associated with target traits. As a result, the number of discoveries of novel genes has increased exponentially [16,17]. In addition, functional [18] and comparative genomic studies [7,19] benefit substantially from progress in sequencing technology, contributing to the accelerated isolation and characterization of genes with impacts on agronomic traits [20,21]. Moreover, due to rapid progress in transcriptome analysis [22,23], chemical genomics [24,25], proteomics [26,27], metabolomics [28,29], and

emerging hormone studies [30,31], understanding of gene and protein function as well as gene networks and metabolic pathways has increased dramatically over the past decade. Traditionally, detailed molecular genetic information of trait expression is exploited by either MAS or transgenic procedures. However, the recent implementation of genomic prediction and selection [32–34] has caused a paradigm shift in plant breeding that questions the need for understanding the underlying molecular genetics (i.e., gene function or pathways) of agronomic traits. It was shown initially in animals and later in plant breeding, that a 'black box approach' based on low-cost and dense coverage markers across the genome [35,36] can efficiently enhance breeding programs. This raises two questions in relation to crop improvement. (i) How relevant is the understanding of gene and pathway information for agronomic trait improvement? (ii) In which ways can the

Glossary

Candidate gene-based association studies: a candidate gene is identified as a possible QTL based on the biochemical or developmental pathways affecting a quantitative trait. Candidate gene-based association studies are testing the hypothesis that there is a correlation between DNA polymorphisms in a candidate gene and the trait of interest. This approach assumes a good understanding of the biochemistry, developmental pathways, and genetics of the trait, and many genes may escape attention.

F2 enrichment: a method used for enrichment of favorable alleles at early generations. If many markers need to be selected, then the frequency of a target homozygous genotype will be low and a large population will be required. A two-stage selection strategy has been proposed to solve the problem. The first step is called F2 enrichment: F2 individuals carrying the entire set of target alleles in either homozygous or heterozygous form are selected, which takes advantage of the expected high frequency (0.75) of carriers (either homozygous or heterozygous) of the desired allele at each locus. The second step is to generate a population of more or less homozygous lines from the selected F2.

Forward genetics: forward genetics is based on phenotypic variation, which is used for gene identification. It seeks to identify the genetic basis of a phenotype or trait. For example, by generating random mutations, mutants with aberrant phenotypes will be isolated; then, by genetic mapping, the underlying mechanism related to a phenotypic change can be determined.

Genome-wide association studies (GWAS): an approach involving testing for trait associations of most of the segments of the genome, by genotyping and rapidly scanning densely distributed genetic marker loci covering the complete sets of DNA, or whole genomes. It is a good choice in the absence of detailed knowledge of the biochemical pathway of target trait expression.

Genomic selection (GS): used for improving quantitative traits in large animal or plant breeding populations based on high-density molecular markers across the whole genome. It is most useful for traits that are controlled by multiple QTL with minor effects rather than a small number of QTL with major effects. It can be described as marker-based selection without QTL mapping.

-Omics approaches: include genomics, metabolomics, proteomics, transcriptomics, and metabolomics; aim to characterize and quantify how biological molecules define the function and dynamics of an organism.

Reverse genetics: begins with DNA sequences, and attempts to assign phenotypes to sequence variation.

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accumulating -omics information be exploited, besides providing low cost markers? Comparable to medical genomics, we propose MOST treatments as alternative and potentially superior routes for exploiting molecular information in plants. Our objectives here are to: (i) systematically introduce the concept of MOST; (ii) compare the advantages and disadvantages of the three avenues for exploiting understanding of the molecular basis of agronomic trait expression (MAS, MOST, and transgenic methods); and (iii) use examples to illustrate the significance of MOST treatments.

Three major avenues to use molecular genomic information for crop improvement

Knowledge of genes affecting agronomic traits is successfully exploited in transgenic and MAS approaches for crop improvement. However, in human genetics, pharmaceutical genomics is the primary route for exploiting gene information [37–40], turning key molecules into drugs to provide health benefits [41,42]. This pharmaceutical approach is less explored in crop improvement, but has the potential to become a third important outlet to fully utilize the accumulating genomic information (Figure 1).

MAS

Once a gene has been identified, linked, gene-derived, or functional markers [43] can be used as diagnostic tools for breeders to select valuable parents or progenies. Currently, major MAS applications include marker-assisted backcrossing, marker-assisted introgression, gene pyramiding, marker-assisted recurrent selection, and F_2 enrichment [44,45]. Successes based on MAS have been reported, such as food quality improvement in tomato (*Solanum lycopersicum*) [46], yield improvement in maize (*Zea mays*) under water-limited conditions [47], gene pyramiding in rice (*Oryza sativa*) [48], and the development of disease-resistant soybeans [*Glycine max* (L.) Merr] [49]. However, successes recorded so far have mainly been for genes with major effects. By contrast, most agronomic traits are quantitatively inherited, with minor contributions from many genes. For those traits, genomic selection seems to be more promising [32], because it does not require prior characterization of genes or quantitative trait loci (QTL) affecting traits of interest.

Transgenics

Since the release of the first genetically modified (GM) crop variety in 1992 ('FlavrSavr' tomato), a massive expansion of GM crops has occurred. In 2013, 173 million hectares were planted with commercial GM crops (<http://isaaa.org/resources/publications/pocketk/16/default.asp>), especially for maize, soybean, and cotton (*Gossypium* spp.) [50]. Most of the transgenes that were introduced to these crops are related to pest, disease, or herbicide resistance. The Bt trait [a transgenic trait conferring resistance to lepidopteran insects found in *Bacillus thuringiensis* (Bt)] in cotton reduces costs relating to pesticides and labor, increases yield, and, thus, leads to economic and health benefits for farmers [51]. The main advantage of transgenic approaches is that they can utilize genes from other species, introducing

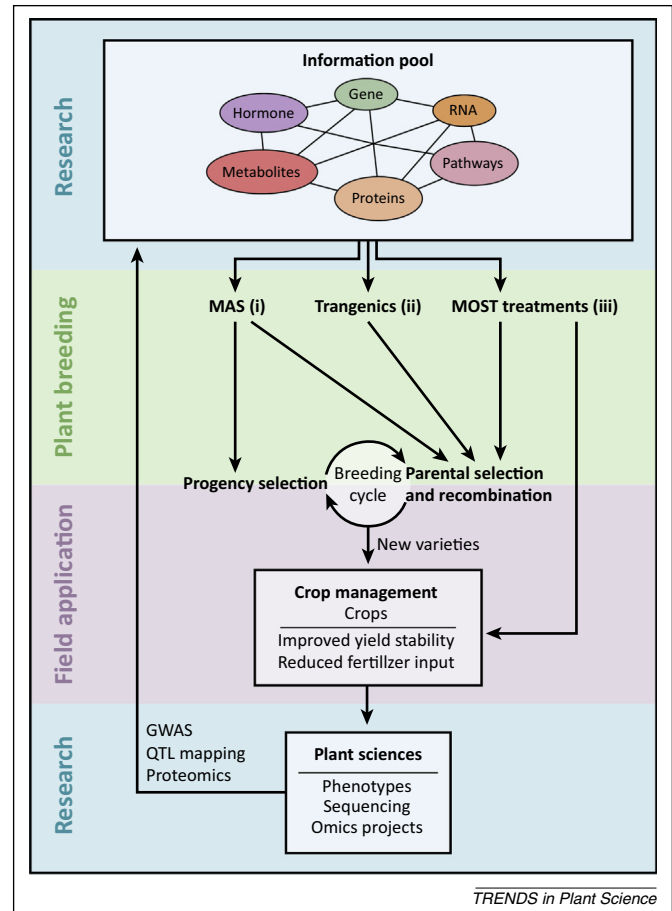


Figure 1. Three ways to utilize detailed molecular genetic information for crop improvement. Phenotypes generated from the field, high-throughput sequencing techniques, and various -omics approaches generate vast amounts of valuable data in the information pool for crop improvement. Traditionally, this detailed molecular genomic information is exploited by marker-aided selection (MAS) (i) and transgenic approaches (ii) for producing better new varieties. MAS can be used for both parental and progeny selection, whereas transgenic methods provide opportunities for introducing novel beneficial traits. Molecular strengthening (MOST) treatments (iii) as a third outlet can facilitate the breeding process (i.e., flowering time regulation or controlled crosses). MOST treatments can also be applied directly in the field for crop management, for reduced fertilizer input, or improved yield stability due to increased biotic and/or abiotic resistance. Abbreviations: GWAS, genome-wide association studies; QTL, quantitative trait loci.

novel beneficial traits. However, legal approval for a new transgenic product costs approximately US\$35 million for the regulatory process (<http://www.isaaa.org/gmaprovaldatabase/default.asp>). As a consequence, only a few transgenic events promising sufficient return on investment are used for crop improvement. This limits the number of genes and crop species for which the use of transgenic varieties is economically feasible. Moreover, public concern about the safety and environmental impact of GM crops prohibits their use in various countries. Novel genome-editing methods [52] might provide a fresh perspective with acceptance of transgene products due to a more targeted manipulation of genomes.

MOST

We will use the term 'MOST' for the nongenetic manipulation of crop improvement, based on understanding of molecular mechanisms. Informed by -omics approaches, molecules can be produced or extracted to target biological

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