



Short Communication

Volume 26 Issue 2 - August 2021
DOI: 10.19080/ARTOAJ.2021.26.556328

Agri Res & Tech: Open Access J

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When Plant Breeding Meets Population Genomics



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Submission: August 19, 2021; **Published:** August 23, 2021

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Abstract

The functional genetic variation of wild relatives has great potential in producing the next generation of crop plants, and fast advances in genome sequencing are facilitating the characterization of the wild and domesticated gene pools. However, the common traditional approaches in plant breeding can hinder the exploitation of this genetic resource. New approaches that attempt to exploit the genetic variation of wild relatives uses a combination of genomic analyses and novel introgression crosses. A key step in the transition from hunting-gathering to agriculture-based societies was the domestication of plants (and animals). This key technological procedure has allowed the evolution of wild plant species into crop species. However, together with the creation of a handful of crop species that now provide 80% of the caloric intake of the human population, the cultivation and selective procedures have gradually depauperated the functional diversity of crop species. In the face of climate changes and growing human population, there is great pressure to improve our stock of domesticated cultivars and the fraction of functional diversity that resides in domesticated plant species is not enough to support future breeding programs. To recover the functional diversity lost during hundreds of years of selective procedures, several studies have been carried out to characterize the gene pool of wild and crop species with the final aim to reintroduce genetic variation of wild donors into the recipient crop plants. Here, I review some novel and exciting routes that make use of the power of population genomics and further narrow the gap between genomic studies and practical breeding.

Keywords: Practical breeding, Ecological adaptation, Environmental conditions, Genomic analyses, Aegilops, Tauschii

Characterizing The Functional Diversity

The advent of genome sequencing resources has greatly facilitated the genome-wide characterization of the functional diversity of elite cultivars, landraces, and ecotypes from wild relatives [10]. In assessing the whole range of the functional diversity that span the wild ecological adaptation, current approaches target the geographical distribution of wild crop relatives that are grown at different environmental conditions. Clines of drought, salinity, altitude are often sought after and exploited in these studies [2]. Genotyping by genome sequencing can powerfully discover genic SNPs and haplotypes associated with plant adaptation [1]. To further assist the process of characterization of the functional diversity, several population parameters have been developed over decades of population genetics studies and are still widely employed in population genomics. Genomic analyses of crop landraces and wild relatives is also of valuable use for understanding the extent of genetic variation lost during domestication and in providing information on the genetic basis of domestication, selection, and adaptation events. Despite the inevitable genetic bottleneck occurring because of the domestication event, evidence is gathering in

suggesting that some variation might have been recovered through historic introgression of alleles from wild relatives into the domesticated lines [3-5]. The first attempts in identifying domestication genes were carried out by QTL mapping but were followed by population genomic and genome-wide association studies [6]. The advantage of using population genomics is that a population-level genome-wide map of SNP variation derived by such studies can be interrogated for other aspects associated with the domestication process. For example, with the analysis of genetic differentiation among populations and the extent of haplotype sharing, one can identify allelic variants subjected to selection during improvement [7].

Introgressing The Functional Diversity

Introgression of the genetic variation of wild relatives into crop species can be seen as the final goal of the characterization of the functional diversity, but it can present substantial challenges for several reasons. Reduced cross ability and incompatibility can prevent the formation of F1 hybrids and ultimately the transfer of useful genetic traits from the wild donor to the receptor.

Reduced meiotic chromosome pairing in hybrids can also prevent the production of further generations, and backcrossing, further impairing the introgression of traits of interest in the crop species. However, cross ability is genetically determined [8, 9], and genomic studies can reveal the chromosomal regions and the genes involved. Second, introgression is not uniform across the genome and is affected by both selections acting on introgressed regions and by the recombination rate [3]. It has long been observed that crossing over frequencies tend to decrease between regions with increased sequence divergence [10]; therefore, introgression of divergent chromosomal regions can be substantially hindered by the local low recombination rate. Some interesting approaches have been developed in challenging crop species such as the hexaploid wheat. The DD wheat genome is known to be derived by ancestors related to *Aegilops tauschii*. A recent paper uses population genomics to describe the overall genetic variation of *A. tauschii*, together with introgression methods for exploiting the wild DD gene pool [11]. To overcome ploidy level differences between wheat and *Aegilops*, together with endosperm abortion that usually occurs in cross-species breeding, the introgression approach included the generation of a synthetic octoploid pool followed by successive backcrossing to obtain wheat hexaploid lines. The breeding approach allowed the transfer of the core *A. tauschii* genetic variation, represented by more than 80 *A. tauschii* natural accessions from five sub lineages, into wheat in 30 months, and the characterization of the introgressed wheat lines by high-throughput genome typing and phenotyping [11]. Another major obstacle arising when introgressing traits of interest into crop species is the occurrence of linkage drag, the transfer of inferior unwanted traits together with the trait of interest. However, it is not always clear whether these unwanted phenotypic traits are the result of linkage drag or pleiotropy. Linkage drag can potentially be overcome by identification of rare recombinants between genes that are tightly linked in repulsion. Negative pleiotropic interactions are also difficult to resolve, and usually require several backcross generations before the pleiotropic effect is reduced. In either scenario, it is often required to determine the cause of the negative outcome of the introgressed genes. Classical breeding approaches use a biparental population, which suffer from low mapping resolution, due to the limited number of recombination events. An alternative strategy is the use of association mapping, which uses linkage disequilibrium data from several populations to localize small- and large-effect QTLs. The low cost of genomic sequences make these approaches now affordable and cost-effective. However, the introduction of possible population structure can obscure the significance of QTLs in these populations. Promising approaches to understanding the genetic negative effect of introgression could also come from the use of multi-parental (MAGIC) crossing populations [12,13]. MAGIC lines are related by crossing several founders in several paired combinations to create a large set of recombinant inbred lines. After a few generations, the descendants will harbor a genetic

mosaic of the multiple founder parents. Successful employment of MAGIC populations provided significant QTL identification for grain yield and other quality traits in rice as well as interaction among traits [13]. Future attempts should target the fine-scale resolution of introgression and the negative effect of it with MAGIC populations.

Box 1 Common Estimators Used in Population Genomics

Genetic diversity (ϕ and π)

To measure the genetic diversity across the genome, two parameters are often used: π measure the pairwise distribution of genetic diversity, whereas ϕ , the Watterson's estimator, counts the number of polymorphic sites. Tabulation of π (and ϕ) are often used to unravel demographic changes that inflate or deflate the effective population size. Genomic variation maps built by comparing π (or ϕ) in wild and cultivated populations can thus provide insights into the extent of the genome-wide domestication bottlenecks and the identification of outliers of reduced diversity that could correspond to domestication-selective sweeps [14, 15]. These outliers could represent genes of functional importance, selected for during the domestication and improvement processes.

The fixation index (F_{ST})

Has been widely used as a measure of population structure, but it has great application in uncovering regional variation of genomic divergence. By scanning the genome for F_{ST} windows of F_{ST} outliers can be identified, which represent genomic regions that have undergone genetic differentiation due to inversions, and generally to lack of historic recombination between homologous regions. Alternatively, elevated F_{ST} can also indicate introgressed regions from an extant or extinct relative.

The F_{IS} statistics

Provides a measure of deviation from the Hardy-Weinberg expectation of heterozygosity. It allows the identification of outlier loci that have a deficit (or an excess) of alleles in the population. A deficit of alleles, or deficit in heterozygosity, usually corresponds to genomic outlier loci that underwent recent selective sweeps. In other words, this estimator is a powerful detector of genomic regions that have swept through the population because of conferring an evolutionary advantage.

Effective population size (N_e)

It is a measure of the number of breeding individuals that live to reproductive age and produce offspring. It reflects the rate of loss of genetic variation and the efficiency of natural selection in purging deleterious mutations and in fixing beneficial mutations. The concept of effective population size is central to plant breeding, as it quantifies the amount of genetic drift in the breeding programmers, the likelihood of inbreeding and the chance of loss of valuable traits.

Linkage disequilibrium (r^2 and D)

Scanning the genome for decay of linkage disequilibrium can be carried out to identify regions of suppressed or reduced recombination. Reduced recombination can evolve to maintain functional haplotypes that can segregate in the population and can be associated with the evolution of ecotype divergence [16]. An important application of linkage disequilibrium analysis is the inference of fine scale localization of QTLs along each chromosome [17].

Patterson's D statistic

Detecting ancient admixture can reveal genomic regions that have been introgressed and maintained because of conferring adaptation. D statistic was developed to infer ancient introgression in human genomes [18,19], but has since been widely used in several model and non-model species, including plants of agricultural interest [20].

Acknowledgment

I am supported by a Challenge fellowship program of SRUC.

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DOI: [10.19080/ARTOAJ.2021.26.556328](https://doi.org/10.19080/ARTOAJ.2021.26.556328)

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