Molecular Plant
Spotlight

A new phase of treasure hunting in plant genebanks

The United Nations has estimated that the world population will surpass 8 billion on Nov. 15, 2022, and will continue to rise to 11.2 billion by 2100. Considering that agricultural resources are limited, it will be a huge challenge to produce sufficient food to feed such a rapidly rising global population. Furthermore, the ongoing climate changes are adding more pressures on worldwide crop productions. To cope with these problems, it is both imperative and urgent to develop the crop cultivars with higher yield potential, improved nutritional quality, and better resilience to environmental stresses.

The crops cultivated today have generally experienced dramatic losses of genetic diversities owing to domestication and breeding selection (McCouch et al., 2020). Consequently, enhancing genetic diversities is a top priority for developing resilient crops with both high yield potential and wide adaptability to changing environmental conditions (McCouch et al., 2020). Furthermore, there are increasing demands for crops with diversified quality attributes for human consumption, livestock feeding, and industrial uses. Thus, it is ideal to have well-characterized plant genetic resources (PGR) that can be readily picked up to develop desired crop varieties both timely and efficiently. This ideal goal can be quickened by making effective uses of the genetic diversities in plant genebanks, most of which are still hidden and untapped at present.

Genebanks: The treasure troves for crop improvement

Scientists and nations have long realized the vital importance of PGR for crop improvement and maintaining food security, with conscientious efforts to collect plant varieties and crop wild relatives starting around 1900 (Dzyubenko, 2018). Currently, there are approximately 1750 genebanks holding about 7.4 million accessions of PGR across the globe (Sofi et al., 2020) (Figure 1A). Over the past 120 years, PGR has made significant contributions to many aspects of crop improvement (McCouch et al., 2020; Varshney et al., 2021). Genes transferred from PGR have facilitated the control of rice blast and bacterial blight epidemics as well as barley powdery mildew and yellow mosaic diseases. Development of wheat with higher grain protein content and rice with improved fragrance also benefited from PGR maintained in genebanks. Despite many successful examples, there are constant concerns regarding how to make more productive uses of PGR to expedite cultivar innovation (Schulthess et al., 2022).

Genomic prediction and genomics-informed selection of elite PGR: A new phase of utilizing PGR

Since 1900s, the journey of PGR exploitation can be roughly divided into four phases (Figure 1B). In phase I (1900s–1970s), Mendelian genetics and cytogenetics are used to study PGR with the aid of morphological, biochemical, and cytogenetic markers in small-scale experiments. This permits the transfer of genes or alien chromatins singularly from PGR to crop plants by conventional crossing, which culminates in the successful breeding of green revolution varieties and elite cultivars with wild introgressions conferring resistance to biotic and/or abiotic stresses (e.g., the short arm of rye 1R chromosome into wheat) (Waines and Ehdaie, 2007). Phase II (1980s–1990s) is steered mainly by molecular genetics, which uses primarily PCR-based DNA markers anchored on genetic linkage maps to characterize PGR in low-throughput experiments. This has facilitated allele mining and utilization of major-effect genes and quantitative trait loci (QTLs) in crop improvement. Notable successes in this phase include the use of PGR genes (alleles) to improve tomato and rice traits, especially disease resistances (Ebert and Schafleitner, 2015; McCouch et al., 2020). Phase III (2000–2015) comes along with early developments in plant genomics, i.e., complete sequencing of *Arabidopsis* and rice genomes and the generation of draft genome sequences for many crop species and crop wild relatives. This phase is typified by the use of single-nucleotide polymorphism (SNP) markers with often limited genome coverage for genotyping PGR populations in moderately high-throughput experiments. The results of genome-wide association studies (GWAS), coupled with those of functional genomics research, have substantially improved our understanding of the genetic architecture of complex agronomic traits and the molecular functions of key trait genes. This allows simultaneous mining and co-transfer of multiple target genes and QTLs from PGR for concordant crop trait improvement. The accomplishments of this phase are illustrated by the insights generated in many large-scale rice GWAS experiments (Wang et al., 2020). Phase IV (2016–present) begins with the pioneering demonstration in sorghum of genomic prediction as a cost-effective global strategy for accelerating PGR evaluation and utilization (Yu et al., 2016), which is further advocated and developed by a recent study in wheat (Schulthess et al., 2022).

In the work by Schulthess et al. (2022), the authors designed and proved the concept of genomics-informed selection of elite PGR based on GWAS and genomic prediction approaches for improving wheat yellow rust (YR) disease resistance and grain yield (GY) (Figure 1C). Central to their study is the availability of a large panel of diverse wheat germplasm accessions with molecular passport data (Mascher et al., 2019), innovative phenotyping practice for the complex trait GY (Longin and Reif, 2014), and proper assembly of a trait-customized core collection

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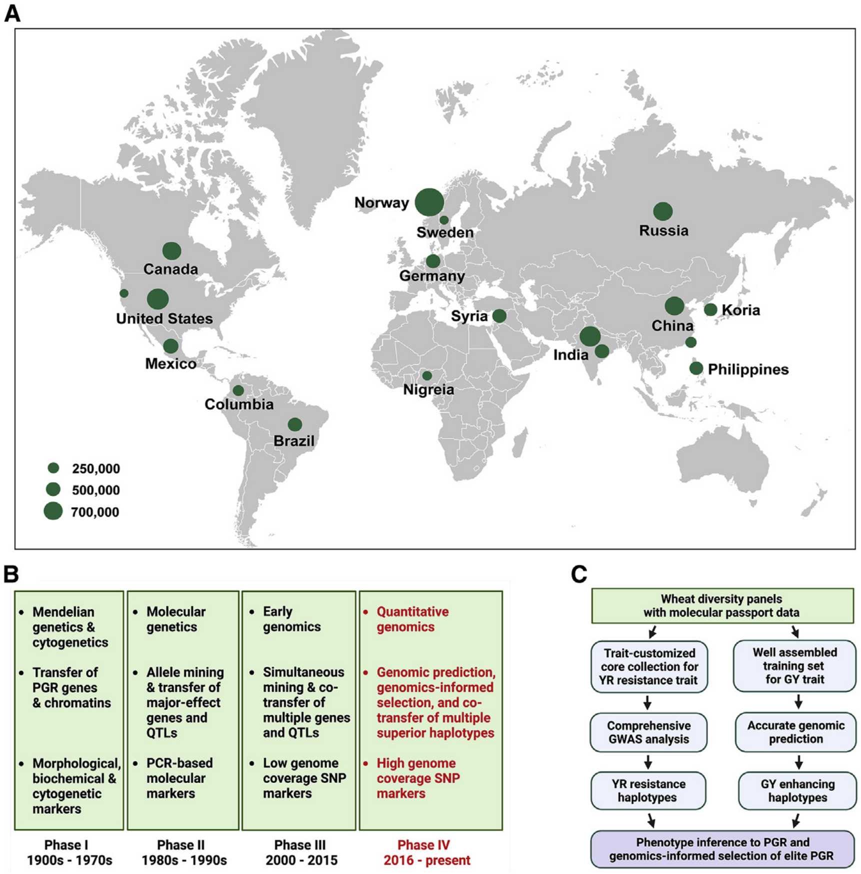

Figure 1. A new phase of plant genebank exploration characterized by genomics-informed selection of elite PGR for crop improvement.

(A) Distribution of major plant genebanks in the world. Number of PGR accessions held in each gene bank is derived from Dzyubenko (2018) and Sofi et al. (2020).

(B) Main features of the four phases of plant genebank exploration, with those of phase IV highlighted in red.

(C) Genomics-informed selection of elite PGR for improving wheat yellow rust (YR) resistance and grain yield (GY) through identifying and co-transferring multiple superior haplotypes.

Figure 1 was created with the software BioRender (BioRender.com).

(T3C) for GWAS or a training set for genomic prediction. Comprehensive GWAS experiments reveal 30 *Yr* resistance-conferring haplotypes specific to T3C PGR but absent from European elite cultivars. Importantly, 23 of the 30 identified haplotypes are likely to represent unutilized YR resistances carried by PGR (Schulthess et al., 2022). This provides ample opportunities for selecting the donor lines appropriate for either isolating new *Yr* genes or enhancing YR resistance in wheat breeding programs, both of which will be highly efficient as the PGR donors already have rich genomic and phenotypic information.

Reliable phenotyping of wheat GY in hundreds and thousands of PGR accessions is a formidable task considering that many of them were collected long ago and have not adapted to current cultivation environments. However, Schulthess et al. (2022) creatively circumvented this problem by using Elite 3 PGR F_1 hybrids to phenotype GY and then to estimate the breeding value of corresponding PGR for GY improvement. By conducting genomic prediction with 29 844 SNP markers and 597 PGR breeding values (estimated using F_1 hybrids) as a training set, GY values are inferred with very high prediction accuracy for hundreds and thousands of wheat accessions within and across genebanks (Schulthess et al., 2022) (Figure 1C). As anticipated, the PGR accessions with higher GY breeding values inferred by genomic prediction tend to be superior parents for producing the offspring with largely elevated yield potential especially in three-way ($Elite_2$ 3 ($Elite_1$ 3 PGR)) crosses.

Perspectives

Just as plant breeding is transitioning to stage 4.0 (Wallace et al., 2018), we have now seen the dawn of phase IV plant genebank exploration (Figure 1), with both being made possible by major advances in plant genomics (Varshney et al., 2021). New technological breakthroughs (such as those in precision genome editing and high-resolution phenomics) and their efficient integration will certainly fast track PGR utilization in further crop breeding programs (Mascher et al., 2019).Thus, millions of PGR accessions stored in genebanks may all have a chance to contribute to global crop innovation and food security in one way or another.

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