Redesigning the exploitation of wheat genetic resources

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More than half a million wheat genetic resources are resting in gene banks worldwide. Unlocking their hidden favorable genetic diversity for breeding is pivotal for enhancing grain yield potential, and averting future food shortages. Here, we propose exploiting recent advances in hybrid wheat technology to uncover the masked breeding values of wheat genetic resources. The gathered phenotypic information will enable a targeted choice of accessions with high value for pre-breeding among this plethora of genetic resources. We intend to provoke a paradigm shift in pre-breeding strategies for grain yield, moving away from allele mining toward genome-wide selection to bridge the yield gap between genetic resources and elite breeding pools.

Strong demand to unlock genetic resources for wheat breeding

Worldwide crop production needs to be doubled to feed an estimated world population of 9 billion by 2050 http://www.fao.org/fileadmin/templates/wsfs/docs/expert_paper/How_to_Feed_the_World_in_2050.pdf, but current yield gain trends are insufficient to meet this rising demand [1]. Wheat (*Triticum aestivum* L.) is one of the most important food and feed crops, providing one-fifth of the total calories for the world's population [2]. Therefore, boosting the rate of genetic improvement of wheat is of high priority, and relies on an efficient exploitation of genetic variation through breeding [3–5]. More than 560 000 wheat accessions are maintained in nearly 40 gene banks globally [3]. Wheat breeding, however, is currently restricted to a highly limited sampling of this genetic diversity [6]. Spatial diversity of wheat is even narrower considering that only a few varieties are widely grown [7]. Consequently, unlocking the biodiversity of wheat genetic resources is crucial for averting future food shortage.

Three-stage strategy to exploit wheat genetic resources

A three-stage strategy has been recently proposed to exploit this barely untapped treasure of diversity [8]. First, accessions should be genotyped to assess their genetic relationships and to provide a basis for systematic selection of representative genotype subsets for detailed studies. Genotyping should also consider major adaption genes to facilitate grouping of accessions. The second step entails phenotyping of gene bank accessions. Combined with genome-wide data, this approach would facilitate targeted selection of specific genotypes from the plethora of plant genetic resources for use in breeding. As a third step, all information accumulated under steps one and two must be made widely available in conjunction with available passport and pedigree data through a capable database platform for exploitation by third parties.

Implementing the first step strongly benefits from rapid developments in sequencing technologies, which have led to drastic increases in genotypic resolution of wheat over the past decade [9–13]. Nevertheless, there still exists the need to establish cost-efficient and high-quality marker systems with a low degree of ascertainment bias [14] that will also allow reliable capture extended structural polymorphisms such as large indels or copy number variation. The enormous amount of sequence data, composed of fingerprints of whole gene bank collections (http://www.breedwheat.fr/, http://www.seedsofdiscovery.org/), has led to the development of biodiversity information facilities (http://www.wheatinitiative.org/research/databases). Intensification of this endeavor is clearly required to meet growing demands for gene bank management and breeding. By contrast, the development of sustainable phenotyping concepts to facilitate and identify the breeding values of genetic resources is still in its infancy. Here, we endeavor to stimulate debate and research

Glossary

Allele: genes at one locus can exist in different forms, which are called alleles.
Breeding values: the breeding value of an individual is defined as the relative performance of its progenies.
Genome-wide selection: genome-wide selection uses estimates of effects of a high number of markers distributed genome-wide to predict the performance of an individual based on its marker profile. Marker effects have to be estimated in large training populations to be reliable.
Harvest index: the harvest index refers to the proportion of grain yield in relation to the total plant biomass.
Hybrid: a hybrid is a cross between two defined parents. Hybrids receive one allele from the male and one allele from the female. If the parents possess different alleles at a particular gene the hybrid is heterozygous at this gene.
Marker-assisted backcrossing: in marker-assisted backcrossing, genetic material from a donor line, such as a genetic resource, is introgressed by repeated crosses to a recipient, such as an elite line. Thus the proportion of genome contribution of the donor line decreases with every backcross generation by one half in comparison to the previous generation.
Marker-assisted selection: marker-assisted selection is based on estimates of marker effects for important genes. The performance of individuals in a population is predicted based on their marker profiles. In contrast to genome-wide selection, marker-assisted recurrent selection focuses on discrete markers linked to known genes with large effects on trait performance.

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on effective phenotyping concepts for grain yield applicable to wheat gene bank accessions readily crossable with elite material, and to provoke a paradigm shift in the way genetic resources are exploited for complex traits.

Uncovering the hidden breeding values of genetic resources

Phenotyping gene bank accessions is considered the most intellectually challenging and resource demanding task for making them accessible to breeding programs [8]. The determination of biotic and abiotic stress traits relies upon high-throughput phenotyping techniques developed for controlled and field conditions [15–17]. By contrast, evaluation of the most important agronomic trait in gene bank accessions, grain yield, is highly challenging considering the presence of major deleterious alleles or the absence of important agronomic genes, which strongly influence lodging, harvest index (see Glossary), and disease susceptibility. Hence, the main effect of these loci and their interactions with other involved genes can hypothetically mask the potential grain yield of genetic resources in evaluations of their performance. The difficulty of uncovering true breeding values is exemplified by the broad introgression of dwarfing genes into elite wheat germplasm during the course of the early green revolution. The use of dwarfing genes enabled breeding of shorter, stiff-strawed varieties with a substantially enhanced harvest index, which spurred an intensification of wheat production [18]. Most available genetic resources in gene banks predate the green revolution and, thus, do not contain dwarfing genes. Consequently, genetic resources are not adapted to the currently used intensive wheat production systems, precluding the accurate determination of their breeding value for grain yield (Figure 1A).

Here, we propose the exploitation of recent advances in hybrid wheat technology [19,20] to unlock the yield potential of genetic resources in hybrid backgrounds (Figure 1B). The principle of this strategy relies on dominance effects of favorable over deleterious alleles for major genes, whereby a predefined elite variety carrying favorable alleles at relevant genes is used as a parent in crosses with novel genetic resources. The heterozygous hybrids of these crosses are expected to be characterized by favorable alleles that annul, or at least reduce, the effects of deleterious alleles. Consequently, less-biased breeding values of genetic resources are unraveled in an otherwise elite-like background rather than by testing the genetic resources *per se*.

The proposed hybrid strategy has been successfully used to evaluate the breeding value of genetic resources of outbreeding crops such as maize [21–23] and rye [24]. Recent large-scale studies on the genotype–phenotype map of hybrid wheat have concurred that the assumption of favorable dominance effects for major adaptation genes is reasonable [25–27]. Consequently, the hybrid strategy proposed here possesses significant potential for uncovering the breeding value of wheat genetic resources.

Alternative phenotyping concepts for grain yield are time-consuming

Evaluating the yield potential of the performance of an inbred line is obscured by the presence of deleterious alleles and/or absence of relevant genes. Instead of employing hybrid wheat technology as proposed in this treatise, key agronomic alleles and genes can be introgressed and fixed by applying marker-assisted selection [28] in conjunction with intensive field evaluation of grain yield performance. Such marker-assisted selection would need to be implemented for every accession, and would represent a costly, laborious, and time-consuming strategy. The same constrain holds true for attempts to evaluate the individual yield potential of particular genome segments from genetic resources in the background of elite lines using, for instance, marker-assisted backcross selection [29].

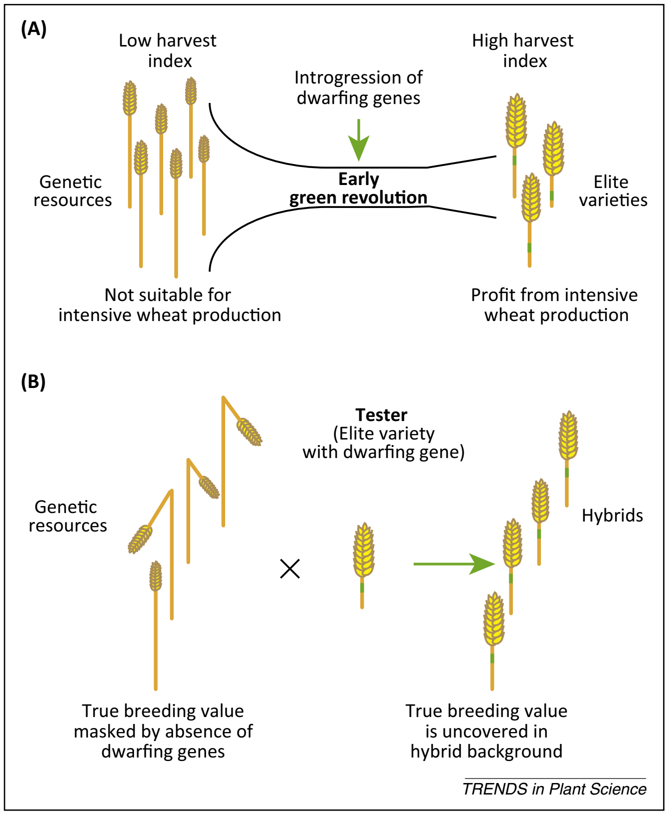

Figure 1. Concept of a hybrid wheat strategy to uncover the masked breeding values of genetic resources. **(A)** Most genetic resources resting in gene banks are tall and exhibit small ears (i.e., have a low harvest index). The early green revolution dwarfing genes were widely introgressed into elite varieties to facilitate intensive wheat production, and to increase grain yield through an enhanced harvest index. Evaluating the yield potential of genetic resources under current intensive wheat production standards is very difficult because lodging and low harvest index mask true breeding values for grain yield. **(B)** In the hybrid wheat strategy, genetic resources are adapted to intensive wheat production in a single step by crossing them to a defined elite variety carrying a dominant dwarfing gene. The dominant action of the dwarfing gene produces an acceptable plant height in hybrids, and allows the accurate estimation of the breeding values of genetic resources for current wheat production systems.

The yield potential of wild wheat relatives that are not directly crossable with hexaploid wheat but require for instance embryo rescue approaches cannot be evaluated with the proposed hybrid strategy. One of the wild relatives, *Aegilops tauschii* as the donor of the D genome, is introgressed via synthetic hexaploid wheat lines [30] typically produced by crossing *A. tauschii* with elite durum wheat (*Triticum turgidum*) lines carrying the A and B genomes, followed by one or two generations of backcrossing to elite lines [31]. Consequently, use of synthetic hexaploid wheat lines is conceptually very similar to the