

## Reinventing the Green Revolution by Harnessing Crop Mutant Resources

The current genetic makeup of crop plants has resulted largely from a narrowing and only recently, a diversification in variation (Abbo et al., 2014). Crop domestication generally has been based on a relatively small number of phenotypic changes that result in the loss of traits important for a wild grass but undesirable for farming (Meyer and Purugganan, 2013). When systematic breeding started a century ago, breeders focused on addressing defects in genotypes, such as disease susceptibility. The transitions from wild grasses to land races and then, to elite genotypes familiar to us as crops were accompanied by a substantial narrowing of genetic diversity (Kovach and McCouch, 2008). Today, breeders seek to improve diversity by tackling specific traits and bringing in novel alleles from land races or wild relatives.

A modern breeding program will have several objectives. The first of these is maintenance breeding and protection of crop yield by managing shifts in pathogens, environmental conditions, farming practices, or quality demands. The breeder will seek to improve yield stability across years and environments. All breeding programs need to release varieties that show improved performance relative to existing lines across a range of conditions. This goal demands new alleles or genetic combinations and in most cases, involves making crosses between elite lines followed by extensive screening of the segregating progeny. The approach has delivered steady yield gains over many years, although breeders always hope for a major change that will result in a big jump in yield. Jumps in yield do happen but rarely do they lead to increases of more than a few percent. When these changes happen, the new germplasm rapidly dominates in breeding programs. Larger yield jumps are known, but their occurrence is even more rare. The introduction of dwarfing genes that underpinned the green revolution for wheat (*Triticum aestivum*) and rice (*Oryza sativa*) is the best known example. It provided a big yield improvement by changing the harvest index, which is the proportion of plant biomass in the harvested grain, and introducing short stiff stems that protect against lodging.

In wheat, the green revolution dwarfing alleles at the *Reduced height1* (*Rht1*) locus, *Rht-B1b* and *Rht-D1b*, which reduce growth in response to GA, have been widely deployed in wheat breeding programs around the world (Peng et al., 1999; Hedden, 2003). Relying on these alleles may not have been the best means to introduce dwarfing, because the *Rht1* mutants reduce biomass across many tissues and can affect growth under some environments. For example, coleoptile length is reduced

in the *Rht1* mutants, and this poses a problem for germination if the seed is sown deep, a common practice in minimum till farming (Rebetzke et al., 2014). Consequently, modern breeding includes a search for new mutants that will reduce overall plant height and maintain a strong stiff stem but also show early vigor, long coleoptiles, and normal root development—in short, a search for new dwarfing mutants.

Before the advent of modern molecular biology and genomics, mutants were a key resource in studying genetic and biochemical processes and pathways. Plants, such as barley (*Hordeum vulgare*), maize (*Zea mays*), and tomato (*Solanum lycopersicum*), were model organisms, because there existed large collections of quite well-defined mutants (well defined in a phenotypic rather than a molecular sense). With the advent of molecular biology, genome size became a major driver in determining which species should be treated as models, simply because of the difficulty of working with large genomes, and mutant resources moved to the background. Nonetheless, maintenance and characterization of barley mutants continued (Franckowiak and Lundqvist, 2012), and a large collection of near-isogenic lines for barley mutants was generated (Druka et al., 2011). As genomics tools developed in barley (Mayer et al., 2012), they became a ready resource for positional cloning of genes associated with the mutations.

In this issue, Dockter et al. (2014) have made use of the mutant resources in barley, the improvements in our knowledge and understanding of the hormonal control of plant development, and the new barley genomic resources to provide a series of options for both generating and screening for new dwarfing mutations. Dockter et al. (2014) began by targeting an alternative pathway to GA sensitivity that underpinned the green revolution dwarfing genes. The brassinosteroid pathway (Bai et al., 2012) had previously been suggested as a potentially useful target for controlling developmental traits in crops (Vriet et al., 2012). The extensive collection of barley mutants was brought into play. Dockter et al. (2014) took advantage of the large number of height and short culm mutants (Franckowiak and Lundqvist, 2012) that could be categorized based on anatomical and developmental traits to identify likely candidates for mutations in the brassinosteroid pathway. From a set of 160 near-isogenic lines, 16 potential brassinosteroid mutants were identified. Dockter et al. (2014) also used a fresh mutant screen to show the efficacy of their selection criteria. In total, mutations in four genes involved in brassinosteroid biosynthesis or signaling were identified.

In short, the study described by Dockter et al. (2014) is important for several reasons. First, it outlines an effective strategy for finding new mutants that can be

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applied in a variety of future studies. Importantly, barley and wheat are very closely related, and the work in barley is readily transferrable to wheat. Second, the work reinforces the value of the barley mutant resources and the genomic information to support gene discovery, and it underscores barley as an attractive crop model. Third, we see in this work an elegant demonstration of the power of combining detailed anatomical studies, physiology, biochemistry, genetics, and genomics to clarify a complex development pathway in a crop plant. No doubt, the results will encourage both wheat and barley breeders and stimulate new and strategic thinking in a search for additional mutations in the brassinosteroid pathway as an alternative to the current dwarfing mutants.

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