

Review

Application of advanced backcross quantitative trait locus (QTL) analysis in crop improvement

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Domestication of crops is widely believed to be accompanied by a bottleneck that greatly reduces genetic diversity. This narrowing of genetic diversity restricts crop plant improvement by limiting the range of valuable traits available for use in modern plant breeding. Wild species are a broad resource to widen the germplasm and improve the traits in crop cultivars. However, genetic variation between species is often related to reproductive isolation or to adaptation to different natural environments and many introgressed genes prove difficult, if not impossible, to use in crop improvement. Advanced Backcross QTL (AB-QTL) analysis is an efficient method to utilize wild species by simultaneous discovery and transfer of valuable QTLs from unadapted germplasm into elite breeding lines. A number of its application in crop genetics and breeding are reviewed in this paper.

Key words: Advanced backcross, QTL, crop plant breeding.

INTRODUCTION

Status of crop diversity in the domesticated germplasm

Crop domestication is a selection process imposed by humans to adapt plants to suit the needs of humans. Favorable traits that arise from spontaneous mutation and recombination occur in wild populations and are continually selected at various stages of growth (Gepts, 2002). Desirable modifications include improved seed fertility, increased seed number, modified plant architecture, altered seed size and shape, flowering times adapted to different areas and decreased seed shattering and dormancy (Pourkheirandish and Komatsuda, 2007). Interestingly, many traits selected under domestication are actually deleterious in the wild. As a consequence, cultigens of many species may not survive without human intervention in planting and harvesting (Gepts, 2002). As such, many domestication genes represent a loss rather than a gain of function as indicated by their recessive nature (Gepts, 2002).

Although domestication has led to many traits in a cultigen that fit the needs or desires of humans such as

increased productivity and better quality, they also came at the price of domestication bottlenecks that generally reduce the gene diversity relative to their wild ancestors (Tanksley and McCouch, 1997). Two key processes that govern the reduction in genetic diversity in a crop lineage during domestication are selection by humans for desirable "domestication traits" and genetic drift in the form of "domestication bottlenecks" (Eyre-Walker et al., 1998).

Following domestication, the genetic diversity variation in crop plants has continued to be reduced by another force—modern plant breeding. Over the past century, the development and successful application of plant breeding methodologies has produced the high-yielding crop cultivars on which modern agriculture is based. Yet, ironically, it is the plant-breeding process itself that threatens the genetic base on which breeding depends. Because new cultivars are usually derived from crosses among genetically related modern cultivars, genetically more variable, but less productive, primitive ancestors are excluded. Wheat is a good example of crops with very narrow genetic bases. The majority of hard red winter wheat varieties in the United States originated from just two lines imported from Poland and Russia (Tanksley and McCouch, 1997). That wheat germplasm with a narrow genetic base might also lead to agronomic disasters first came into concern from several severe epidemics of shoot fly (*Atherigona* spp.) and karnal

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bunt (*Tilletia indica*) in India in the 1970s (Reif et al., 2005).

The continual genetic erosion in modern germplasm could result in broad susceptibility to abiotic hazards or newly emerging biotic hazards like insect pests and disease, thereby threatening long-term food and feed security. The outbreak of Southern corn leaf blight in 1970 brought this risk sharply into focus. This disease drastically reduced corn yields in the United States and was attributed to extensive use of a single genetic male sterility factor that, unfortunately, was genetically linked to disease susceptibility (Tanksley and McCouch, 1997). Investigation of trends in cotton yield improvement showed that the rate of change in cotton yields declined from 1985 to 1998. Furthermore, from 1992 through 1998, the actual yield also declined and appears to be closely associated with increasing genetic vulnerability (Paterson et al., 2004). Growing concerns about genetic vulnerability have stimulated renewed interest in utilizing the more distant gene pools as a source of genetic variation in breeding programs. The wild progenitors and closely related species often contain novel alleles and thereby represent an important source of the genetic variation for crop improvement.

Extracting valuable alleles from wild species

There are three reasons which hinder the wide use of wild species in conventional crop improvement program for many crops. First, in conventional breeding, the phenotype (physical appearance) of the crop is always considered in selection. This approach works well for the traits of interest controlled by one or a few genes, such as simply inherited resistance to diseases and insects (Tanksley and McCouch, 1997). However, the agronomic performance of crop cultivars such as yield and quality components is mainly influenced by complex quantitative traits. Also, wild plants in general have smaller fruits, produce fewer seeds that often shatter and other undesirable traits compared to cultivars. Consequently, they appear to be deceptively poor as donors for enhancing yield. Finally, it can be difficult and time consuming to obtain interspecific hybrids and introgress useful traits selectively.

The development of molecular markers and molecular linkage maps has made it possible to study the effects of the individual loci that control a quantitatively inherited trait (quantitative trait loci, or QTLs) and to utilize these QTLs for crop improvement. Genetic mapping of major genes and QTLs for many important agricultural traits have allowed the integration of biotechnology with conventional breeding process. Exploitation of information from the map position of traits with agronomical importance can be achieved through marker -assisted selection (MAS) of the traits during the breeding process.

Several types of segregating populations can be utilized for performing QTL analysis. The two most popular

populations for QTL analysis are F_2 and BC_1 populations (backcrosses to one or both parents), because they are easy and relatively quick to develop. Each of these populations has different strengths with regard to QTL analysis. These populations have the most complete genetic construction, which provides the most abundant genetic information and both dominant and additive effects can be analyzed. However, they are temporary populations in the sense that the segregating unit is a single plant, therefore it is impossible to perform experiments with replications and the population genetic construction will change if further selfing or backcrossing is carried out. In addition, the effects of favorable QTL alleles are often lost due to the high level of epistatic interactions between QTLs and other donor genes in early generations. These interactions might be fixed in advanced generations thus leading to possible silencing of the measured QTL effects (Pillen et al., 2003).

To overcome these problems, immortalized mapping populations have been constructed to address the problems of these two major obstacles associated with the identification of quantitative trait loci, low heritability and high experimental error. Recombinant inbred lines (RILs) that are developed by single seed decent methods and doubled haploid (DH) populations are such immortalized populations. In these populations, the same genotype that is represented by infinite individuals and replications can be realized so as to obtain more stringent data and the same population can be shared among different research groups. However, such populations are time consuming to develop and since each locus is homozygote in these populations, dominant effects cannot be detected. An immortalized F_2 population that was constructed by intercrosses between RILs can produce a permanent population that is useful for heterosis and QTL analysis (Hua et al., 2002, 2003). Advantages of this population include the fact that genotype proportions in this population are similar to those of the F_2 population. Additionally, replicated trials in multiple environments can be investigated as each genotype was represented by a limitless number of plants as opposed to a single individual per genotype represented in an ordinary F_2 population (Hua et al., 2003).

With regards to plant breeding involving wild species, the populations mentioned above all share two common weaknesses: first, the population segregates for a large percentage of genes from the wild parent, thus resulting in lower statistical power to detect QTLs with small effects (Chee et al., 2005a). Secondly, once potentially valuable QTLs are discovered, substantial backcrossing and intercrossing are likely to be required for the development of commercial cultivars. Separating QTL discovery and cultivar development into discrete and sequential steps not only increases the time required for new cultivar development, but also reduces the likelihood that the QTL information is used to create a superior crop cultivar (Tanksley and Nelson, 1996).

Tanksley and Nelson (1996) proposed the advanced backcross QTL (AB-QTL) analysis as a potential solution by combining the discovery and transfer of valuable QTLs from unadapted germplasm into elite breeding lines into a single process. In the advanced backcross (AB) design, QTL analysis will be delayed until a later generation like the BC₂ or BC₃ generation. The logic behind this approach is that the effect of individual QTLs can be more precisely measured because undesirable effects of wild species on the elite background are reduced since later generation progenies such as BC₂ or BC₃ carry a smaller number of genes from the donor parent. In addition, if epistasis plays a major role in hybrid trait performance, MAS performed in AB progeny may be more effective than in the F₂ because recombination can break the assembly of favorable epistatic gene combinations accumulated by traditional breeding (Allard, 1996). Because an AB population is skewed toward the recurrent parent genome, favorable epistatic interactions among recurrent parent and tester alleles are less likely to be disrupted. AB-QTL analysis is especially suited for crops in which cultivars are inbred. AB-QTL analysis would be most readily applied to annual crops with relatively short generation times rather than long-generation perennial crops due to the development and exploitation of the necessary advanced backcross populations and near-isogenic lines with QTLs (QTL-NILs). It would be difficult to apply the method to highly heterozygous, out-crossing crops like alfalfa or clonally propagated crops like potato for which inbred lines are not commonly employed in breeding programs (Tanksley and Nelson, 1996).

The utility of the AB-QTL approach has been tested in numerous crops species and proved to be a feasible method in crop breeding (Grandillo and Tanksley, 2005). The objective of this paper is to review the recent application of AB-QTL approach for QTL detection in germplasm development and extraction of valuable and novel alleles from exotic germplasm. The achievements in applying AB-QTL analysis in a number of major crops are reviewed here.

APPLICATION OF THE AB-QTL APPROACH IN CROP GENETICS AND BREEDING

Tomato

Solanum subsection *Lycopersicon* consists of nine species, *Solanum lycopersicum* L. (cultivated tomato), *Solanum pimpinellifolium* L., *Solanum cheesmaniae*, *Solanum chmielewskii*, *Solanum neorickii*, *Solanum peruvianum*, *Solanum chilense*, *Solanum habrochaites* and *Solanum pennellii* (Tam et al., 2007). Cultivated tomato is known to have a narrow genetic base partly due to population genetic processes such as genetic bottlenecks and natural and artificial selection during domestication (Labate et al., 2006), whereas the wild

species represent considerable genetic diversity.

Tanksley et al. (1996) analyzed approximately 170 BC₂ plants from a cross between an elite inbred and the wild species *L. pimpinellifolium* 'LA1589' (Table 1). QTLs controlling horticultural traits were measured on BC₂F₁ and BC₃ families derived from the BC₂ individuals. They found that *L. pimpinellifolium* possesses QTL alleles capable of enhancing most traits that are important in producing tomatoes for processing. In their research, they also constructed QTL-NILs that contained specific QTLs that modified fruit size and shape that displayed the transgressive phenotypes predicted from the original BC₂ QTL analysis. Fulton et al. (1997) analyzed QTLs using a BC₃ population previously developed from a backcross of a wild relative of tomato *L. peruvianum* 'LA1706' into the cultivated variety *L. esculentum* 'E6203' (Table 1). They scored about 200 BC₄ families for 35 traits. QTL results showed that in many cases the wild alleles were associated with an agronomically beneficial effect despite the inferior phenotype of the wild parent. They also found eight stringent QTLs for fruit weight that could be followed through the BC₂, BC₃, and BC₄ generations.

Bernacchi et al. (1998a) applied the AB-QTL strategy to cultivated tomato using the wild species *L. hirsutum* 'LA1777' as the donor parent (Table 1). Genotype data of 315 BC₂ plants and phenotypic data for 19 agronomic traits from about 200 derived BC₃ lines were collected. A total of 121 QTLs were identified for all traits. It is interesting that despite that *L. hirsutum* is overall phenotypically inferior to the elite parent, *L. hirsutum* alleles were associated with an improvement of the traits from a horticultural perspective for many of the QTLs. Wild alleles were also associated with increases in total yield, soluble solids, and other traits. Bernacchi et al. (1998b) further produced NILs contained unique introgressions of wild alleles originating from two donor wild species *L. hirsutum* (LA1777) and *L. pimpinellifolium* (LA1589) by the molecular breeding strategy of AB-QTL analysis (Table 1). Their results revealed that 88% of the quantitative factors showed the phenotypic improvement predicted by QTL analysis of the BC₃ populations. Evaluation of the agronomic performance of the NILs showed that the per-location gains over the elite control ranged from 6 to 59% for different traits. Fulton et al. (2000) used AB-QTL strategy to detect QTLs affecting traits of agronomic importance in an interspecific cross between an elite tomato inbred and the wild species *L. parviflorum* (Table 1). With a total of 170 BC₂ plants that were genotyped by means of 133 genetic markers and about 170 BC₃ families that were scored for 30 horticultural traits, a total of 199 QTLs were identified for all traits. For 19 traits, at least one QTL was identified for which the *L. parviflorum* allele was associated with an agronomically favorable effect despite the overall inferior phenotype of this wild species.

Besides identifying QTLs for agronomic traits such as yield and fruit color, the AB strategy was also used to assess an important quality characteristic such as tomato

Table 1. Some examples of AB-QTL analysis in crop genetics and breeding.

Crop	^aPopulation(s)	Traits/Genes evaluated	Authors
Tomato	BC ₂ and BC ₃	A battery of horticultural traits	Tanksley et al. (1996)
	BC ₃ and BC ₄	A battery of horticultural traits	Fulton et al. (1997)
	BC ₂ and BC ₃	19 agronomic traits	Bernacchi et al. (1998a)
	NILs derived from AB populations	A battery of important agronomic traits	Bernacchi et al. (1998b)
	BC ₂ and BC ₃	30 horticultural traits	Fulton et al. (2000)
	BC ₂ and BC ₃	Biochemical properties	Fulton et al. (2002)
	RIL, BC ₃ S ₁ , BC ₃ S ₃ , QTL-NILs	Six quality traits	Chaïb et al. (2006)
	BC ₂ , IL and RIL	Ascorbic acid content	Stevens et al. (2007)
Rice	BC ₂ testcross population	12 agronomically important quantitative traits	Xiao et al. (1998)
	BC ₄ F ₂ , BC ₄ F ₃ and NILs	Heading date	Yamamoto et al. (2000)
	BC ₂ F ₁ and BC ₂ F ₂	Yield, yield components and morphological traits	Thomson et al. (2003)
	BC ₂ F ₂	Yield and yield component traits	Septiningsih et al. (2003a)
	BC ₂ F ₂	14 seed quality traits	Septiningsih et al. (2003b)
	BC ₃ F ₃ and BC ₃ F ₄	Blast resistance	Wu et al. (2004)
	BC ₃ F ₁ hybrid families	Grain quality and grain morphology	Li et al. (2004)
	RILs and BC ₃ F ₃	Rice blast disease	Liu et al. (2004)
	BC ₂ testcross progeny	13 agronomic traits pertaining to yield and its components	Marri et al. (2005)
	F _{2:3} developed from BC ₅ F ₆ line	Agronomic traits	Yoon et al. (2006)
	BC ₃ F ₄ NILs	Yield-related traits	Xie et al. (2008)
	A set of 12 BC ₂ F ₆ progenies	Yield and yield components	Cheema et al. (2008)
	A BC ₃ F ₃ line named BC116	Rice blast disease	Manosalva et al. (2009)
Barley	BC ₂ F ₂	Yield, yield component and quality	Pillen et al. (2003)
	BC ₃ F ₃	Grain yield and its components	Li et al. (2006)
	BC ₂ F _{6:8}	Resistance to seedling disease and adult plant spot blotch	Yun et al. (2006)
	BC ₂ F ₈	Morphological and agronomical traits	Gyenis et al. (2007)
	BC ₂ DH populations and candidate ILs	The major photoperiod response gene <i>Ppd-H1</i>	von Korff et al. (2004)
	BC ₂ DH population	Powdery mildew, leaf rust resistance and scald resistance	von Korff et al. (2005)
	BC ₂ DH population S42	9 agronomic traits	von Korff et al. (2006)
	BC ₂ DH population S42	7 malting parameters	von Korff et al. (2008)
	ILs derived from the AB population S42	Resistance to powdery mildew and leaf rust	Schmalenbach et al. (2008)
	ILs derived from the AB population S42	7 Agronomic traits	Schmalenbach et al. (2009)
Wheat	BC ₂ F ₂ and BC ₂ F ₃	Yield and yield components	Huang et al. (2003)

Table 1. Contd.

	BC ₂ F ₁	Seven agronomic traits	Huang et al. (2004)
	BC ₂ F _{2,4}	12 Agronomic traits	Narasimhamoorthy et al. (2006)
	BC ₂ F ₃	Quality traits	Kunert et al. (2007)
	BC ₂ F ₃	Leaf rust resistance	Naz et al. (2008)
Maize	BC ₂ testcrosses	Grain yield, grain moisture and plant height	Ho et al. (2002)
	BC ₂ F ₂ and NILs	Grain yield components	Li et al. (2007)
	BC ₂ S ₁ , F _{2:3} and NILs	9 plant traits	Li et al. (2008)
	BC ₂ F ₁	Root aerenchyma formation	Mano and Omori (2008)
Cotton	BC ₃ F ₂	Fiber elongation	Chee et al. (2005a)
	BC ₃ F ₂	Fiber length	Chee et al. (2005b)
	BC ₃ F ₂	Fiber fineness and micronaire	Draye et al. (2005)

^aNotes: NIL, near-isogenic line; IL, introgression line; BC₂DH, advanced backcross (BC₂) doubled haploid population; RIL, recombinant inbred line; AB populations, advanced backcross populations.

flavor. Fulton et al. (2002) applied the AB-QTL strategy to four AB populations to identify QTLs for biochemical properties that may contribute to the flavor of tomatoes such as sugars and organic acids (Table 1). QTLs with significant effects associated with the ratio of sugars/glutamic acid, a trait highly correlated with improved flavor, was identified as good targets for future work in improving the flavor of tomatoes. Fresh fruit and vegetables are a major source of another organic acid ascorbic acid (vitamin C), an important antioxidant for the human diet. Ascorbic acid content in tomato fruit exhibits quantitative inheritance. Stevens et al. (2007) mapped QTLs for ascorbic acid content in three tomato populations derived from crosses between cultivated tomato varieties and three related wild species or subspecies (Table 1). The three populations are (1) introgression lines (ILs) derived from *S. pennellii*, (2) an AB population derived from a cross between a cultivated tomato and a *S. habrochaites* accession, and (3) a recombinant

inbred line (RIL) population derived from the cross between a cherry tomato line and a large fruited line. They identified some common regions controlling ascorbic acid content on chromosomes 2, 8, 9, 10, and 12. Most QTLs appeared relatively stable over years and in different environments. A few co-locations between genes and QTLs were revealed.

The efficiency of marker-assisted backcrossing for the introgression of a QTL from a donor line into a recipient line depends on the stability of QTL expression. Chaïb et al. (2006) studied QTLs for six quality traits in tomato in order to investigate their individual effect and their stability over years, generations, and genetic backgrounds (Table 1). Five chromosome regions carrying fruit quality QTLs were transferred following a marker-assisted backcross scheme from a cherry tomato line into three modern lines with larger fruits. Three sets of genotypes corresponding to three generations were compared: namely an RIL population, three BC₃S₁ populations, and three sets of QTL-NILs

(BC₃S₃ lines). About half of the QTLs detected in QTL-NILs were detected in two years. Eight of the ten QTLs detected in RILs were recovered in the QTL- NILs with the genetic background that was used for the initial QTL mapping experiment.

Rice

Distributed throughout the tropics and subtropics, the *Oryza* genus comprises two cultivated species (*Oryza sativa* L. and *Oryza glaberrima* Steud) and 21 wild species that are grouped under four sections and four complexes (Veasey et al., 2004). Cultivars of common rice (*O. sativa* L.) are divided into indica and japonica subspecies (Oka, 1958). The modern rice cultivars have low genetic variation for most of the agronomically important traits. To sustain the demand of ever increasing populations in the world, new varieties have to be developed to increase the yield of rice. Wild species present potential donor sources for complex

traits such as yield and quality and would help to realize the dream of sustained food security.

To identify trait-improving QTL alleles from wild species, Xiao et al. (1998) selected an accession of *Oryza rufipogon*, a relative of cultivated rice and developed an interspecific BC₂ testcross population (Table 1). The *O. rufipogon* accession was phenotypically inferior for all 12 agronomically important traits evaluated. However, transgressive segregation that outperformed the original elite hybrid parent was observed for all traits examined. Li et al. (2004) developed an interspecific AB population from a cross between *O. sativa* 'V20A' and *O. glaberrima* and identified QTLs associated with grain quality and grain morphology (Table 1). Eleven QTLs associated with grain-related traits were detected with the favorable allele coming from *O. glaberrima* at eight loci. Favorable *O. glaberrima* alleles were associated with improvements in grain shape and appearance. Yamamoto et al. (2000) developed a BC₄F₂ from a cross between a japonica rice variety 'Nipponbare', and an indica rice variety 'Kasalath' (Table 1). QTL analysis revealed that two QTLs Hd6 and Hd7 were involved in variation of days to heading. They further developed a QTL-NIL with Hd6 prominently increasing the days to heading under a 13.5 h day length as compared with the recurrent Nipponbare parent. Thomson et al. (2003) developed an AB population between an accession of *O. rufipogon* (IRGC 105491) and the U.S. cultivar 'Jefferson' (*O. sativa* ssp. *japonica*) to identify QTLs for yield, yield components and morphological traits (Table 1). Seventy-six QTLs were identified for the 13 traits examined. The *O. rufipogon* allele was favorable for 53% of the yield and yield component QTLs. Several QTLs were localized to putative homologous regions in maize where QTLs for these traits have been previously reported, supporting the hypothesis of functional conservation of QTLs across the grasses. Septiningsih et al. (2003a) developed a BC₂F₂ population from an interspecific cross between *O. sativa* (cv IR64) and *O. rufipogon* (IRGC 105491) (Table 1). Two hundred and eighty-five families were evaluated for 12 agronomic traits and despite its inferior performance, 33% of the QTL alleles originating from *O. rufipogon* had a beneficial effect for yield and yield components in the IR64 background. Several QTLs for plant height, grain weight and flowering time detected in this study corresponded to homologous regions in maize containing previously detected maize QTLs for these traits. Septiningsih et al. (2003b) also evaluated 14 seed quality traits using this set of AB population in order to identify QTLs associated with grain quality in rice (Table 1). However, for the twenty-three independent QTLs that were identified, most of the *O. rufipogon*-derived alleles of these QTLs contributed an undesirable effect.

Marri et al. (2005) used AB method to introgress and map new QTLs relating to yield and its components from transgressive segregation was observed for all the yield and yield-component traits. Thirty nine QTLs were

identified with *O. rufipogon* alleles contributing positively to 74% of the QTLs in spite of its inferiority for most of the traits studied. Yoon et al. (2006) made introgressions from wild species *Oryza grandiglumis* into *O. sativa* subsp. *japonica* cv. 'Hwaseongbyeo' as a recurrent parent. They produced an advanced IL HG101 from a single plant from BC₅F₃ families that resembled Hwaseongbyeo (Table 1). An F_{2:3} population including 150 families from the cross Hwaseongbyeo/HG101 was developed and evaluated for 13 agronomic traits. A total of 39 QTLs and 1 gene conferring resistance to blast isolate were identified. For 18 QTLs identified in this study, the *O. grandiglumis*-derived alleles contributed a desirable agronomic effect despite the overall undesirable characteristics of the wild phenotype. Xie et al. (2008) constructed a high-resolution physical map targeting a cluster of yield-related QTLs on the long arm of rice chromosome 9 across a 37.4 kb region containing seven predicted genes (Table 1). A total of seven QTLs for 1,000-grain weight, spikelets/panicle, grains/panicle, panicle length, spikelet density, heading date, and plant height were identified in the cluster by using a series of BC₃F₄ NILs derived from a cross between the *japonica* cultivar Hwaseongbyeo and *O. rufipogon* (IRGC 105491). Alleles from the low-yielding *O. rufipogon* parent were beneficial in the Hwaseongbyeo background for all seven QTLs. BC₃F₄ NILs containing a homozygous *O. rufipogon* introgression in the target region out-yielded sibling NILs containing Hwaseongbyeo DNA and the Hwaseongbyeo parent by 14.2 - 17.7 and 16.2 - 23.7% respectively. Cheema et al. (2008) used a limited backcross strategy to introgress QTLs associated with yield and yield components from *O. rufipogon* (acc. IRGC 105491) to cultivated rice *O. sativa* cv 'IR64' (Table 1). A set of 12 BC₂F₆ progenies, selected from among them, more than

100 BC₂F₅ progenies, were evaluated for yield and yield components. Nine of the 12 ILs showed significantly higher yield (19 - 38%) than the recurrent parent IR64. Based on marker trait association it appears that some of the QTLs are stable across the environments and genetic backgrounds and can be exploited universally.

Plant disease resistance governed by QTLs is predicted to be effective against a broad spectrum of pathogens and long lasting (Manosalva et al., 2009). Use of these QTLs to improve crop species, however, is hindered because the genes contributing to the trait are not known. Wu et al. (2004) developed an AB population consisting of 80 BC₃F₃ lines from rice cultivars 'Vandana' and 'Moroberekan' and analyzed for blast resistance and genotyped with 50 candidate genes and 23 simple sequence repeat (SSR) markers (Table 1). Candidate defense response (DR) genes and SSR markers significantly associated with partial blast resistance in rice were detected. Analysis of BC₃F₄ progeny using genotypes of BC₃F₃ confirmed the phenotypic contribution of these markers. Three lines in a cluster with a high similarity to vandana expressed a high level of partial blast resistance in the field. Liu et al. (2004) used candidate

DR genes to dissect quantitative resistance in rice with RILs and AB populations derived from a blast-resistant cultivar 'Sanhuangzhan 2' (SHZ-2) (Table 1). Based on DNA profiles of DR genes, RILs were clustered into two groups corresponding to level of resistance and several DR genes were found to be co-localized with resistance QTLs identified by interval mapping. AB lines with four to five effective DR genes showed enhanced resistance under high disease pressure in field tests. Manosalva et al. (2009) accumulated five disease resistance QTLs that co-localized with DR genes by marker-aided selection to develop blast-resistant varieties (Table 1). One AB line carrying a major-effect QTL on Chr. 8, which included a cluster of 12 germin-like protein (*OsGLP*) gene members, exhibited resistance to rice blast disease over 14 cropping seasons. A highly conserved portion of the *OsGLP* coding region was used as an RNA interference trigger to silence a few to all of the expressed Chr. 8 *OsGLP* family members. They revealed that as more Chr. 8 *OsGLP* genes were suppressed disease susceptibility of the plants increased.

Barley

The genus *Hordeum* consists of 32 species and 45 taxa including diploid ($2n = 2x = 14$), tetraploid ($2n = 4x = 28$) and hexaploid ($2n = 6x = 42$) cytotypes (von Bothmer et al., 1995). Barley was grown initially as a food crop; however, the most common uses of barley in modern times are for animal feed and malting for alcohol production (Pickering and Johnston, 2005). It is often perceived that because barley breeders are restricted to crossing within the primary gene pool, which consists of cultivated barley *Hordeum vulgare* ssp. *vulgare* L. ($2n = 2x = 14$) and its wild diploid progenitor *H. vulgare* ssp. *spontaneum*, the genetic base of cultivated varieties is quite restricted (Russell et al., 2000).

AB-QTL analysis has been widely used in barley. Pillen et al. (2003) developed a BC₂F₂ population from the initial cross 'Apex' (ssp. *vulgare*) × 'ISR101-23' (ssp. *spontaneum*) (Table 1). Field data for 136 BC₂F₂ families were collected for 13 quantitative traits. Among the 86 putative QTLs detected, favorable effects were identified from spp. *spontaneum* for 29 of the QTLs. In one case, the spp. *spontaneum* allele was associated with a yield increase of 7.7% averaged across the six environments tested.

Von Korff et al. (2004) reported on the selection of two sets of candidate introgression lines (pre-ILs) in spring barley (Table 1). Two AB doubled haploid (BC₂DH) populations, S42 and T42, were generated by introgressing an accession of ssp. *spontaneum* (ISR42-8) into two different spring barley cultivars, 'Scarlett' (S) and 'Thuringia' (T). From these BC₂DH populations two sets with 49 (S42) and 43 (T42) pre-ILs were selected. The selected pre-ILs represents a first promising step towards

the assessment and utilization of genetic variation present in exotic barley. Von Korff et al. (2005) mapped new resistance genes against powdery mildew, leaf rust and scald in the AB doubled haploid (BC₂DH) population S42 (Table 1). They detected nine QTLs for powdery mildew, six QTLs for leaf rust resistance, and three QTLs for scald resistance. The presence of the exotic QTL alleles reduced disease symptoms by a maximum of 51.5, 37.6, and 16.5% for powdery mildew, leaf rust, and scald, respectively. For a majority of resistance QTLs (61.0%), the wild barley contributed the favorable allele thus demonstrating the usefulness of wild barley in the quest for resistant cultivars. In order to identify favorable exotic QTL alleles for the improvement of agronomic traits in the BC₂DH population S42, von Korff et al. (2006) detected 86 QTLs for nine agronomic traits (Table 1) in which the exotic alleles improved performance in 31 (36%) of 86 QTLs detected for agronomic traits. The exotic alleles had favorable effects on all analyzed quantitative traits. Von Korff et al. (2008) applied the AB-QTL strategy to detect QTLs for malting quality traits and using the BC₂DH population S42. QTL analysis in S42 for seven malting parameters measured in two different environments yielded 48 QTLs. The exotic genotype improved the trait performance at 18 (37.5%) of 48 QTLs. Favorable transgressive segregation was recorded for four traits. These studies therefore demonstrate that wild barley does harbor valuable alleles and can enrich the genetic basis of cultivated barley and improve malting quality traits.

Schmalenbach et al. (2008) developed a set of 59 spring barley ILs from the AB population S42 (Table 1). The ILs were generated by three rounds of backcrossing, two to four subsequent selfings, and MAS in parallel. Each line includes a single marker-defined chromosomal segment of the wild barley accession 'ISR42-8', whereas the remaining part of the genome is derived from the elite barley cultivar 'Scarlett'. Altogether 57% and 75% of QTLs conferring resistance to powdery mildew and leaf rust, respectively, were verified by ILs. A co-localization of two favorable QTLs was identified in line S42IL-138 and a reduction effect was revealed for powdery mildew as well as for leaf rust severity. This line might be a valuable resource for transferring new resistance alleles into elite cultivars. Schmalenbach et al. (2009) used a set of 39 wild barley ILs to study QTLs to verify genetic effects for agronomic traits that were previously detected in the BC₂DH population S42 (Table 1). A total of 47 QTLs were localized in the S42IL set for seven agronomic traits, among which 39 QTLs were significant across all tested environments. For 19 QTLs (40.4%), the wild barley introgression was associated with a favorable effect on trait performance. One introgression line S42IL-107 carried an introgression on chromosome 2H and was found to carry QTLs for multiple phenotypes. This line exhibited improved performance across all tested environments for the traits days-until-heading, plant height, and thousand grain weight. Since S42IL-107 can

be directly used to transfer valuable ssp. *spontaneum* alleles into modern elite cultivars, it will be valuable for the breeding of improved cultivars.

Li et al. (2006) developed a total of 207 BC₃ lines using the 2-rowed German spring cultivar ssp. *vulgare* 'Brenda' as a recurrent parent and the ssp. *spontaneum* accession 'HS584' as a donor parent (Table 1). The BC₃ lines were evaluated for grain yield and its components as well as heading date and plant height with a total of 100 QTLs detected. Based on genotypic data obtained from this population, 55 ILs carrying 1 or 2 donor segments were selected to develop a set of doubled-haploid lines that will be used to reconfirm and investigate the effects of 100 QTLs for future genetic studies.

Yun et al. (2006) developed and genetically characterized an AB population (BC₂F_{6:8}) with 'OUH602', ssp. *spontaneum*, as the donor parent and 'Harrington', ssp. *vulgare*, as the recurrent parent (Table 1). They validated all major QTLs previously identified in the OUH602/Harrington RIL population. A previously unidentified QTL conferring adult plant spot blotch resistance was identified on Chr. 4 (4H). The resistance alleles for each of the QTLs were contributed by OUH602. The AB population is a valuable resource for further genetic studies and breeding applications. To map the genetic factors that morphologically and agronomically differentiate wild barley from modern barley cultivars, Gyenis et al. (2007) identified QTLs associated with morphological and agronomical traits in a Harrington/OUH602 AB (BC₂F₈) population (Table 1). Thirty QTLs were identified of which 16 were newly identified in this study. Their results revealed the genetic architecture of morphological and agronomic traits that differentiate wild from cultivated barley.

Wheat

Roughly 95% of the wheat crop is common wheat (*Triticum aestivum* L.), used for making bread, cookies, and pastries, whereas the remaining 5% is durum wheat (*T. turgidum* ssp. *durum*), used for making pasta and other semolina products (Dubcovsky and Dvorak, 2007). Common wheat has been a genetically narrow species throughout its entire existence due to the genetic bottlenecks associated with interspecific hybridization, polyploidization, and selection. As a result, lower levels of genetic variation are observed for many traits in common wheat in comparison with its progenitor species.

Huang et al. (2003) made the first report on the use of AB-QTL analysis in wheat (Table 1) to identify QTLs for yield and yield components in a BC₂F₂ population derived from a cross between the German winter wheat variety 'Prinz' (*T. aestivum* L.) and the synthetic wheat line 'W-7984'. A total of 72 pre-selected BC₂F₂ plants were genotyped and phenotypic data were collected for five agronomic traits from corresponding BC₂F₃ families. A total of 40 putative

QTLs were detected and for 24 (60%) of them, alleles from the synthetic wheat W-7984 were associated with a positive effect on agronomic traits despite the fact that the synthetic wheat line was overall inferior to Prinz with respect to agronomic appearance and performance. In their second AB-QTL analysis carried out in winter wheat, Huang et al. (2004) studied seven agronomic traits in a BC₂F₁ population derived from a cross between the German winter wheat variety 'Flair' (*T. aestivum* L.) and the synthetic wheat line 'XX86' (Table 1). They selected 111 BC₂F₁ lines for genotyping with microsatellite markers as well as being evaluated in the field for seven agronomic traits. A total of 57 putative QTLs for yield and yield components were detected, of which 24 (42.1%) were found to have a positive effect from the synthetic wheat XX86. Many QTLs for correlated traits were mapped in similar chromosomal regions. Narasimhamoorthy et al. (2006) used AB-QTL analysis to identify QTLs for yield and yield components in a backcross population developed from a cross between the hard red winter wheat variety 'Karl 92' (*T. aestivum* L.) and the synthetic wheat line 'TA 4152-4' (Table 1). Phenotypic data were collected for agronomic traits on 190 BC₂F_{2:4} lines. Severity of wheat soil borne mosaic virus reaction was evaluated at one location with seven of ten putative QTLs found on homoeologous group 2 and 3 chromosomes. The favorable allele was contributed by cultivated parent Karl 92 at seven QTLs, which included a major locus for wheat soil borne mosaic virus resistance, and three QTLs by the synthetic parent.

Kunert et al. (2007) utilized AB-QTL strategy to locate QTLs for baking quality traits in two BC₂F₃ populations of winter wheat (Table 1). The backcrosses were derived from two German winter wheat cultivars 'Batis' and 'Zentos' (*T. aestivum* L.) and two synthetic, hexaploid wheat accessions 'Syn022' and 'Syn086'. From a total of 400 BC₂F₃ lines that were evaluated, 38 QTLs were significant for a marker main effect. The exotic alleles improved trait performance for 14 QTLs while the elite genotype contributed a favorable effect at 24 QTLs. At the locus on chromosome 4B, the exotic allele increased the falling number by 19.6%, and at the QTL on chromosome 6D, the exotic allele increased the sedimentation volume by 21.7%. The results indicate that synthetic wheat carries favorable QTL alleles for baking quality traits and could be useful for breeding improved wheat varieties by MAS.

Naz et al. (2008) localized exotic QTL alleles for the improvement of leaf rust resistance in an AB population B22, which is derived from a cross between the winter wheat cultivar 'Batis' (*T. aestivum*) and the synthetic wheat accession 'Syn022L' (Table 1). A total of 250 BC₂F₃ lines were assessed for seedling resistance against the leaf rust isolate 77WxR under controlled conditions. In addition, field resistance against leaf rust was evaluated by assessing symptom severity under natural infestation across multiple environments. The QTL analysis revealed six putative QTLs for seedling resistance and seven for field resistance.

For seedling resistance, the effects of exotic QTL alleles improved resistance at all detected loci. The strongest effects were detected at marker locus Xbarc149 on chromosome 1D at which the exotic allele decreased seedling symptoms by 46.3% and field symptoms by 43.6%. Several of the detected QTLs co-localized with known resistance genes while others appear to be novel resistance loci. Therefore, the exotic wheat accession Syn022L is likely to be useful for the improvement of leaf rust resistance in cultivated wheat.

Maize

Modern domestic maize (*Zea mays* L. *mays*) was derived from *Zea mays* ssp. *parviglumis*, also known as a teosinte (Doebley, 2004). In contrast to tomato, rice, or wheat; maize is an allogamous crop species that encompasses abundant genetic variation (Darrah and Zuber, 1986) despite a domestication bottleneck (Eyre-Walker et al., 1998) followed by intensive breeding.

Ho et al. (2002) applied an AB breeding strategy to identify QTLs of agronomic importance in a cross between two elite inbreds of maize, 'RD6502' and 'RD3013' (Table 1). Two hundred and four BC₂ families were scored with molecular markers. BC₂ testcrosses (TC) with 'B73' were phenotyped at six locations. They detected four grain yield, six grain moisture, and three plant height QTLs at which the RD3013 allele had a favorable effect. All four yield QTLs were selected as target introgressions in the development of BC₃TC families. As predicted by BC₂TC analysis, BC₃TC entries containing introgressions at the yld3.1 and yld10.1 QTLs significantly outperformed non-carrier entries by 11.1 and 6.7%, respectively. Their work demonstrated that the AB-QTL method can be applied to identify and manipulate useful QTLs in heterotic inbreds of elite maize. Genetic gains by this approach can be coupled with the maintenance and selection of favorable epistatic gene complexes by traditional hybrid breeding for maize improvement.

Li et al. (2007) evaluated 220 selected BC₂F₂ families developed from a cross between 'Dan232' and an elite popcorn inbred 'N04' for six grain yield components, and genotyped the families by 170 SSR markers (Table 1). A total of 19 significant QTLs were detected. Eighteen QTL had favorable alleles contributed by the parent Dan232. Six QTLs were also detected in the F_{2:3} population. Improved N04 could be developed from 210 and 208 families with higher grain weight/plant and/or 100-grain weight, respectively, and 35 families with the same or higher popping expansion volume than N04. In addition, QTL-NILs for grain weight/plant and/or 100-grain weight could be obtained from 12 families. Li et al. (2008) further identified trait-improving QTL alleles from Dan232, a dent-type maize inbred, and compared the detection of QTL in the BC₂S₁ population with QTL results using F_{2:3} families of the same population. Two hundred and twenty

BC₂S₁ families developed from a cross between Dan232 and N04 were evaluated for nine plant traits. A total of 28 significant QTLs were detected with 23 of them having favorable alleles contributed by Dan232. Nine QTLs detected in the BC₂S₁ population were also located in or near the same chromosome intervals in the F_{2:3} population.

Root aerenchyma formation is considered to be one of the most important characteristics for adapting to flooding. Mano and Omori (2008) used an elite maize 'Mi29' × a teosinte *Z. nicaraguensis* population with 214 BC₂F₁ individuals for AB-QTL analysis (Table 1). A QTL for aerenchyma formation under non-flooding conditions exhibiting a larger effect was located on chromosome 1; the position was close to the previously identified QTL Qaer1.07. Two QTLs with minor effects were mapped to a different position on chromosomes 1 and 5. These aerenchyma QTLs might be of special value in marker-assisted maize breeding.

Cotton

The cotton genus *Gossypium* L. consists of about 45 diploid and 5 tetraploid species forming a monophyletic group (Fryxell, 1992; Wendel and Cronn, 2003). Among these there are four species of cultivated cottons, namely *Gossypium herbaceum*, *Gossypium arboreum*, *Gossypium hirsutum*, and *Gossypium barbadense*, which provide the world's most important nature textile fiber (Wendel et al., 1992). Among the four species, modern cultivars of *G. hirsutum*, commonly referred to as Upland cotton, supplies the overwhelming majority of the world's cotton fiber. Although cotton domestication has led to increased productivity and better fiber quality, it is widely believed that the transformation has been accompanied by an extreme reduction in genetic diversity. For example, Wendel et al. (1992) revealed that the modern Upland cotton gene pool is narrow and concluded that a relatively severe genetic bottleneck accompanied the development of modern Upland cultivars. Furthermore, they observed that although introgression from other cotton species was involved in Upland cotton, most exotic genes have been selectively eliminated through post-introgression breeding programs.

Chee et al. (2005a) first developed an advanced-generation backcross population by intercrossing *G. hirsutum* cv. 'Tamcot 2111' with *G. barbadense* cv. 'Pima S6' followed by independently backcrossing the F₁ plants to the *G. hirsutum* parent for three cycles (Table 1). They modified the backcross-self mating design from the advanced backcross-QTL analysis proposed by Tanksley and Nelson (1996) in two ways. They started by developing a series of 24 independently derived BC₃ plants by backcrossing a randomly selected individual from each lineage to its original recurrent parent. Then, they imposed a generation of selfing prior to QTL

mapping. In principle, the selfing process would ensure an equal frequency of the *G. barbadense* and *G. hirsutum* alleles for any markers segregating in each BC₃F₂ family. Introgressed alleles at an average of 7.3% of loci in each BC₃F₁ plant were revealed by genome-wide mapping, collectively representing *G. barbadense* introgression over about 70% of the genome. Twenty-four BC₃F₁ plants were selfed to generate 24 BC₃F₂ families with a total of 2,976 plants that were field-evaluated for fiber elongation and genetically mapped. One-way analysis of variance detected 22 non-overlapping QTLs distributed over 15 different chromosomes, explaining from 8% to 28% of phenotype variance. Although the *G. barbadense* parent has lower fiber elongation than the *G. hirsutum* parent, the *G. barbadense* allele contributed to increased fiber elongation at 64% of the QTLs for elongation. Two-way analysis of variance detected significant among-family genotype effects and genotype × family interactions in two and eight regions, respectively, suggesting that the phenotypic effects of some introgressed chromosomal segments are dependent upon the presence/absence of other chromosomal segments.

Using the same advanced-generation backcross populations (Chee et al., 2005a), Chee et al. (2005b) dissected the molecular basis of genetic variation governing 15 parameters that reflect fiber length (Table 1). A total of 28 QTLs were detected for fiber length, 9 QTLs for length uniformity and 8 for short fiber content. For eight, six, and two chromosomal regions containing QTLs for fiber length, length uniformity, and short fiber content, respectively, two-way analysis of variance showed a significant among-family genotypic effect; therefore these same QTLs can be detected in multiple genetic backgrounds. A total of 13, 2, and 4 loci showed genotype × family interaction, illustrating the complexity in introgression of exotic germplasm into the gene pool of cultivated cotton. Co-location of many QTLs for fiber length, length uniformity, and short fiber content accounted for correlations among these traits, while the discovery of many QTLs unique to each trait suggests that maximum genetic gain will require breeding efforts that target each trait.

Draye et al. (2005) dissected the molecular basis of genetic variation governing two parameters reflecting lint fiber fineness and to compare the precision of these two measurements. By utilizing the same AB populations described by Chee et al. (2005a, b) (Table 1), a total of 32 and 9 QTLs for fiber fineness and micronaire were detected respectively. More QTLs were found in this study than previously found in other studies based on F₂ populations, reflecting the ability of the backcross-self design to resolve smaller QTL effects. Seven of the 9 micronaire QTLs were also associated with fiber fineness although the two measurements differed dramatically in the number of QTLs detected. This supports other data in suggesting that fiber fineness more accurately reflects the underlying physical properties of cotton fibers and consequently, is a preferable trait for selection.

CONCLUSION

Growing concerns about genetic vulnerability have motivated plant breeders to look to wild relatives for new sources of genetic variation to broaden the genetic diversity of crop germplasm. QTL analysis using early generation hybrids has been successful in identifying favorable genes from wild species; however, much work remains in order to introduce and utilize the beneficial genes identified using these populations in a mainstream breeding program. Due to issues related to barriers to gene introgression commonly encountered with wild species such as segregation distortion, suppression of recombination, and linkage drag, the genetic improvement potential of many beneficial genes identified from wild species have not been realized. The AB-QTL approach, which advocates delaying QTL analysis until BC₂ or BC₃, was proposed as a strategy that in principle has the advantage of detecting and integrating favorable QTLs from wild species into elite breeding lines. In the last 15 years, AB-QTL populations have been created for most major crop species, and the examples presented herein have collectively demonstrated that this approach has made significant contributions in unlocking favorable alleles from the wild species parents. In particular, the AB-QTL approach has shown that the genetic potential of exotic germplasm cannot be predicted based on phenotype alone. Because segregation has broken the donor genome into smaller components, the action of individual genetic loci is more clearly resolved than in earlier generation hybrids, resulting in more QTLs being identified and the genetic effects of individual loci more accurately estimated in the AB-QTL populations. Also, once a favorable QTL has been identified, NILs can quickly be developed with as little as one additional backcrossing to the recurrent parent when performed in conjunction with selection using linked DNA markers. These NILs can then directly be used as donor parents in cultivar development without much of the risks associated with standard interspecific gene introgression. Finally, with the target QTL becoming the major genetic source of variation due to the absence of other segregating QTLs, the NILs are a powerful resource for further genetic dissection of QTLs, including the eventual map-based cloning of the underlying gene, which has now been accomplished in a number of crop species.

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