Marker-Assisted Selection (MAS) in Major Cereal and Legume Crop Breeding: Current Progress and Future Directions

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ABSTRACT

With the development of molecular markers in crops, genetic and physical maps have been constructed in several important crops. Genes or QTL conditioning important agronomic traits were mapped onto chromosomes or genetic linkage groups through analyses of mapping populations. This paper reviews the application of marker-assisted selection (MAS) in three major cereal crops, wheat (*Triticum aestivum* L.), maize (*Zea mays* L.) and rice (*Oryza sativa* L.), as well as two legume crops, soybean (*Glycine max* L.) and common bean (*Phaseolus vulgaris* L.). The important traits mapped in biotic stresses include resistances to bacterial, viral and fungal diseases; resistances to insects, such as aphids, green bugs, and Hessian flies; and resistance to nematodes. Other traits include tolerance to abiotic factors like drought, high temperature, and soil nutrient deficiency; seed quality and nutrient components; as well as yield and its components. The advantages and disadvantages of using MAS in crop breeding are discussed. This paper is a summary of available MAS strategies and potential application of MAS in tracking more traits in practical breeding. Future utilization of MAS is also discussed. As a review of MAS in five important crops across cereals and legumes, we believe it provides useful information to crop breeders and molecular geneticists.

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INTRODUCTION

Morphological markers were the first type of markers used in genetic maps in maize (*Zea mays* L.) (Creighton and McClintock 1931). Isoenzyme markers were later used in maize (Schwartz 1960). Due to the limited number of these two types of markers, they could not be used widely in constructing genetic maps. Botstein *et al.* (1980) developed restriction fragment length polymorphism (RFLP) markers. As co-dominant markers they could distinguish between the homozygotes and heterozygotes. Due to the complicated procedures and radioactive materials involved in RFLP markers, polymerase chain reaction (PCR) markers, like randomly amplified polymorphic DNA (RAPD) markers, were soon developed. These markers were used by breeders very often in marker-assisted selection (MAS) in bean (*Phaseolus vulgaris* L.) and other crops (Williams *et al.* 1990; Kelly and Miklas 1998). Due to their poor repeatability, RAPD bands were cloned and sequenced to design sequence characterized amplified region (SCAR) markers (Haley *et al.* 1994; Yu *et al.* 2000a). These SCAR markers had longer primer sequences and amplified single target

bands with better stability and repeatability, making them popular with breeders.

As more genomic DNA sequences became available in crops, simple sequence repeats (SSR) or microsatellites were developed in wheat (Röder *et al.* 1998; Somers *et al.* 2004; Song *et al.* 2005), maize (Davis *et al.* 1999), rice (Wu and Tanksley 1993), soybean (Cregan *et al.* 1999a), and bean (Yu *et al.* 1999, 2000b; Gaitan-Solis *et al.* 2002; Metais *et al.* 2002; Blair *et al.* 2003). Although SSR markers have multiple loci, their polymorphism is limited, especially in mapping populations from parents with narrow genetic backgrounds. To increase the polymorphism, Vos *et al.* (1995) proposed amplified fragment length polymorphic (AFLP) markers. This type of marker combined the advantages of both RFLP and PCR. It has been applied in genetic map constructions of most crops in combination with other types of markers. For any given core map in crops, all of the markers mentioned above were involved (Röder *et al.* 1998; Freyre *et al.* 1998; Cregan *et al.* 1999a; Davis *et al.* 1999; McCouch *et al.* 2002; Song *et al.* 2005). As more sequences from genomic DNA, expressed sequence tags (EST), cDNA, bacterial artificial Chromosome (BAC) and yeast artificial chromosome (YAC) clones for many crops became available, single nucleotide polymorphic (SNP) markers were designed. SNP markers became a powerful tool to detect polymorphism and for use in MAS in crops (Gupta and Rustgi 2004; Chen G *et al.* 2005). Four SNP genotyping assays including single-base extension (SBE), allele-specific primer extension (ASPE), oligo-nucleotide ligation (OL), and direct hybridization (DH) were compared by Lee SH *et al.* (2004). SBE and ASPE were more accurate and ASPE was more cost-effective and simple, however, OL was faster and DH was even more economical. SNPs were attractive to breeders because of their abundance and potential for use in automated high-throughput genotyping with no-gel assay (Gupta *et al.* 2001). The transition from random DNA markers to markers developed from transcriptomes and other coding sequences, and their application in MAS were reviewed by Gupta and Rustgi (2004). Hayashi *et al.* (2004) studied SNPs and small insertion/deletion (InDels) polymorphisms at *Piz* and *Piz-t* regions, two resistance genes to rice blast. On average, there was one SNP in every 248 bp. SNPs could be used to generate numerous markers within a target region and were simple to assay. SNP genotyping with allele-specific PCR has become valuable for genetic mapping, map-based cloning and MAS.

As core maps have been constructed in most important crops, breeders and molecular geneticists can study the traits of interest using their own mapping population with references from the core maps. They can either use available markers on those core maps or design their own specific markers to be used in MAS in their own breeding populations.

As new types of markers were developed, technologies to detect them have changed in the following areas: 1) from regular agarose to polyacrylamide gel to increase the precision of detected bands, 2) DNA staining methods from ethidium bromide, SYBR Safe, and silver to florescent to increase the feasibility, and 3) from gel to non-gel assays to facilitate automation and high-throughput screening. Non-electrophoresis-based PCR assays for allelic discrimination using fluorogenic 5′-nuclease procedure (TaqMan) were described by Salvi *et al.* (2001). This automation facilitates large-scale screening and MAS.

In the following sections of the paper, we review some progress on MAS in breeding in five important crops.

MAS FOR RESISTANCE TO BIOTIC STRESSES

We summarize those studies in which MAS has been applied or where there is high potential for MAS to be used in wheat, maize, rice, soybean and common bean for resistance to biotic stresses caused by bacteria, virus, fungi, nematodes, and several insects including aphids, Hessian

flies, and green bugs (**Table 1**).

MAS in wheat

Fusarium head blight (FHB, mainly caused by *Fusarium graminearum*) and rust (caused by *Puccinia* spp.) resistances as well as resistance to Hessian fly [*Mayetiola destructor* (Say)], Russian wheat aphid (RWA, *Diuraphis noxia*), and green bug (*Schizaphis graminum*), are very important in wheat breeding.

For FHB resistance in wheat, A 3BS QTL conditioning type II FHB resistance (resistance to Fusarium spread) from Sumai 3 has been intensively studied and applied in breeding (Anderson *et al.* 2001). This QTL, fhb1, was validated using near-isogenic lines (NILs) from 13 different populations (Pumphrey *et al.* 2007). More recent studies focus on the type III (resistance to accumulation of deoxynivalenol (DON)) (Somers *et al.* 2003; Lemmens *et al.* 2005; Paul *et al.* 2005) and type IV (kernel quality) resistances (Abate *et al.* 2007). Combinations of different types of FHB resistances are being studied (Abate *et al.* 2007; Miedaner *et al.* 2006). The FHB resistant sources from local adapted varieties have been identified and studied (Rudd *et al.* 2001; Liu S *et al.* 2005a, 2007a; Abate *et al.* 2007). Chen J *et al.* (2006) studied two major QTL on 3BS and 5AS from the Chinese cultivar W14. Markers Xbarc133 and Xgwm493 flanking the QTL on 3BS (Anderson *et al.* 2001) and Xbarc56 and Xbarc117 flanking the QTL on 5AS were used in MAS to pyramid these two QTL to develop cultivars with resistance to initial infection, disease spread, kernel damage and deoxynivalenol (DON) accumulation. Fhb2 on 6BS flanked by Xgwm133 and Xgwm644 were confirmed by field spray experiments (Cuthbert *et al.* 2007). In durum wheat, Qfhs.ndsu-3AS was mapped on 3AS of *T. dicoccoides* and not homologous to Qfhs.ndsu-3BS. Flanking markers Xfcp401 and Xfcp397.2 can improve MAS of this QTL (Chen XF *et al.* 2007). Some adapted and unadapted FHB resistant sources have more than two types of resistances which will facilitate MAS in breeding for multiple FHB resistances as well as in integration with other disease resistances.

Leaf rust (*Puccinia triticina*) is one of the most damaging diseases of wheat worldwide. Sequenced tagged Site (STS) markers linked to *Lr9*, *Lr10*, *Lr19*, *Lr24*, *Lr29* and *Lr35* were highly specific and very useful in MAS for these genes (Baszczyk *et al.* 2004). Three markers, Xwmc764, Xgwm210 and Xwmc661 are the most suitable markers to select *Lr16* in breeding programs or to pyramid it with other leaf rust resistance genes (McCartney *et al.* 2005). Four SSR markers Xgwm95, Xgwm47, Xgwm372 and Xgwm122 co-segregating with *Lr45*, were identified (Zhang N *et al.* 2007). Tightly linked markers have been used to select lines with two genes, *Lr19* and *Lr24* (Slikova *et al.* 2004) and three genes, *Lr10*, *Lr26*, and *Lr37* (Singh and Tiwari *et al.* 2005) and four genes, *Lr1*, *Lr9*, *Lr24* and *Lr47* (Nocente *et al.* 2007). Slow leaf rusting resistance is very important in breeding due to its durability compared to race-specific resistance. SSR markers linked to QTL for decreasing final severity, infection rate, and infection duration in CI 13227 have potential to be used in MAS for these traits (Xu *et al.* 2005). Flanking markers linked to *Yr5* was identified (Smith *et al.* 2007). Peng *et al.* (2000) identified SSR markers linked to a stripe rust (caused by *Puccinia striiformis*) resistance gene, *YrH52*, at a distance of 0.33 cM. Markers within 5 cM are efficient to select homozygous resistant plants. Xbarc101 co-segregates with *Yr36*, a gene for adult-plant resistance to stripe rust on chromosome 6B. As another flanking marker of *Yr36*, Xucw71 is also linked to the grain protein content locus $Gpc-B_1$, MAS for two traits is possible (Uauy *et al.* 2005). SCAR markers SC-gp1 and SC-D04 co-segregated with a barley yellow dwarf (BYD) viral resistance gene, *Bdv2*, which can be used in MAS to breed BYD resistant cultivars (Zhang *et al.* 2004).

Winter wheat cultivar, Massey, has three QTL on 1B, 2A, and 2B associated with resistance to powdery mildew

Table 1 Markers tightly linked to some important traits for marker-assisted selection in wheat, maize, rice, soybean and common bean.

Crops	Traits	Resistance QTL/genes[1]	Markers for MAS	References
Wheat	Fusarium head blight	*Qfhs.ndsu-3BS*; QTL on 5AS; *Qfhs.ndsu-3AS*; *Fhb2*	Xwgm533.1, Xbarc147, Xbarc133 and Xgwm493; Xbarc56 and Xbarc117; Xfcp401, Xfcp397.2; Xgwm133, Xgwm644	Anderson *et al.* 2001; Chen J. *et al.* 2006; Chen *et al.* 2007; Cuthbert *et al.* 2007
	Stem rust	*Sr2*	Xgwm533	Hayden *et al.* 2004
	Leaf rust	*Lr16*; *Lr1*, *Lr47*; *Lr45*; *Lr9*, *Lr10*, *Lr29*, *Lr26*, *Lr37*, *Lr19*, *Lr24*	Xwmc764, Xgwm210, Xwmc661; PTAG621, PS10; Xgwm47.133, Xgwm372.180, Xgwm122.110	McCartney *et al.* 2005; Nocente *et al.* 2007; Zhang N *et al.* 2007; Slikova *et al.* 2004; Baszczyk *et al.* 2004; Singh and Tiwari 2005
	Slow leaf rusting	QTL		Xu *et al.* 2005
	Powdery mildew	*Pm3*; *Pm4a*, *Pm21*; *Qpm.vt-2A*, *Qpm.vt-2B*	Pm3FR; BCD292; NAU/Xibao16; Xgwm304, Xgwm501	Tommasini *et al.* 2007; Ma *et al.* 1994; Liu *et al.* 2001; Gao *et al.* 2005; Chen YP *et al.* 2006; Tucker *et al.* 2006
	Stripe rust	*Yr5*; *Yr36*; *YrH52*	Xwmc175; Xbarc101, Xucw71; Xgwm413-Xgwm273a	Smith *et al.* 2007; Peng *et al.* 2000; Uauy *et al.* 2005
	Barley yellow dwarf	*Bdv2*	SC-gp1, SC-D04	Zhang *et al.* 2004
	Septoria tritici blotch	*Stb2*	Xgwm389, Xgwm533.1	Adhikari *et al.* 2004
	Spot blotch	QTL	Xgwm67, Xgwm469, Xgwm570	Sharma *et al.* 2007
	Karnal bunt	QTL	gwm538snp.152, OPM-20	Brooks *et al.* 2006 Kumar *et al.* 2006
	Green bug	*Gb3*; *Gbx1*, *Gba*, *Gbb*, *Gbc*, *Gbd*, *Gbz*	Xwmc 634	Weng *et al.* 2002, 2005; Zhu *et al.* 2005
	Russian wheat aphid	*Dn4*; *Dn2*, *Dn6*, *Dn7*, *Dn1*, *Dn5*	Xgwm106, Xgwm337, red glum gene *Rg2*; Xgwm437; Xrems1303.320; Xgwm44, Xgwm111	Arzani *et al.* 2004; Miller *et al.* 2001; Lapitan *et al.* 2007; Liu *et al.* 2002
	Hessian fly	*H9*; *H16*, *H17*; *H22*; *H10*; *H11*; *H13*; *H32*	Xbarc263, Xcfa2153, SOPO05.909; Xpsp2999, Xwem6b; Xhor2kv, Xgdm33	Kong *et al.* 2005, 2007; Zhao *et al.* 2006; Liu XM *et al.* 2005a, 2005b; Sardesai *et al.* 2005
	Cereal cyst nematode	*Cre3*; *CreX*; *CreY*	Xgwm301; OpY16-(1065)	Martin *et al.* 2004; Barloy *et al.* 2007
	Root-lesion nematode	QTL	Xbcd1821, Xcdo456	Zwart *et al.* 2006
	Dough strength, loaf volume, protein content	QTL; *Gpc-B1*	Xbarc15-2A, Xgwm666-3A, Xpsp2999-1A; Xucw71	Uauy *et al.* 2005; Kuchel *et al.* 2006
	Grain texture, protein quantity	QTL	Xpsr3261, Xbarc141	Turner *et al.* 2004
	Protein	*HWM-GS 5 + 10*		Zhang *et al.* 2003
	Low polyphenol oxidase activity	QTL	Xgwm312	Watanabe *et al.* 2006
	Stem strength; stem diameter, pith diameter, culm wall thickness for lodging	*QSs-3A*, *QSs-3B(QSd-3B)*; *QPd-1A*, *QPd-2D (QCwt-2D)*	Xwmc527-Xwmc21, Xgwm108-Xwmc291; Xgwm135-Xwmc84, Xgwm311-Xgwm301	Hai *et al.* 2005
	Yield (drought)	QTL	Xwmc89; Xgwm261	Kirigwi *et al.* 2007; Kumar *et al.* 2007
	Dwarfing	*Rht-B1b*, *Rht-D1b*; *Rh4*, *Rh5*, *Rht9*, *Rht12*, *Rht13*	BF-MR1, DF-MR2	Ellis *et al.* 2002
	Aluminum tolerance	OTL	Xbarc164, Xwmc331	Zhou *et al.* 2007
	Southern corn leaf blight	*rhm*	rhm-F/R	Cai *et al.* 2003
Maize	European corn borer	QTL	umc123, umc110	Flint-Garcia *et al.* 2003; Cardinal *et al.* 2006
	Southwestern corn borer	QTL	Umc63; csu173-umc126a, csu26a-umc68; umc140#2, umc65a-umc21; umc103a; csu145a	Bohn *et al.* 1998
	Corn earworm	QTL, *p1*	csu1066-umc176	Butron *et al.* 2001
	Downy mildew	QTL	bnl 8.23-bnl 5.47a	George *et al.* 2003
	Gibberella ear rot	QTL	BC559.120, BC324.1400	Ali *et al.* 2005
	Anthesis-silking interval (ASI)	QTL		Ribaut *et al.* 1996, 2007
	Cell membrane stability	QTL		Frova *et al.* 1998
	Vertical root pulling	QTL		Landi *et al.* 2002
	Ear setting percentage, grain yield	QTL		Li *et al.* 2003
	Carotenoid accumulation	*Yellow 1*, *viviparous 9*	Dupssr18-bnlg249, zdsRFLP-phi034	Wong *et al.* 2004
	Lysine	*o2*, *o16*	Umc1066, umc1041	Yang *et al.* 2005
	Bacterial leaf blight	*Xa23*; *Xa21*; *xa13*; *Xa4*; *xa5*; *Xa7*, *xa29(t)*	C189; pTA248; RG136; MP12; RG556, RG207	Sanchez *et al.* 2000; Singh *et al.* 2001; Joseph *et al.* 2004; Tan *et al.* 2004; Phan *et al.* 2005, Iyer-Pascuzzi and McCouch 2007; Wang CL *et al.* 2005; Deng *et al.* 2006a
Rice	Rice blast	*Pi-1*; *Pi-k^h*; *Pi-b*, *Pi-k*; *pi-5(t)*; *Piz*; *Pigm(t)(Pi2, Pi9)*; *Pi-ta*; *Piz (Piz-t)*, *Pit*, *Pik*, *Pik-m*, *Pik-p*, *Pi-ta*, *Pi-ta2*, *Pib*	MRG4766; S-129.700; RM208, RM224; JJ80-T3; MRG5836; C5483, C0428; YL155/YL87; z4794 -z60510, t256, k3951, k2167, k3957, ta3, b2	Chen ZW *et al.* 2005; Sharma *et al.* 2005; Fjellstrom *et al.* 2004; Yi *et al.* 2004; Conaway-Bormans *et al.* 2003; Deng Y *et al.* 2006; Wang *et al.* 2007; Hayashi *et al.* 2006

Table 1 (Cont.)

Crops	Traits	Resistance QTL/genes[1]	Markers for MAS	References
Rice	Green rice leaf hopper	*Grh5*	RM3754, RM3761	Fujita *et al*. 2006
	Brown plant-hopper	*Bph2*; *Bph13(t)*; *Bph9*; *Qbph11*; *Bph17*	RM7102, RM463; AJ09.230; RM463, RM5341; XNpb202, C1172; RM8213, RM5953	Renganayaki *et al*. 2002; Su *et al*. 2005; Sun *et al*. 2005, 2006
	Drought tolerance, yield	QTL	RG939-RG476-RG214	Babu *et al*. 2003
	Root thickness	*brt5b*	RM161-R521	Li *et al*. 2005
	Deep root, root thickness	QTL	RG256-RG151	Kamoshita *et al*. 2002
	Drought tolerance	QTL	RM223, RM263	Kumar *et al*. 2005
	Low glutelin content	QTL	SSR2-004, RM1358	Wang YH *et al*. 2005
	Rice protein and fat content	*qRPC-5*; *qRFC-2*; *qRFC-5*	RG435-RG172a; RG241b-RG324; RG470-RG474	Hu *et al*. 2004
	Ferrous iron toxicity			Wan *et al*. 2003
	Elongating ability	QTL		Gregorio *et al*. 2002
	Thermo-sensitive genetic male sterile	*rtms1*; *tms3(t)*	Rev1, RM239-RG257; F18F/F18RM	Lang *et al*. 1999; Jia *et al*. 2001
	Seed dormancy	*qSdn-1*	RM104	Guo *et al*. 2004; Wan *et al*. 2006
	Seed vigor	*qSV-7*	RM214 - G20 - C285	Zhang ZH *et al*. 2005
	Heading date	*Hd1*; *Hd2*; *Hd3*; *Hd6*; *Hd7*; *Hd4*; *Hd5*, *Hd9*	S2539; C728; C764; R3226; C560; R1485; S1633A	Lin *et al*. 2000; Yamamoto *et al*. 2000; Lin *et al*. 2002, 2003
	Cold tolerance	*Qsct-11*	RM202	Chen W *et al*. 2005
Soybean	Soybean cyst nematode	*rhg-1*; *rhg-t1*	Satt309, Sat168; Satt038, Satt130	Mudge *et al*. 1997; Cregan *et al*. 1999b; Ferdous *et al*. 2006
	Soybean mosaic virus	*Rsv3*; *Rsv4*	A519F/R, M3Satt; Satt542, Satt558, AW471852R, Satt634	Hayes *et al*. 2000; Jeong *et al*. 2002, 2004; Hwang *et al*. 2006
	Frogeye leaf spot	*Rcs3*	Satt244, Satt547	Mian *et al*. 1999
	SDS	QTL	SAT99, SATT6	Njiti and Lightfoot 2006
	Root and stem rot	*Rps8*, *Rps3*	Sat_154	Sandhu *et al*. 2005
	Brown stem rot	*Rbs1*; *Rbs2*	Satt431; Satt244	Tamulonis *et al*. 2001
	Soybean rust	*Rpp1*	Barc_Sct_187, Barc_Sat_064	Hyten *et al*. 2007
	Soybean aphid	*Rag1*	Satt435, Satt463	Li *et al*. 2007
	Protein	*Glycinin (11S, G4)*; *beta-conglycinin (7S)*	Satt461, Satt292, Satt156; Satt461, Satt249	Panthee *et al*. 2004
	Isoflavones	QTL	Satt201 – Satt540 – Satt245	Primomo *et al*. 2005
	Fatty acid content	QTL		Hyten *et al*. 2004b
	Palmitate acid	*fap*(nc)	GmFATB1a	Cardinal *et al*. 2007
	Linolenic acid	QTL	Satt534, Satt560	Spencer *et al*. 2004
	Alpha-tocophenol	QTL	Sat342, Sat167	Dwiyanti *et al*. 2007
	Iron-deficiency chlorosis		Satt481	Charlson *et al*. 2005
	Salt tolerance		Sat_091, Satt237	Lee GJ *et al*. 2004
Common bean	Common bacterial blight	QTL	UBC420, SU91, SAP6	Jung *et al*. 1997; Miklas *et al*. 2000a; Yu *et al*. 2000b
	Bean common mosaic virus	*I*	SW13	Melotto *et al*. 1996
	Bean common mosaic necrosis virus	*bc-1[2]*, *bc-2[2]*, *bc-3*	SBD5.1300, RCO11	Miklas *et al*. 2000b
	Bean gold mosaic virus	*bgm-1*	SR2	Blair *et al*. 2007
	Anthracnose	*Co-4[2]*	SAS13	Melotto and Kelly 2001
	White mold	QTL	AFLP	Ender *et al*. 2007

[1] Gene, linked markers, and references are separated by ";" if they are corresponded specifically.

(caused by *Erysiphe graminis* f. sp. *tritici*). They can explain more than 50% of the phenotypic variation for adult plant resistance (Liu *et al*. 2001). Plants selected through MAS using markers linked to two QTL on 2A and 2B gave a high level of resistance in the field (Tucker *et al*. 2006). QTL mapping using lines from USG3209 confirmed that it has the QTL from Massey (Tucker *et al*. 2007). Gao *et al*. (2005) used MAS to pyramid *Pm2*, *Pm4a* and *Pm21* (Ma *et al*. 1994). Plants with *Pm21* showed immunity. Plants with *Pm2* and *Pm4a* showed greater levels of resistance than those with only one gene. A co-dominant marker linked to *Pm21* and developed from cDNA is very useful in MAS for this gene (Chen YP *et al*. 2006). Perfect markers were designed and tested for *Pm3* gene where seven alleles confer resistance (Tommasini *et al*. 2006). This can improve the efficiency in breeding.

Sharma *et al*. (2007) identified SSR markers linked to resistance to spot blotch (caused by *Cochliobolus sativus*) in *G162* and they may be useful in MAS. SSR loci Xgwm389 and Xgwm533.1 were about 1cM distal to *Stb2*,

a gene conferring resistance to Septoria tritici blotch (caused by *Mycosphaerella graminicola*) (Adhikari *et al*. 2004). Hayden *et al*. (2004) also reported that Xgwm533 was linked to the stem rust (caused by *Puccinia graminis*) resistance gene, *Sr2*. These two markers are also associated with a major QTL for Fusarium head blight resistance (Anderson *et al*. 2001). Using markers linked to multiple disease resistances should benefit breeders in developing multiple resistant cultivars. Zeng *et al*. (2005) conducted MAS for simultaneous resistance to powdery mildew, stripe rust and yellow dwarf virus in wheat and pyramided 3 to 5 genes (*Pm* + *Yr* + *Bdv*) into individual plants.

Marker Xgwm538 is linked to a QTL for Karnal bunt (caused by *Tilletia indica Mitra*) resistance in wheat line HD29. A new SNP designed as gwm538snp.152 selectively amplifies one target fragment, improving the consistency for MAS (Brooks *et al*. 2006). A RAPD marker OPM-20 is associated with a resistance QTL allele from Line HD29 (Kumar *et al*. 2006), which could be useful in MAS.

Two AFLP markers and one SSR marker, Xwmc 634,

co-segregate with *Gb3*, a green bug resistance gene on 7D (Weng *et al.* 2002, 2005). The converted STS markers from these two AFLPs and the SSR marker should be useful in MAS. Markers linked to other green bug resistance genes *Gbx1*, *Gba*, *Gbb*, *Gbc*, *Gbd*, *Gbz* on 7DL can be used to pyramid them into adapted wheat cultivars (Zhu *et al.* 2005).

Markers Xbarc263, Xcfa2153, and SOPO05.909 were specific to the Hessian fly resistance gene, *H9* (Kong *et al.* 2005). Markers linked to a gene cluster including *H9*, *H10*, *H11* on 1AS (11 more *H11*-like genes), *H13* on 6DS (Liu XM *et al.* 2005a, 2005b) *H22* on 1DS (Zhao *et al.* 2006) and *H32* on 3D (Sardesai *et al.* 2005) have been identified. Markers Xpsp2999 and Xwem6b flanking *H16* and *H17* were reported on 1AS by Kong *et al.* (2007). This region contains gene clusters of other Hessian fly resistance genes as well as *Pm3* and *Lr10*. They should be very useful for pyramiding multiple disease resistances in breeding.

SSR markers Xgwm106 and Xgwm337 flank *Dn4* (a resistance gene for RWA), on 1DS by 5.9 and 9.2 cM, respectively (Arzani *et al.* 2004). The red glum color gene *Rg2* is also linked to *Dn4*. Using combinations of markers and the *Rg2* gene can provide 100% accuracy and 75% efficiency in MAS to select homozygous *Dn4* plants. Marker Xgwm437 is linked to *Dn2* at 2.8 cM (Miller *et al.* 2001). Two SSR markers, Xgwm44 and Xgwm111, are linked to *Dn6* on 7DS at 14.6 and 3 cM, respectively. *Dn6* is allelic or tightly linked to *Dn1*, *Dn2*, and *Dn5* (Liu *et al.* 2002). *Dn7* was transferred from rye and it is the only one resistant to biotype 2. Marker Xrems1303.320 is very useful in MAS breeding (Lapitan *et al.* 2007). These markers are used in breeding programs either identifying or pyramiding these linked genes for RWA resistance.

SSR marker Xgwm301 is tightly associated with the cereal cyst nematode (*Heterodera avenae* Woll., CCN) resistance gene, *Cre3*, on 2DL. It has been used in MAS for selecting a nematode resistant wheat cultivar in Australia (Martin *et al.* 2004). Two new CCN resistance genes, *CreX* and *CreY*, were transferred from *Aeigilops variabilis* Accession No. 1 into wheat using MAS (Barloy *et al.* 2007). SSR markers linked to two QTL conditioning root-lesion nematode (*Pratylenchus neglectus*) resistances on 6DS and 2BS are used in breeding wheat cultivars of different genetic backgrounds (Zwart *et al.* 2006).

MAS in maize

An STS marker converted from AFLP tightly linked to the *rhm* gene for southern corn leaf blight (caused by *Bipolaris maydis*) resistance is useful in MAS or for map-based cloning of this gene (Cai *et al.* 2003).

Flint-Garcia *et al.* (2003) compared phenotypic selection and MAS for stalk strength and 2nd generation of European corn borer (2-ECB) [*Ostrinia nubilalis* (Hubner)] resistance and demonstrated that MAS could be an effective tool to select for stalk strength and 2-ECB resistance. Cardinal *et al.* (2006) mapped the QTL for leaf-feeding by ECB. If only interactions between QTL with significant main effects are tested, important epistatic interactions will be missed. They concluded that MAS will be most efficient for this trait when main effects and interaction effects of QTL are included in the selection.

A marker linked to QTL resistance to southwestern corn borer (*Diatraea grandiosella*) from maize line CML139 were incorporated into MAS breeding (Khairallah *et al.* 1998). Scientists at the International Maize and Wheat Improvement Centre (CIMMYT) applied MAS to select stem borer [*Scirpophaga incertulas* (Walker)] resistance and pyramid *Bacillus thuringiensis* (*Bt*) resistance genes into breeding populations to increase the durability of maize resistance to these pests (Bergvinson and Hoisington 2001).

Maysin and related compounds are plant produced antibiotic compounds against corn earworm (*Helicoverpa zea*). Markers linked to QTL *p1* on chromosome 1S and a novel QTL at the interval of csu1066-umc176 on chromosome 2C-2L, together with markers linked to husk tightness, can be used in MAS breeding (Butron *et al.* 2001).

George *et al.* (2003) identified SSR markers linked to a major QTL on chromosome 6 from Ki3 conditioning resistance to downy mildew (caused by *Peronosclerospora* spp.), which is stable across environments of four countries in Asia. They used these markers in MAS.

Markers linked to major QTL for silk and kernel resistance to Gibberella ear rot (caused by *Fusarium* spp.) detected in more than one experiment in maize line CO387 can be used in MAS for these traits (Ali *et al.* 2005).

MAS in rice

Resistances to bacterial blight (caused by *Xanthomonas oryzae* pv. *oryzae*) and rice blast (caused by *Pyricularia grisea*) have been intensively studied in rice. Since rice is a model cereal crop, its molecular genetic studies and the application of available knowledge may provide some useful insights to other cereal crops.

There are 21 dominant and 9 recessive genes for bacterial blight resistance in rice. Among them, four dominant and two recessive genes have been used in practical MAS breeding. A single major gene, *Xa21*, with broad spectrum resistance, is very effective. Through MAS, it has been introduced into a rice hybrid restorer line in China, 'Minghui 63' (Chen *et al.* 2000) and a photoperiod-sensitive genetic male sterile line, '3418S' (Luo *et al.* 2003) and other hybrids (Cao *et al.* 2003). An EST marker linked to *Xa23* and markers linked to *Xa29*(*t*) were identified and are being used in MAS for blight resistance (Tan *et al.* 2004; Wang CL *et al.* 2005).

Combinations of several dominant and recessive genes have given a high level of resistance. MAS has been used to pyramid resistance genes into rice hybrids or restorer lines in the following combinations: two genes, *xa13* and *Xa21* (Joseph *et al.* 2004), *Xa4* and *Xa21* (Deng QM *et al.* 2006), or *Xa7* and *Xa21* (Zhang *et al.* 2006); three genes, *xa5*, *xa13* and *Xa21* (Sanchez *et al.* 2000; Singh *et al.* 2001); four genes, *Xa4, xa5, xa13*, and *Xa21* (Huang *et al.* 1997) or *Xa4*, *xa5*, *Xa7* and *Xa21* (Phan *et al.* 2005). It is very difficult to pyramid multiple genes in conventional breeding because they can mask the effects of each other. Furthermore, functional markers were designed from *xa5* to facilitate the MAS for this recessive gene (Iyer-Pascuzzi and McCouch 2007).

Phenotypic screening results also verified the successful pyramiding of genes using MAS. AFLP detected 80.4% to 86.7% recurrent parent alleles in BC_1F_3 for the gene transfers of *xa13* and *Xa21* in line IRBB55 (Joseph *et al.* 2004). The EST marker C189 linked to *Xa23* gave 100% efficiency (Wang CL *et al.* 2005). In another case, an F_3 line test found that MAS reached an efficiency larger than 90% to identify homozygous resistant plants for *Xa4*, *xa5*, *Xa7* and *Xa21* (Phan *et al.* 2005). Chu *et al.* (2006) used map-based cloning to fine map the *xa13* to 14.8 kb region. Newly designed tightly linked markers may improve the efficiency of MAS for *xa13* in breeding.

Xa21 and a fused *Bt* gene *cry1Ab/cry1Ac* were introduced into cytoplasm male sterile (CMS) restorer line 'Minghui 63' using MAS (Jiang *et al.* 2004). This will improve both disease and pest resistances.

Rice blast is a serious disease of rice, especially Japonica type. There are many blast resistance genes deployed in rice breeding. Several single dominant genes have been used or are being used in MAS including *Pi-1* (linked with marker MRG4766 at 1.3 cM, Chen ZW *et al.* 2005), *Pi-k*[h] (linked to marker S-129.700 at 2.1 cM, Sharma *et al.* 2005), *Pi-2*(*t*) (Hittalmani *et al.* 1995), *Pi-5*(*t*) (linked to JJ80-T3, Yi *et al.* 2004), *Pi-b* and *Pi-k* (co-segregates with RM208 and RM224, Fjellstrom *et al.* 2004), *Pi-z* (linked to MRG5836, Conaway-Bormans *et al.* 2003), and *Pigm(t)*, *Pi2*, *Pi9* (linked to C5483 and C0428, Deng *et al.* 2006) as well as *Pi-ta* (linked to YL155/YL87, Wang *et al.* 2007). Marker-based prediction for resistant plants can reach 95-98% (Hittalmani *et al.* 1995; Chen ZW *et al.* 2005). Liu SP

et al. (2003) transferred *Pi-1* into an elite hybrid maintainer line, Zhenshan 97, using flanking markers.

Pyramiding several blast resistance genes through MAS has been used in rice breeding. *Pigm*(*t*) on chromosome 6 may be either allelic or tightly linked to *Pi2* and *Pi9*. *Pi26*(*t*) was also mapped at that region (Deng Y *et al.* 2006). Fjellstrom *et al.* (2004) suggested that MAS can be used to pyramid *Pi-b*, *Pi-k*, and *Pi-ta2* into new rice cultivars and elite lines. Another set of three major genes including *Pi-1*, *Pi-z5*, and *Pi-ta*, was transferred into agronomically superior rice cultivars using MAS (Hittalmani *et al.* 2000). Recently, SNP and InDel markers co-segregating with 9 rice blast resistance genes including *Piz*, *Piz-t*, *Pit*, *Pik*, *Pik-m*, *Pik-p*, *Pi-ta*, *Pi-ta2* and *Pib* were identified (Hayashi *et al.* 2004, 2006). Wang Z *et al.* (2007) demonstrated that markers from a resistant/susceptible *Pi-ta* hapolytes are useful in MAS. These markers should be useful in developing cultivars with one or several genes.

Genes for rice blast and bacterial blight resistances were also pyramided. Two major genes (*Piz-5 + Xa21*) and three genes (*Pi-1 + Pi-5 + Xa21*) were stacked into plants using MAS and transformation in rice (Narayanan *et al.* 2002, 2004).

Leaf hoppers [*Nephotettix cincticeps* (Uhler)] and plant hoppers [BPH, *Nilaparvata lugens* (Stal)] are very serious problems in rice. SSR markers, RM3754 and RM3761, linked to the green rice leafhopper resistance gene, *Grh5*, are useful in breeding to improve the resistance to this insect (Fujita *et al.* 2006). Five genes conditioning brown plant-hopper have been used in MAS breeding. Using SSR markers, RM7102 and RM463, linked to *bph2* in MAS, the selection efficiencies are 89.9% and 91.2%, respectively (Sun *et al.* 2006). The other four genes are: *Bph9* (linked to SSR markers RM463 and RM5341) on chromosome 12 (Su *et al.* 2006), *Qbph11* (flanked by markers *XNpb202* and *C1172*) for BPH resistance in 'DV85' (Su *et al.* 2005), *Bph13*(*t*) (linked by AJ09230(b) on chromosome 3 (Renganayaki *et al.* 2002), and *Bph17* (flanked by RM8213 and RM5953) (Sun *et al.* 2005).

MAS in soybean

MAS has been used in soybean breeding for resistances to soybean cyst nematode (SCN, *Heterodera glycines* Inchinoe), soybean mosaic virus (SMV), leaf spot (*Cercospora sojina* Hara), sudden death syndrome [SDS, caused by *Fusarium solani* (Mart.)] as well as root and stem rot (caused by *Phytophthora sojae*) diseases.

SCN is the most economically significant soybean pest. Conventional breeding for SCN resistant cultivars is difficult and expensive. Mudge *et al.* (1997) identified two SSR markers, Satt038 and Satt130, flanking the SCN resistance on linkage group (LG) G. They can be used in MAS to efficiently identify plants with SCN resistance. Subsequently, SSR marker, Satt309, was identified 0.4 cM from the *rhg1* locus conferring SCN resistance. It can be used to distinguish most of SCN-susceptible genotypes from those *rhg1* carriers derived from resistant sources 'Peking', PI 437654, and PI 90763. A different marker, Sat168, can be used for MAS in breeding populations involving typical southern US cultivars crossed with PI 88788 and PI 209332 (Cregan *et al.* 1999b). Ferdous *et al.* (2006) identified a major QTL (*rhg-t1*) from the Japanese cultivar Toyomusume and con-cluded that the combination of *rhg1* on LG G and *rhg-t1* on LG B_1 provides a high level resistance to SCN race 3. In total, over 60 markers associated with SCN resistance QTL have been identified (Concibido *et al.* 2004).

For SMV, *Rsv3* gene confers resistance to three of the most virulent strains of SMV. PCR markers were designed to pyramid it with other disease resistance genes (Jeong *et al.* 2002). SNPs linked to *Rsv1* and *Rsv3* were designed using allele-specific PCR to facilitate the MAS for these two genes (Jeong and Maroof 2004). *Rsv4*, which confers resistance to all known strain groups of SMV, is flanked by the SSR markers, Satt542 at 4.7cM and Satt558 at 7.8cM on

LG D1b, greatly facilitating breeding for this resistance (Hayes *et al.* 2000). Hwang *et al.* (2006) used comparative genomics and developed EST markers AW471852R which is 2.4 cM away from *Rsv4* gene and Satt634 which is 2.2 cM from the other side. These tightly linked markers are being used in MAS breeding.

Resistance gene, *Rcs3*, provides resistance to all known races of *Cercospora sojina* Hara, which causes frogeye leaf spot on soybean. The linked markers offer the opportunity for breeders to use MAS in the development of resistant cultivars (Mian *et al.* 1999).

Field trials to select SDS-resistant cultivars are expensive and time-consuming. MAS selection for loci of SDS resistance from Forrest is well established. SSR markers linked to SDS resistance from Minsoy were identified to combine different resistance QTL (Njiti *et al.* 2006).

Root and stem rot is caused by *Phytophthora sojae*. A series of *Rps* genes have been identified and *Rps8* confers resistance to most *P. sojae* isolates. *Rps8* and *Rps3* were mapped to the gene-rich region on LG F (Sandhu *et al.* 2005). MAS using Satt431 for brown stem rot (caused by *Phialophora gregata* f. sp. *sojae*) resistance gene *Rbs1* and Satt244 for *Rbs2* can predict 88 and 82% of the phenotypes, respectively (Tamulonis *et al.* 2001).

Soybean rust, caused by *Phakopsora pachyrhizi*, has the potential to be one of the major diseases. Markers Barc_Sct_187 and Barc_Sat_064 are linked to one resistant gene *Rpp1* from line PI 200492, which can be used in MAS (Hyten *et al.* 2007).

Marker Satt435 and Satt463 on LG M are flanking soybean aphid (*Aphis glycines Matsumurd*) resistance gene *Rag1* from Dowling and resistance gene from Jackson (Li *et al.* 2007).

Pyramiding resistance to insects was also conducted. Walker *et al.* (2004) found that introgression of a *Bt* transgene *cry1Ac* and the PI 229358 allele at a QTL using MAS makes soybean lines more resistant.

MAS in common bean

Marker-assisted selection has been used in common bean for bacterial, virus, and fungal disease resistances (Kelly *et al.* 2003; Liu *et al.* 2005b; Miklas *et al.* 2006a). For common bacterial blight (caused by *Xanthomonas campestris* pv. *phaseoli*) resistances, several SCAR markers have been found linked to resistance QTL from different sources: UBC420 linked to the QTL on chromosome 1 with resistant alleles from XAN 159; SU91 linked to the QTL on chromosome 3 from the same source; SAP6 linked to QTL on chromosome 8 with resistance from great northern Nebraska No. 1 Sel. 27 (Jung *et al.* 1997; Yu *et al.* 2000a; Miklas *et al.* 2000a; Pedrosa *et al.* 2003). These markers have been used in practical breeding to pyramid CBB resistances. Pinto and red kidney beans with both SAP6 and SU91 linked QTL through MAS are available (Mutlu *et al.* 2005; Miklas *et al.* 2006b). More tightly linked markers to the CBB resistance QTL on chromosome 1 of XAN 159 have been designed and validated to be useful in different genetic backgrounds for MAS of this QTL (Liu *et al.* 2007b).

SW13 is linked to the *I* gene for resistance to *Bean common mosaic virus* (BCMV) and has proved very reliable in different genetic backgrounds (Melotto *et al.* 1996; Miklas *et al.* 2006a). SCAR marker SBD5.1300 tightly linked to *bc-1²*, which confers resistance to specific strains of BCMV and bean common mosaic necrosis virus (BCMNV). However, its resistance is masked by *bc-2²* and *bc-3* (Miklas *et al.* 2000b). Therefore, the marker should be useful in MAS breeding. A recessive gene, *bgm-1*, confers bean gold mosaic virus resistance. Its tightly linked marker SR2 is also close to bc-1 (Blair *et al.* 2007). The linkage between two loci may facilitate the MAS of them.

Breeding for anthracnose (caused by *Colletotrichum linemuthianum*) resistance from different sources using MAS to combine different genes (*Co-1* to *Co-10*) conferring resistance to various predominant races based on geo-

graphic regions is practical and realistic (Balardin and Kelly 1998). SAS13 is linked to the *Co-4²* gene which has the broadest resistance to fungal races (Melotto and Kelly 2001). However, application in MAS using this marker is not very consistent and reliable (Liu S *et al.* 2005b; Miklas *et al.* 2006a).

Pyramiding different resistance genes or QTL with different disease resistances is very common. Integration of UBC420 linked QTL for CBB resistance, SW13 linked I gene for BCMV resistance, and SAS13 linked to *Co-4²* gene for anthracnose resistance to breed bean varieties with multiple disease resistances in several market classes including navy, black, pinto, red kidney and cranberry beans is underway (Park and Yu 2004; Liu S *et al.* 2005b, 2006).

In white mold resistance breeding, marker-assisted backcrossing successfully transferred a B_7 QTL from G122 and a B_8 QTL from NY6020-4 into susceptible pinto bean (Miklas and Bosak 2006c). Ender *et al.* (2007) applied markers linked QTL for resistance to white mold from Bunsi to enhance the selection of resistance in breeding. MAS in bean breeding for different disease resistances have been reviewed by Kelly *et al.* (2003) and Miklas *et al.* (2006a) in detail.

MAS FOR RESISTANCE TO ABIOTIC STRESSES

MAS for drought tolerance

Abiotic stress resistance is more complex and subject to large environmental effects. It is controlled by multiple genes/QTL with quantitative inheritance and may involve multiple resistance or tolerance mechanisms (Miklas *et al.* 2006a). This makes it hard to study both physiologically and genetically.

In wheat, breeding drought tolerance has been focused on improving crop water use efficiency, rapid early leaf area development and high osmotic adjustment (Quarrie *et al.* 1999). Kirigwi *et al.* (2007) identified one QTL on 4AL where tolerant alleles come from 'Dharwar Dry'. Marker Xwmc89 is associated with all QTL for grain yield, grain fill rate, spike density, biomass production, drought susceptibility index (DSI) and explained 20-40% phenotypic variations of these traits. However, potential markers linked to these traits need to be evaluated for MAS.

Drought is the second most severe limitation to maize production after soil fertility. Four QTL were found for common anthesis-silking interval (ASI), male flowering and female flowering under water-stress conditions (Ribaut *et al.* 1996). MAS to improve yield under drought should combine important traits like ASI, yield components, or other traits significantly correlated with yield (Ribaut *et al.* 1997). Frova *et al.* (1998) identified markers linked to QTL associated with cell membrane stability in maize under water stress and high temperature. Markers linked to QTL associated with vertical root pulling resistance in maize were identified and may be useful to improve root strength and yield under water stress (Landi *et al.* 2002). Under drought conditions, an MAS strategy for yield improvement can be established by combining QTL associated with decreased ASI and increased ear setting percentage and grain yield (Li XH *et al.* 2003). Marker-assisted backcross (MABC) selection has been used to improve yield under drought conditions by selecting fewer genotypes (10-20 each cycle) and fewer generations (Ribaut *et al.* 2007).

Babu *et al.* (2003) identified two QTL on chromosome 4 and 9 for drought tolerance in rice. They also had pleiotropic effects on yield. Linked markers can be useful in MAS for these traits. Boopathi *et al.* (2003) developed a SCAR marker linked to root thickness for rice drought tolerance screening. Moreover, root traits were studied in upland and lowland environments (Li *et al.* 2005). Basal root thickness is significantly correlated with the index of drought resistance. Markers linked to QTL for deep root and root thickness in rice create the potential for MAS to select these traits in rainfed lowlands (Kamoshita *et al.*

2002). Using 38 rice accessions from diverse genetic backgrounds, markers RM223 and RM263 co-segregated in all individuals in the drought tolerance bulk so they may be useful in MAS for improvement of rainfed rice (Kumar *et al.* 2005). MAS can be used to introduce QTL for tolerance to submergence and drought into cultivars with a broad range of adaptation or in a specific region for rice (Mackill *et al.* 1999). Co-localized QTL for different traits will facilitate MAS for them in rice breeding.

MAS for drought tolerance has been used in common bean breeding programs to combine alleles from races Durango and Mesoamerica (Schneider *et al.* 1997a). Using MAS to improve drought tolerance in common bean showed that the effectiveness of MAS is inversely proportional to the heritability (Schneider *et al.* 1997b).

Lodging resistance

QTL associated with lodging resistance in wheat were detected (Keller *et al.* 1999). Based on the correlations among phenotypic traits, they suggest that indirect selection of plant height and culm stiffness combined with two QTL for lodging resistance is the most efficient way to improve lodging resistance. Hai *et al.* (2005) identified markers linked to QTL for stem strength, stem diameter, and culm wall thickness and suggested using them as an index in MAS to improve lodging resistance in wheat.

Perfect markers linked to two dwarfing genes *Rht-B1b* and *Rht-D1b* were identified for MAS of these genes in wheat (Ellis *et al.* 2002). SSR markers linked to other wheat height-reducing genes, *Rh4* on 2BL, *Rh5* on chromosome 3BS, *Rht9* on 2DS, *Rht9* on 5AL, *Rht12* on 5AL, *Rht13* on 7BS, were also identified for MAS to breed cultivars with reduced heights.

Cold tolerance

RAPD marker OPT8.511 was confirmed to have a strong association with cold tolerance of rice. It is linked in repulsion to the cold tolerance from japonica cultivar 'Toyohatamochi' (Kim *et al.* 2000). SSR marker RM202 is closely linked to a QTL (Qsct-11) for cold tolerance from rice line 'Lemont' and is used in MAS breeding (Chen W *et al.* 2005).

MAS FOR IMPROVEMENT OF OTHER TRAITS

High protein and other nutrition improvement

Wheat grain protein content (GPC) is a major end-use quality in wheat. Zhang *et al.* (2003) reported that they transferred *HWM-GS 5 + 10* subunit into wheat cultivars with different maturities and quality types combining backcrosses with biochemical marker-assisted selection. Markers linked to QTL conditioning grain texture and protein quantity were used in MAS for these traits (Turner *et al.* 2004). Kuchel *et al.* (2006) identified QTL associated with dough strength on chromosome 2A and 3A, loaf volume on 2A and 3A, protein content on 6A. The linked markers can be used in MAS to improve bread-making quality. Marker Xgwm312 is linked to lower polyphenol oxidase activity on 2AL and MAS for this trait in breeding is promising (Watanabe *et al.* 2006).

QTL associated with carotenoid accumulation in maize kernels were mapped to the regions with candidate genes, *yellow 1* and *viviparous 9*. The linked markers could be used in an efficient MAS to increase levels of carotenoids in maize grain (Wong *et al.* 2004). High lysine in maize was controlled by both *o2* and *o16* genes. The double recessive mutants have 30% more lysine than maize with just one mutation (Yang *et al.* 2005).

Tightly linked markers could greatly reduce breeding time and effort depending on phenotypic measurement. Markers SSR2-004 and RM1358 linked to low glutelin content can provide 96.8% and 92.7% efficiency in rice MAS

breeding (Wang YH *et al*. 2005).

QTL associated with rice protein content and rice fat content were identified (Hu *et al*. 2004) and have the potential to be applied in MAS. The major QTL, *qRPC-5*, is at the interval of RG435-RG172a while *qRFC-2* and *qRFC-5* are linked by marker intervals RG241b-RG324 and RG470-RG474, respectively. These two traits are negatively correlated. The PCR-Acc I marker can be used to lower the amylase content through backcrossing and MAS in rice (Zhang SL *et al*. 2005).

QTL associated with protein, oil and seed size were mapped using RILs from the cross Essex/Williams in soybean. MAS can help breeders to retain these QTL and pyramid additional QTL from new germplasm (Hyten *et al*. 2004a). Glycinin (11S) and beta-conglycinin (7S) are important seed storage proteins in soybean. Markers linked to both subunits were identified and can be used in MAS to improve the nutritional quality of soybean (Panthee *et al*. 2004). QTL associated with isoflavones in soybean seeds were identified and linked markers are useful to develop soybean varieties with desirable isoflavone content through MAS (Primomo *et al*. 2005). Yu *et al*. (2005) studied the G4 glycinin subunit using base excision sequence scanning and discussed the design of SNPs for MAS of a recessive null allele.

Altering fatty acid (FA) content in soybean oil is of interest to breeders. One marker interval on LG L linked to QTL for palmitic, oleic, linoleic, and linolenic acids with R^2 from 13 to 50%. MAS can help breeders to increase the genetic gains for desirable FA composition of soybean (Hyten *et al*. 2004b). Spencer *et al*. (2004) identified SSR markers, Satt534 and Satt560, which are linked to QTL on LG B_2 for decreased linolenic (18:3) acid. These markers can be used in MAS for low-18:3 soybean genotypes. Marker GmFATBla, linked to locus *fap*, accounted for more than 60% of phenotypic variation in palmitate content and was designed from cDNA (Cadinal *et al*. 2007), which should be benefit to MAS. Genetic manipulation of balanced amino-acid and carbohydrate composition through genomics will enhance the nutritional value of legume crops (Babu *et al*. 2004). Tocopherols are major lipophilic antioxidants in soybean. Markers Sat_243 and Sat_167 were significantly associated with α-tocopherol concentration and can be used in MAS (Dwiyanti *et al*. 2007).

Plant nutrition and other traits

In soybean breeding for resistance to iron-deficiency chlorosis (IDC), conventional approaches were used but not effective. Many IDC-resistant cultivars have lower yield and the environmental effects are large. SSR marker Satt481 is associated with IDC resistance across environments. MAS should increase breeding efficiency (Charlson *et al*. 2005). Salt tolerance was studied using 'S-100' which is one of major ancestors of soybean cultivars in southern USA. Markers Sat_091 and Satt237 were always associated with salt tolerance in descendent cultivars of S-100, indicating its usefulness in MAS in commercial soybean breeding (Lee GJ *et al*. 2004).

Markers linked to ferrous iron toxicity can be used in MAS for rice cultivars (Wan *et al*. 2003). Salinity is compounded by mineral deficiencies (Zn, P) and toxicities (Al), submergence and drought. Gregorio *et al*. (2002) identified markers linked to QTL for elongating ability under these stresses. MAS may help the selection for tolerance to these traits in rice. QTL associated with aluminum tolerance in Atlas66 were mapped on 4D and 3BL (Zhou *et al*. 2007). The associated markers can be used in MAS for this trait.

Male sterility is very important in the development of hybrid cultivars in rice. Markers linked to thermo-sensitive genetic male-sterile (TGMS) genes, *rtms1* and *tms3(t)*, can be used in MAS to select TGMS plants at seedling stage of rice (Jia *et al*. 2001; Lang *et al*. 1999).

Identification of QTL and application of MAS in rice breeding for seed dormancy, heading date and yield-related traits were also summarized in the following. Seed dormancy is associated with pre-harvesting sprouting resistance in rice. Wan *et al*. (2006) identified markers linked to *qSdn-1* on chromosome 1 across different populations and they may be useful in MAS for this trait. Guo *et al*. (2004) identified markers linked to seed dormancy QTL on chromosome 3 which has been found in different genetic backgrounds in rice. *qSV-7* has the largest main effects and its linked marker can be used in MAS for seed vigor of rice (Zhang ZH *et al*. 2005).

MAS was used to develop near-isogenic lines (NILs) containing QTL controlling heading date, *Hd1*, *Hd2*, *Hd3*, *Hd4*, *Hd5*, *Hd6*, *Hd7*, *Hd9* in rice (Lin *et al*. 2000; Yamamoto *et al*. 2000; Lin *et al*. 2002, 2003). SSR markers have also been identified for the maturity genes E1, E3, E4 and E7 in soybean (Molnar *et al*. 2003) to facilitate conversion of later maturity group lines to earlier maturing lines.

In order to breed for rice heterosis, Liu and Wu (1998) suggested assembling favorable alleles and removing unfavorable alleles from the parental lines. Both indica/indica and indica/japonica hybrids can be improved by use of MAS. Markers linked to panicle number per plant and spikelet number per panicle are useful in MAS for high-yield panicle type (Luo and Li 2001). Li *et al*. (1998) suggested that the important QTL affecting the source leaves can be manipulated through MAS to increase sink capacity to improve yield in rice. In bread wheat, mapping of QTL for yield and seven yield contributing traits in two populations showed that QTL for spikelets per spike was common between two populations. HomeoQTL were detected. Six QTLs were identified pleiotropically or coincidentally for more than one trait and consistent over environments. Markers associated with these traits will be efficient in MAS (Kumar *et al* 2007).

PROS AND CONS OF MAS

Advantages of MAS

Co-location of QTL and genes conferring different disease resistances have been found in common bean and other crops (Kelly *et al*. 2003; Miklas *et al*. 2006a). This may result in one marker linked to several target traits, which will be very efficient in MAS. MAS can also help retain the available resistance and incorporate new sources of resistance. MAS may improve mass selection and increase efficiency through progeny testing and decreasing the number of replications and increasing selection intensity (Gallais and Charcosset 1994).

Tuvesson *et al*. (2006) studied the application of MAS in European plant breeding and pointed out that MAS is very useful to monitor the gene transfer and the genetic background. Simple and rapid DNA extraction methods are needed for MAS to be used broadly. For example, a protocol to extract DNA from seeds was developed to simplify the MAS application in soybean (Bolton *et al*. 2005).

Single large-scale marker-assisted selection (SLS-MAS) can be used to select plants at early generations with a fixed and favorable genetic background at specific loci while segregation at other loci is maintained (Ribaut and Betrán 1999). It is very useful in maize to combine conventional breeding and markers. Edwards and Page (1994) compared MAS and phenotypic recurrent selection (PRS) and concluded that MAS can provide rapid gain for the first 2-3 generations of recurrent selection in maize. Enrichment of frequency of desirable traits in F_2 or BCF_1 through MAS can reduce the minimum required population size and sequential culling can be used to decrease marker screening cost (Wang JK *et al* 2007). Liu PY *et al*. (2006) studied the effects of genotype x environment (GE) interactions on genetic response to MAS. It is more efficient than phenotypic selection (PS) when GE interactions exist. For QTL confirmed in multiple environments, MAS gave higher general response.

Knapp (1998) compared phenotypic selection (PS) and

MAS, and found that the breeder must test up to 17 times more progenies using PS than using MAS to ensure obtaining at least one superior genotype. When the heritability of a trait is low to intermediate and the selection intensity is high, MAS is beneficial in accomplishing a selection goal. Through simulation, van Berloo and Stam (1998) found that MAS is promising when dominant alleles at QTL are present and linked in coupling phase.

For bean common mosaic virus resistance, a marker linked to the *I* gene (Melotto *et al*. 1996) has been proved as a breeder-friendly marker in MAS across a wide genetic background in both gene pools in many laboratories (Miklas *et al*. 2006a). Tar'an *et al*. (2003) applied MAS for complex traits in bean, like yield, using a QTL-based index and showed that it can help breeders to select lines with important QTL in a desirable genetic background. Zhang YM *et al*. (2005) mapped QTL based on pedigree information, trait value and marker information. The MAS procedure, implemented via best linear unbiased predictors (BLUP), may be routinely used by breeders to select superior lines and line combinations.

Considerations in use of MAS

Verification of putative QTL and its magnitude of effects and accurate map chromosome location are very important to realize the potentials of MAS (Liu PY *et al*. 2003). Some markers linked to disease resistances in bean are only useful in one gene pool. Those markers will have limited usefulness (Miklas *et al*. 2006a). For example, a SCAR marker tightly linked to resistance to angular leaf spot [*Phaeoisariopsis griseola* (Sacc.) Ferraris] can only be used in MAS for introgression in Andean backgrounds (Mahuku *et al*. 2004).

Marker-assisted selection requires polymorphisms in the parents. This can limit its usefulness in populations from relatively narrow genetic backgrounds, from which most conventional breeding populations are generally derived. On the other hand, phenotypic selection tries to combine different sources of disease resistances or other traits of interest. Therefore, breeders have to evaluate the advantages and limitations when applying MAS in breeding. It depends on the target traits, genetic backgrounds, and environmental effects (Miklas *et al*. 2006a).

For some traits phenotypic selection is more efficient than MAS. Bohn *et al*. (2001) concluded that MAS using only marker information is less efficient than conventional phenotypic selection for maize stem borer resistance unless QTL have larger effects or the cost of marker assays is considerably reduced (Yu *et al*. 2000a). Due to the low consistency of QTL across populations, MAS is not recommended to improve ECB resistance in early maturing dent germplasm (Papst *et al*. 2001; Jampatong *et al*. 2002).

The efficiency of MAS is affected by the number of loci, sample size, genetic parameters and the selection schemes (Thompson 1990). MAS is inferior to phenotypic selection in most of the selection schemes when the cost ratio (r) of obtaining measurements on phenotypic characters to scoring marker loci is less than one and the heritability is greater than 0.3 (Xie and Xu 1998). The optimal heritability for MAS of a trait is 0.2. For traits with heritability lower than this, the efficiency of MAS is reduced (Moreau *et al*. 1998). Simulation of the efficiency of MAS showed that the response to MAS is more variable than the response to phenotypic selection. The higher efficiency of MAS on QTL with large effects in early generations is balanced by a higher rate of fixation of unfavorable alleles of QTL with smaller effects in later generations (Hospital *et al*. 1997). Frisch and Melchinger (2001) studied the number of marker data points required to recover the recurrent parent genome when two genes were simultaneously introduced. Application of three or four selection steps, large population size starting from early generation, and merging target genes in early generation will improve the efficiency of MAS.

Gimelfarb and Lande (1995) noted that markers used for selection are not necessarily the most tightly linked to the QTL controlling the trait. The additive effects of the markers estimated by the regression may not accurately reflect the contributions of the most tightly linked markers. MAS for complex traits was limited due to the inability to detect and quantify marker-trait relationships, especially for the gene-by-gene and gene-by-environment effects (Podlich *et al*. 2004). Breeders should be very cautious when using QTL detected from only one environment (Liu PY *et al*. 2006).

Advantages of combination of MAS and phenotypic selection

MAS for disease resistance should be verified by disease inoculation to ensure that the resistance is being transferred (Miklas *et al*. 2006a). The most effective breeding strategy to improve bean CBB resistance combines MAS and periodic phenotypic selection. Phenotypic selection is needed to retain minor QTL and to select epistatic interactions that contribute to improved disease resistance (Miklas *et al*. 2006a). Davies *et al*. (2006) compared the MAS and phenotypic selection for high grain protein content. Phenotypic selection is more effective in some environments because it can select both major and minor QTL (Miklas *et al*. 2006a). However, MAS has more advantages to help in transferring the high GPC QTL through backcrossing. A selection index including both molecular marker information and phenotypic values with suitable weights is the best selection strategy (Sala *et al*. 2006). Liu *et al*. (2004) studied the efficiency of MAS in breeding selfed crops. They proposed an index to select superior genotypes and suggested that combination of MAS in early generations with phenotypic selection in later generations would be most efficient. In wheat breeding in Australia, MAS, phenotype and pedigree information was integrated to improve the efficiency of selection and increase the rate of genetic gain (Christopher *et al*. 2007).

Dreher *et al*. (2002) from CIYYMT used *opaque2* controlling maize protein as a case to study the cost-effectiveness of MAS. They concluded that in those cases where phenotypic screening is expensive and difficult, including breeding for multiple genes, recessive genes, traits associated with adult plants, and traits with seasonal or geographical limitations, MAS has advantages. However, conventional breeding can be cost-effective for those traits which depend on visual selections. Kuchel *et al*. (2005) simulated the processes of applying MAS in a BC_1F_1 population, gene selection in haploid and selection for recurrent background. Incorporation of MAS in the first two stages increased genetic gain and reduced the overall cost by 40% compared with phenotypic selection.

Hoeck *et al*. (2003) studied the QTL associated with seed size of soybean and concluded that phenotypic selection was effective and less expensive than MAS.

Inconsistent QTL across environment was due to weak expression of QTL, and to significant QTL × environment interaction effects in the opposite direction to QTL main effects. In application of MAS for quantitative traits, QTL × environment interaction effects must be considered (Li ZK *et al*. 2003).

FUTURE DIRECTIONS

MAS depends on several important factors, including the number of target genes to be selected, the genetic distances between the markers and the target genes, the number of genotypes selected in each generation, and the genetic background in which the target gene is transferred (Babu *et al*. 2004; Francia *et al*. 2005). The continuous development of marker technologies and improved genetic understanding of complex traits, relations among traits and between target trait and environments will make MAS breeding more broadly-usful and efficient, as well as cost-effective. Koebner and Summers (2003) predicted that when SNP technology is sufficiently developed to facilitate marker-based

genotyping of the number of plants that breeders handle routinely in the field, it will profoundly change breeding strategies. SNP markers will show the power and efficiency of MAS in plant breeding. It promises the high throughput assay and multiplexing that will decrease the cost for selection of multiple traits in crop breeding (Dubcovsky 2004). For complex traits like yield and abiotic stress, however, several constraints limit the efficiency of MAS in plant breeding (Francia *et al.* 2005).

Current QTL analyses depend on populations developed from two inbred lines. The detected QTL only represent a small part of the genetic architecture of the trait. However, the general breeding population is pedigree derived and remains unexploited. Crepieux *et al.* (2004) developed a framework which is based on two-step identity-based-descendant (IBD) variance component and applicable to any type of breeding population from inbred parents. The consideration of relatedness between parents improved the power and accuracy of the QTL analyses.

More perfect markers associated with important agronomic traits will be developed for MAS. In wheat, gene cloning has led to the development of perfect markers based on allelic variation responsible for the differences in the traits (Dubcovsky 2004). These traits include glutenin genes, waxy genes, vernalization genes, *Rht* genes for plant height and leaf rust resistance genes *Lr10* and *Lr21*.

One major area of future plant breeding will focus on improving the nutrition, and enriching antioxidants for human health using functional and nutritional genomics (Datta 2000). In this phase, MAS will be a useful tool in selection.

The application of knowledge from model crops to other crops or orphan crops less studied may be effective in the following areas: 1) analyses of crop diversities and identification of useful alleles; 2) specific allele integration using MAS; 3) cloning and transfer of desirable alleles among taxa (Nelson *et al.* 2004). Comparative studies can use both similarities and differences to accelerate the studies of orphan crops.

With the advanced technology and information available, the competition will be on the speed to incorporate these technologies into crop breeding programs (Dubcovsky 2004). As breeders and molecular geneticists, we are very glad to see the great progress that has been and will be made combining conventional breeding with available molecular technologies.

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