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

Shuyu Liu¹ • Mitali Banik¹ • Kangfu Yu¹† • Soon J. Park¹ • Vaino Poysa¹ • Yanan Guan²

¹ Greenhouse and Processing Crops Research Centre, Agriculture and Agri-Food Canada, 2585 County Rd. 20, Harrow, Ontario, N0R 1G6, Canada
² Institute of Crop Science, Shandong Academy of Agricultural Sciences, 28 Sangyuan Rd. Jinan, 250100, Shandong, China

Corresponding author: * yuk@agr.gc.ca

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.

Keywords: disease resistance, drought tolerance, Glycine max L., insect resistance, marker-assisted selection, Oryza sativa L., Phaseolus vulgaris L., single nucleotide polymorphism, Triticum aestivum L., Zea mays L.

CONTENTS

INTRODUCTION...................................................................................................................................................................................... 74
MAS FOR RESISTANCE TO BIOTIC STRESSES.................................................................................................................................... 75
- MAS in wheat.................................................................................................................................................................................. 75
- MAS in maize.................................................................................................................................................................................. 78
- MAS in rice.................................................................................................................................................................................. 78
- MAS in soybean........................................................................................................................................................................... 79
- MAS in common bean............................................................................................................................................................ 79
MAS FOR RESISTANCE TO ABIOTIC STRESSES................................................................................................................................. 80
- MAS for drought tolerance.................................................................................................................................................... 80
- Lodging resistance.................................................................................................................................................................. 80
- Cold tolerance........................................................................................................................................................................ 80
MAS FOR IMPROVEMENT OF OTHER TRAITS..................................................................................................................................... 80
- High protein and other nutrition improvement.................................................................................................................. 80
- Plant nutrition and other traits............................................................................................................................................. 81
PROS AND CONS OF MAS................................................................................................................................................................. 81
- Advantages of MAS............................................................................................................................................................... 81
- Considerations in use of MAS................................................................................................................................................. 82
ADVANTAGES OF COMBINATION OF MAS AND PHENOTYPIC SELECTION.................................................................................. 82
FUTURE DIRECTIONS............................................................................................................................................................................. 83
ACKNOWLEDGEMENTS...................................................................................................................................................................... 83
REFERENCES.................................................................................................................................................................................. 83

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 (Schwert 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. 2001; 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; Whitman-Solis et al. 2002; Muck 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, 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. OL and DH were faster and more economical, while ASPE was more cost-effective and simple, howev-

To detect FHB resistance in wheat, a 3BS QTL conditioning type II FHB resistance (resistance to Fusarium spread) from Sunmai 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 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 Xbarn133 and Xgwm493 flanking the QTL on 3BS (Anderson et al. 2001) and Xbarn36 and Xbarn117 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 (Cutiberti 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 (Baszczynski 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 Xgwm493, Xwmc764, Xgwm575, Xgwm644 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 (Sillikov 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, YrH152, at a distance of 0.33 cm. Markers within 5 cm are efficient to select homozygous resistant plants. Xbarn101 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-B1, 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.

<table>
<thead>
<tr>
<th>Crops</th>
<th>Traits</th>
<th>Resistance QTL/genes</th>
<th>Markers for MAS</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wheat</td>
<td>Fusarium head blight</td>
<td>Qfhk.ndsu-3BS; QTL on S5; Qfhk.ndsu-3AS; Fhb2</td>
<td>Xwgm533.1, Xbarc147, Xbarc133 and Xwgm493, Xbarc56 and Xbarc117; Xfep401, Xfep397.2; Xwgm133, Xwgm644</td>
<td>Anderson et al. 2001; Chen J. et al. 2006; Chen et al. 2007; Cuthbert et al. 2007</td>
</tr>
<tr>
<td></td>
<td>Stem rust</td>
<td>Sr2</td>
<td>Xwgm533</td>
<td>Hayden et al. 2004</td>
</tr>
<tr>
<td></td>
<td>Leaf rust</td>
<td>Lr16, Lr1, Lr47, Lr45; Lr9; Lr10, Lr29, Lr26, Lr37; Lr19, Lr24</td>
<td>Xwmc764, Xwgm210, Xwmc661; PTAG621, PS10; Xwgm473.133, Xwgm372.180, Xwgm122.110</td>
<td>McCarty et al. 2005; Nocentini et al. 2007; Zhang N et al. 2007; Sliškova et al. 2004; Baszczyk et al. 2004; Singh and Tiwari 2005</td>
</tr>
<tr>
<td></td>
<td>Slow leaf rust</td>
<td>QTL</td>
<td></td>
<td>Xu et al. 2005</td>
</tr>
<tr>
<td></td>
<td>Powdery mildew</td>
<td>Pm3; Pm4a; Pm21;</td>
<td>Pm3FR; BCD292; NAU/Xibao16; Xwgm304, Xwgm501</td>
<td>Tommasini et al. 2007; Ma et al. 1994; Liu et al. 2001; Gao et al. 2008; Chen et al. 2008; Tucker et al. 2006</td>
</tr>
<tr>
<td></td>
<td>Stripe rust</td>
<td>QTL</td>
<td></td>
<td>Zhang et al. 2005</td>
</tr>
<tr>
<td></td>
<td>Barley yellow dwarf</td>
<td>Bd2</td>
<td>SC-gp1, SC-D04</td>
<td>Smith et al. 2007; Peng et al. 2000; Uauy et al. 2005</td>
</tr>
<tr>
<td></td>
<td>Septoria triticic blotch</td>
<td>Sb2</td>
<td></td>
<td>Adhikari et al. 2004</td>
</tr>
<tr>
<td></td>
<td>Spot blotch</td>
<td>QTL</td>
<td></td>
<td>Sharma et al. 2005</td>
</tr>
<tr>
<td></td>
<td>Karnal bunt</td>
<td>QTL</td>
<td></td>
<td>Brooks et al. 2006</td>
</tr>
<tr>
<td>Green bug</td>
<td></td>
<td></td>
<td>Xwmc634</td>
<td>Weng et al. 2002, 2005; Zhu et al. 2005</td>
</tr>
<tr>
<td>Russian wheat aphid</td>
<td></td>
<td></td>
<td>Xwgn106; Xwgm337; red glum gene Rg2; Xwgm437; Xrems1303;320; Xwgm44, Xwgm111</td>
<td>Arzani et al. 2004; Miller et al. 2001; Lapitan et al. 2007; Liu et al. 2002</td>
</tr>
<tr>
<td>Russian wheat aphid</td>
<td></td>
<td></td>
<td>Xbarc263, Xfca2153, SPO005.909; Xspsp999, Xwem66B, Xhoa2ks, Xgdm33</td>
<td>Kong et al. 2005, 2007; Zhao et al. 2005; Liu et al. 2006, 2005b; Saradesi et al. 2005</td>
</tr>
<tr>
<td>Russian wheat aphid</td>
<td></td>
<td></td>
<td>Xgsm301; OpV16(1065)</td>
<td>Martin et al. 2004; Barloy et al. 2007</td>
</tr>
<tr>
<td>Russian wheat aphid</td>
<td></td>
<td></td>
<td>Xwmc512-Xwmc21, Xwgm108-Xwmc291; Xwgm135-Xwmc84, Xwgm311-Xwmc301</td>
<td>Dong et al. 2006</td>
</tr>
<tr>
<td>Russian wheat aphid</td>
<td></td>
<td></td>
<td>Xwmc89; Xwmg261</td>
<td>Kirigwi et al. 2007; Kumar et al. 2007</td>
</tr>
<tr>
<td>Russian wheat aphid</td>
<td></td>
<td></td>
<td>Xwmc182; Xdcm456</td>
<td>Ellis et al. 2002</td>
</tr>
<tr>
<td>Russian wheat aphid</td>
<td></td>
<td></td>
<td>Xbarc164, Xwmc331</td>
<td>Zhou et al. 2007</td>
</tr>
<tr>
<td>Russian wheat aphid</td>
<td></td>
<td></td>
<td>umc123, umc110</td>
<td>Cai et al. 2003</td>
</tr>
<tr>
<td>Russian wheat aphid</td>
<td></td>
<td></td>
<td>Umc363; csu173-umc126a, csu26a-umc68; umc1402u; umc65a-umc21; umc103a; csu145a</td>
<td>Bohn et al. 1998</td>
</tr>
<tr>
<td>Russian wheat aphid</td>
<td></td>
<td></td>
<td>cs1066-umc176</td>
<td>Butron et al. 2001</td>
</tr>
<tr>
<td>Russian wheat aphid</td>
<td></td>
<td></td>
<td>bnl8.23-bnl 5.47a</td>
<td>George et al. 2003</td>
</tr>
<tr>
<td>Russian wheat aphid</td>
<td></td>
<td></td>
<td>BC539.120, BC324.1400</td>
<td>Ali et al. 2005</td>
</tr>
<tr>
<td>Russian wheat aphid</td>
<td></td>
<td></td>
<td></td>
<td>Frova et al. 1998</td>
</tr>
<tr>
<td>Russian wheat aphid</td>
<td></td>
<td></td>
<td></td>
<td>Landi et al. 2002</td>
</tr>
<tr>
<td>Russian wheat aphid</td>
<td></td>
<td></td>
<td></td>
<td>Li et al. 2003</td>
</tr>
<tr>
<td>Russian wheat aphid</td>
<td></td>
<td></td>
<td></td>
<td>Wong et al. 2004</td>
</tr>
<tr>
<td>Russian wheat aphid</td>
<td></td>
<td></td>
<td></td>
<td>Yang et al. 2005</td>
</tr>
<tr>
<td>Rice</td>
<td>Rice blast</td>
<td>Pj-I; Pj-ka; Pj-b; Pj-k; Pj-5t; Pj-z; Pgm4(t); P12; P9; Pj-tar; Pj-(P12-5); Pj-tik; Pj-tik; Pj-tik; Pj-tik; Pj-tik; Pj-tik</td>
<td>MRG4766; S-129.700; RM208, RM224; JX80-T3; MRG9836; CS483; C0428; YL155/YL87; Z4794 -z60510, i256, k3951, k2167, k3957, ta3, b2</td>
<td>Chen et al. 2005; Sharma et al. 2005; Fjellstrom et al. 2004; Yu et al. 2004; Conaway-Bornans et al. 2003; Deng et al. 2006; Wang et al. 2007; Hayashi et al. 2006</td>
</tr>
<tr>
<td>Crops</td>
<td>Traits</td>
<td>Resistance QTL GENES</td>
<td>Markers for MAS</td>
<td>References</td>
</tr>
<tr>
<td>-------</td>
<td>--------</td>
<td>----------------------</td>
<td>-----------------</td>
<td>------------</td>
</tr>
<tr>
<td>Rice</td>
<td>Green leaf resistance</td>
<td>Ghr5</td>
<td>RM3754, RM3761</td>
<td>Fujita et al. 2006</td>
</tr>
<tr>
<td></td>
<td>Brown plant hoppers</td>
<td>Bph2, Bph13(t), Bph6, Qphb11, Bph17</td>
<td>RM7102, RM463, AJ09.230; RM463, RM5341; XNph202, C1172; RM8213, RM5953</td>
<td>Renganayagi et al. 2002; Su et al. 2005; Sun et al. 2005, 2006</td>
</tr>
<tr>
<td></td>
<td>Drought tolerance, yield</td>
<td>QTL</td>
<td>RG939-RG476-RG214</td>
<td>Babu et al. 2003</td>
</tr>
<tr>
<td></td>
<td>Root thickness</td>
<td>brs2b</td>
<td>RM161-R521</td>
<td>Li et al. 2005</td>
</tr>
<tr>
<td></td>
<td>Deep root, root thickness</td>
<td>QTL</td>
<td>RG256-RG151</td>
<td>Kamoshita et al. 2002</td>
</tr>
<tr>
<td></td>
<td>Drought tolerance</td>
<td>QTL</td>
<td>RM223, RM263</td>
<td>Kumar et al. 2005</td>
</tr>
<tr>
<td></td>
<td>Low glutel content</td>
<td>QTL</td>
<td>SSR2-004, RM1358</td>
<td>Wang YX et al. 2005</td>
</tr>
<tr>
<td></td>
<td>Rice protein and fat content</td>
<td>qRfC-5, qRfC-2, qRfC-5</td>
<td>RG435-RG172a, RG241b-RG324, RG470-RG474</td>
<td>Ha et al. 2004</td>
</tr>
<tr>
<td></td>
<td>Ferrous iron toxicity</td>
<td>QTL</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Elongating ability</td>
<td>QTL</td>
<td>Rev1, RM239-RG257, F18F/F18RM</td>
<td>Lang et al. 1999; Jia et al. 2001</td>
</tr>
<tr>
<td></td>
<td>Thermo-sensitive genetic male sterile</td>
<td>rms1, rms3(t)</td>
<td>RM104</td>
<td>Guo et al. 2004; Wan et al. 2006</td>
</tr>
<tr>
<td></td>
<td>Seed dormancy</td>
<td>qSdb-1</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Seed vigor</td>
<td>qSV-7</td>
<td>RM214 - G20 - C285</td>
<td>Zhang ZH et al. 2005</td>
</tr>
<tr>
<td></td>
<td>Heading date</td>
<td>Hdl1; Hdl2; Hdl3; Hdl6; Hdl7; Hdl4; Hdl5; Hdl9</td>
<td>S2539; C728; C764; R3226; C560; S1485; S1633A</td>
<td>Lin et al. 2000; Yamamoto et al. 2000; Lin et al. 2002, 2003</td>
</tr>
<tr>
<td></td>
<td>Cold tolerance</td>
<td>Qct-11</td>
<td>RM202</td>
<td>Chen W et al. 2005</td>
</tr>
<tr>
<td>Soybean</td>
<td>Soybean cyst nematode</td>
<td>RHG-1, RHG-4</td>
<td>Satt309, Sat168; Satt038, Satt130</td>
<td>Mudge et al. 1997; Cregan et al. 1999b; Ferdous et al. 2006</td>
</tr>
<tr>
<td></td>
<td>Frogeye leaf spot</td>
<td>Rcs3</td>
<td>Satt244, Satt547</td>
<td>Man et al. 1999</td>
</tr>
<tr>
<td></td>
<td>SDS</td>
<td>QTL</td>
<td>SAT99, SATT6</td>
<td>Njitte and Lightfoot 2006</td>
</tr>
<tr>
<td></td>
<td>Root and stem rot</td>
<td>Rsps8, Rsps3</td>
<td>Sat_154</td>
<td>Sandhu et al. 2005</td>
</tr>
<tr>
<td></td>
<td>Brown stem rot</td>
<td>Rbs1; Rbs2</td>
<td>Satt431, Satt244</td>
<td>Tamonilus et al. 2001</td>
</tr>
<tr>
<td>Soybean</td>
<td>Soybean rust</td>
<td>Rpl1</td>
<td>Sat435, Satt467</td>
<td>Li et al. 2007</td>
</tr>
<tr>
<td></td>
<td>Soybean aphid</td>
<td>Rgol1</td>
<td>Satt461, Satt292, Satt156; Satt461, Satt249</td>
<td>Panthee et al. 2004</td>
</tr>
<tr>
<td></td>
<td>Protein</td>
<td>Glycinin (11S, G4), betaconglycinin (7S)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Isoflavones</td>
<td>QTL</td>
<td>Satt201 – Satt540 – Satt245</td>
<td>Primomo et al. 2005</td>
</tr>
<tr>
<td></td>
<td>Fatty acid content</td>
<td>QTL</td>
<td></td>
<td>Hyten et al. 2004b</td>
</tr>
<tr>
<td></td>
<td>Palmitate acid</td>
<td>sap(nc)</td>
<td>GmFATB1a</td>
<td>Cardinal et al. 2007</td>
</tr>
<tr>
<td></td>
<td>Linolenic acid</td>
<td>QTL</td>
<td>Satt534, Satt560</td>
<td>Spencer et al. 2004</td>
</tr>
<tr>
<td></td>
<td>Alpha-tocopherol</td>
<td>QTL</td>
<td>Sat342, Sat167</td>
<td>Dwiyanti et al. 2007</td>
</tr>
<tr>
<td></td>
<td>Iron-deficiency chlorosis</td>
<td>QTL</td>
<td>Satt481</td>
<td>Charlson et al. 2005</td>
</tr>
<tr>
<td></td>
<td>Salt tolerance</td>
<td>QTL</td>
<td>Sat_091, Sat237</td>
<td>Lee et al. 2004</td>
</tr>
<tr>
<td>Common Bean</td>
<td>Common bacterial blight</td>
<td>UBC420, SU91, SAP6</td>
<td></td>
<td>Jung et al. 1997; Miklas et al. 2000a; Yu et al. 2000b</td>
</tr>
<tr>
<td></td>
<td>Bean common mosaic virus</td>
<td>I</td>
<td>SW13</td>
<td>Melotto et al. 1996</td>
</tr>
<tr>
<td></td>
<td>Bean common mosaic necrosis virus</td>
<td>bc-1, bc-2, bc-3</td>
<td>SBD5.1300, RCO11</td>
<td>Miklas et al. 2000b</td>
</tr>
<tr>
<td></td>
<td>Bean gold mosaic virus</td>
<td>bgm-1</td>
<td>SR2</td>
<td>Blair et al. 2007</td>
</tr>
<tr>
<td></td>
<td>Anthracnose</td>
<td>Co-4</td>
<td>SAS13</td>
<td>Melotto and Kelly 2001</td>
</tr>
<tr>
<td></td>
<td>White mold</td>
<td>QTL</td>
<td>AFLP</td>
<td>Ender et al. 2007</td>
</tr>
</tbody>
</table>

*Gene, linked markers, and references are separated by “;” if they are corresponded specifically.

(called by Erysiphe graminis f. sp. tritici). They can explain more than 50% of the phenotypic variance 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 DNA is very useful in MAS. SSR loci Xgwm389 and Xgwm533.1 were about 1cM distal to Srh2, 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, Xwm6c 343,
co-segregate with Gb3, a green bug resistance gene on 7D (Weng et al. 2002, 2005). The converted STS markers from these two AFLP markers and the SSR marker should be useful in MAS. Markers linked to other green bug resistance genes Gbx1, Gba, Gbb, Gbc, Gbd, Ghz 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. 2002). A major gene cluster MAS 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 Xsp9299 and Xwem6f 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 populations to increase the durability of maize resistance to downy mildew (caused by Peronosclerospora ssp.), 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 ssp.) 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

Resistance 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 major cereal crop, it may fulfill 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), or 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-Pasquier 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 BC1F2 for the gene transfers of xa13 and Xa21 in line IRBB55 (Joseph et al. 2004). An EST marker C189 linked to Xa23 gave 100% efficiency (Wang CL et al. 2005). In another case, an F3 line test found that MAS reached an efficiency larger than 90% to identify homoyzogous 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 Japanese 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-t (linked with marker MRG4766) and Pi-t1 (linked with marker S-129.700 at 2.1 cM, Sharma et al. 2005), Pi-t2 (Hittalmani et al. 1995), Pi-t5(t) (linked to J80-T3, Yi et al. 2004), Pi-b and Pi-k (co-segregates with RM208 and RM224, Fjellstrom et al. 2004), Pi-z (linked to MRG8536, Conway-Bormans et al. 2003), and Pigm(t), P12, P19 (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 genes, 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, Pi-z5, Pik, Pik-m, Pik-p, 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 haplotype 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, Nilapavarta 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, Satt463 and RM5341) on chromosome 12 (Su et al. 2006), Bphp11 (flanked by markers XNp6202 and C1172) for BPH resistance in ‘DV85’ (Su et al. 2005), Bphp13(t) (linked by AJ09230(b) on chromosome 3 (Renganayaki et al. 2002), and Bphp17 (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 Inchi- noe), 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 rng1 locus conferring SCN resistance. It can be used to distinguish most of SCN-susceptible genotypes from those rng1 carriers derived from resistant parent ‘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 (rng1) from the Japanese cultivar Toyomusume and con-complained that the combination of rng1 on LG G and rng2 on LG B provides a high level resistance to SCN. Conventional breeding from resistant sources 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). SNP 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 Sat634 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 (Tamaloniis et al. 2001).

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 the different genetic backgrounds for MAS of this QTL (Liu et al. 2007b).

SW13 is linked to the F 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-1f, which confers resistance to specific strains of BCMV and bean common mosaic necrosis virus (BCMN). However, its resistance is neither in bc-1f nor in bc-3 (Miklas et al. 2000b). Therefore, the marker should be useful in MAS breeding. A recessive gene, bmg-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 lindenuthianum) 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-4 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 UBC240 linked QTL for CBM resistance, SW13 linked J gene for BCMV resistance, and SAS13 linked to Co-4 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 B1 QTL from G122 and a B2 QTL from NY620-4 into susceptible pinto bean (Miklas and Bosak 2006c). Ender et al. (2007) applied markers linked QTL for resistance to white mold from Bursi 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 (Quarré et al. 1999). Kirigvi 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 QTL into 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, MAS strategy for improvement can be established by combining QTL associated with decreased ASI and increased ear setting percentage and grain yield (Li 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).

Baba et al. (2003) identified two QTL on chromosome 4 and 6 that affect 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, Rrh9 on 2DS, Rrh9 or 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 ‘Toyohata-mochi’ (Kim et al. 2000). SSR marker RM202 is closely linked to a QTL (Qsc-t-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 HWMS-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-Ace1 marker can be used to lower the amylose 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 pyramidal 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 glycycin 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 R² 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 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 Sat243 and Sat167 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 Sat091 and Sat237 were always associated with salt tolerance in descendent cultivars of S-100, indicating its usefulness in MAS in commercial soybean breeding (Lee GI 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 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, rtm1 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 qSbr-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, Hdl1, Hdl2, Hdl3, Hdl4, Hdl5, Hdl6, Hdl7, Hdl9 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 coincidently 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).

Tuveson 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 F₁ or BCF₁ 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 common mosaic virus resistance, a marker linked to the J 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 (Sace.) 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 borers resistance unless QTL have larger effects or the cost of marker assays is considerably reduced (Yu et al. 2000a). Due to the low consis- tent QTL expression 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 rate of fitness is less than one. One allele of QTL with 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 CIYMT used opaque2 controlling maize protein as a case to study the cost-effective-ness 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 BC1F1 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 selec- tion 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-useful and efficient, as well as cost-effective. Koeb- ner and Summers (2003) predicted that when SNP technol-ogy 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 (Franca 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 genomic traits will be developed for MAS. In wheat, gene cloning has led to the development of perfect markers based on the traits in the traits (Dubcovsky 2004). These traits include glutenin genes, waxy genes, vernalization genes, allelic variation responsible for the differences in the traits 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.

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.

ACKNOWLEDGEMENTS

The authors thank the funding support from the Improving Farming System Practice Initiative project of Agricultural Agri-Food Canada and the Ontario White and Coloured Bean Growers.

REFERENCES


Charlton DV, Bailey; Ciancio SR, Shoemaker RC (2005) Molecular marker Sat481 is associated with iron deficiency chlorosis resistance in a soybean breeding population. Crop Science 45, 2394-2399


Hyten DL, Hartman GL, Nelson RL, Frederick RD, Concibido VC, Narvel


Kelly JD, Gepts P, Milkas PN, Coyne DP (2003) Tagging and mapping of genes and QTL and molecular-marker assisted selection for traits of econo-
Theoretical and Applied Genetics 111, 243-249


Luo LJ, Li ZK (2001) QTL dissection of panicle number per plant and spikelet number per panicle in rice (Oryza sativa L.). Acta Genetica Sinica 28, 752-759


Ma QZ, Sorrells ME, Tanklesy SD (1994) RFLP markers linked to powdery mildew resistance genes Pm1, Pm2, Pm3, and Pm4 in wheat. Genome 37, 871-875


Paul PA, Lipps PE, Madden LV (2005) Relationship between visual estimates of Fusarium head blight intensity and deoxynivalenol accumulation in harvested wheat grain: A meta analysis. Phytopathology 95, 1225-1236


Prevey MO, Borrero R, Anderson JS (2007) Validating the Fhil1 QTL for fusarium head blight resistance in near-isogenic wheat lines developed from breeding populations. Crop Science 47, 200-206


Sanchez AC, Brar DS, Huang N, Li Z (2000) Sequence tagged site marker-assisted selection for three bacterial blight resistance genes in rice. Crop Science 40, 792-797


86

MAS in major cereal and legume crop breeding. Liu et al.
Schneider KA, Brothers ME, Kelly JD (1997a) Marker-assisted selection to improve resistance in common bean. Crop Science 37, 53-60
Schwartz D (1960) Electrophoretic and immunochromical studies with endo-sperm proteins of maize mutants. Genetics 45, 1419-1427
Williams JGK, Kubelik AR, Livak KJ, Rafalski JA, Tingey SV (1990) DNA polymorphisms amplified by arbitrary primers are useful as genetic markers. Nucleic Acids Research 18, 6353-6355
Xie C, Xu S (1998) Efficiency of multistage marker-assisted selection in the improvement of multiple quantitative traits. Heredity 80, 489-498
Yu K, Park SJ, Posa V, Geps P (200b) Integration of simple sequence repeat (SSR) markers into a molecular linkage map of common bean (Phaseolus vulgaris L..). Journal of Heredity 91, 429-434
Zeng ZG, Zhang ZY, Du LP, Xin ZY, Chen X (2005) Development of wheat germplasm with multi-resistance to powder mildew, stripe rust and yellow
MAS in major cereal and legume crop breeding. Liu et al.

dwarf virus by molecular marker-assisted selection. *Scientia Agricultura Sinica* 38, 2380-2386


Zhang YB, Sun LF, Xin WL, Song QJ, Zhang CL, Zhao HB, Xiao ZM, Qi SY (2003) Effect of HMW-GS 5+10 on quality parameters in four leading wheat cultivars. *Agricultural Sciences in China* 2, 483-488


Zhao HX, Liu XM, Chen MS (2006) H22, a major resistance gene to the Hessian fly (*Mayetiola destructor*) is mapped to the distal region of wheat chromosome 1Ds. *Theoretical and Applied Genetics* 113, 1491-1496


88