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Phenotypic versus marker-assisted selection for stalk strength and second-generation European corn borer resistance in maize

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Abstract Maize (*Zea mays* L.) stalk lodging is breakage of the stalk at or below the ear, which may result in loss of the ear at harvest. Stalk lodging is often intensified by the stalk tunneling action of the second-generation of the European corn borer (2-ECB) [*Ostrinia nubilalis* (Hübner)]. Rind penetrometer resistance (RPR) has been used to measure stalk strength and improve stalk lodging resistance, and quantitative trait loci (QTL) have been identified for both RPR and 2-ECB damage. Phenotypic recurrent selection (PS) increases the frequency of favorable alleles over cycles of selection. Several studies have indicated that marker-assisted selection (MAS) is also a potentially valuable selection tool. The objective of this study was to compare the efficiency of PS versus MAS for RPR and 2-ECB. Marker-assisted selection for high and low RPR was effective in the three populations studied. Phenotypic selection for both high and low RPR was more effective than MAS in two of the populations. However, in a third population, MAS for high RPR using

QTL effects from the same population was more effective than PS, and using QTL effects from a separate population was just as effective as PS. Marker-assisted selection for resistance and susceptibility to 2-ECB using QTL effects from the same population was effective in increasing susceptibility, but not in increasing resistance. Marker-assisted selection using QTL effects from a separate population was effective in both directions of selection. Thus, MAS was effective in selecting for both resistance and susceptibility to 2-ECB. These results demonstrated that MAS can be an effective selection tool for both RPR and 2-ECB resistance. These results also validate the locations and effects of QTL for RPR and 2-ECB resistance identified in earlier studies.

Keywords Corn · Quantitative genetics · Host-plant resistance · Standability · Lodging resistance

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Introduction

Stalk lodging resistance is an important aspect of plant standability in maize (*Zea mays* L.). Stalk lodging is breakage of the stalk at or below the ear, which may result in loss of the ear at harvest. Sibale et al. (1992) described use of a modified electronic rind penetrometer to measure stalk strength. Rind penetrometer resistance (RPR) has been significantly and negatively correlated with stalk lodging in several studies (Chesang-Chumo 1993; Dudley 1994; Spiess 1995; Jampatong 1999b; Kang et al. 1999; McDevitt 1999; Hondroyianni et al. 2000) and is being used to study stalk quality in the seed industry (J. Arbuckle, 2003, personal communication). The rind penetrometer, therefore, has become a valuable tool for measuring stalk strength. One insect pest of maize that increases stalk lodging by stalk tunneling is the European corn borer (ECB) [*Ostrinia nubilalis* (Hübner)], which causes losses of \$1 billion annually in the United States due to control costs and yield losses (Mason et al. 1996).

One of the most efficient tools for improving breeding populations for quantitative traits is phenotypic selection

(PS), where the frequency of favorable alleles is increased within a population over cycles of selection (Hallauer 1992). Phenotypic recurrent selection has been very successful in improving RPR in the synthetic 'MoSCSSS' (Alsirt 1993). Phenotypic selection has also been successful in developing second-generation European corn borer (2-ECB)-resistant maize. Several inbred lines have been released with native host-plant resistance from various sources, including tropical maize accessions (Barry et al. 1995).

Composite interval mapping has been employed to identify quantitative trait locus/loci (QTL) for both RPR and 2-ECB resistance in an effort to understand the genetic basis of these traits. In a previous study, we found that RPR was controlled by many genes with small-to-moderate effects (Flint-Garcia et al. 2003). Cardinal et al. (2001), Flint-Garcia (2001) and Jampatong et al. (2002) found that resistance to 2-ECB was conferred by several genes with small-to-moderate effects.

Once QTL are identified, they can be manipulated by marker-assisted selection (MAS) to indirectly select for favorable QTL alleles. Several studies have indicated that MAS has the potential to be a valuable selection tool. However, only a limited number of studies have provided results comparing PS with MAS. Encouraging results were reported for yield, ear height and ear number in maize (Stuber 1994), for malting quality in barley [*Hordeum vulgare* (L.)] (Han et al. 1997), for drought resistance in common bean [*Phaseolus vulgaris* (L.)] (Scheider et al. 1997), for transfer of acylsugar accumulation from wild tomato to cultivated tomato [*Lycopersicon esculentum* (Mill.)] (Lawson et al. 1997), for flowering time in *Arabidopsis thaliana* (Van Berloo and Stam 1999), for yield in barley (Romagosa et al. 1999), for seedling emergence and kernel-eating quality characteristics in sweet corn (Yousef and Juvik 2001) and for resistance to southwestern corn borer [*Diatraea grandiosella* (Dyar)] (Wilcox et al. 2002).

A criticism of QTL mapping is the difficulty in distinguishing between a true QTL and a statistical false positive (erroneous declaration of a QTL). Approaches to verifying the effects of previously identified QTL include development of nearly isogenic lines (NILs) varying for a single QTL and testing of candidate genes. Marker-assisted selection can also be used to validate QTL effects by testing whether selection based on QTL changes the mean trait value when compared to a non-selected entry.

The objectives of this study were (1) to compare the efficiency of PS versus MAS for high and low RPR, and resistance and susceptibility to 2-ECB in multiple populations, and (2) to use MAS to verify QTL for RPR and 2-ECB. Comparisons between PS and MAS were made for selections from a population (1) based on QTL from the respective population, i.e., when QTL from population 3 were used for MAS in population 3, and (2) based on QTL from a separate population, i.e., when QTL from populations 2 or 4 were used to make selections in population 3.

Materials and methods

Plant materials and selection

This study is based on the phenotypic family means and the predicted gene effects for QTL from four $F_{2:3}$ mapping populations. Populations 1, 2, and 3 (Flint-Garcia 2001; Flint-Garcia et al. 2003) and population 4 (Jampatong 1999a; Jampatong et al. 2002) were used to make selections for high and low RPR, and resistance and susceptibility to 2-ECB. The pedigrees of the four populations are population 1, 'MoSCSSS-High RPR' × 'MoSQB-Low SCS' (stalk crushing strength, an alternative measurement of stalk strength; 282 families); population 2, 'MoSCSSS-High RPR' × 'MoSCSSS-Low RPR' (291 families); population 3, 'MoSCSSS-High RPR' × 'Mo47' (291 families); and population 4, 'Mo47' × 'B73' (244 families).

Populations 1 and 2 were originally created to map stalk rind strength QTL since both parents of each population were selected for high ('MoSCSSS-High RPR') and low ('MoSCSSS-Low RPR' and 'MoSQB-Low SCS') stalk strength phenotypes. Population 4 was initially created to map QTL for resistance to both first- and second-generation ECB, with 'Mo47' as the source of resistance. We decided to evaluate RPR in this population, where neither parent had been selected for stalk strength per se. Finally, population 3 was designed to bridge the gap between populations 1 and 2 and population 4.

To accommodate collection of different types of data, the PS versus MAS evaluation was designed and planted as two separate experiments: a stalk strength experiment and a 2-ECB experiment. The naming convention for entries was (1) the population in which selection was conducted, (2) the trait selected for (high or low RPR, resistance or susceptibility to 2-ECB), and (3) the selection criterion (population used for selection and PS or MAS) (Fig. 1). The stalk strength experiment included selections based solely on RPR from populations 1, 2, and 3. For populations 1 and 2, selections for high and low RPR were based on both phenotype and QTL from their respective populations. For population 3, selections were made for high and low RPR, each based on phenotype, QTL from population 3, QTL from population 2, and QTL from population 4. The 2-ECB experiment included selections based solely on ECB tunneling damage from population 3. Selections were made for resistance and susceptibility to 2-ECB, each based on phenotype, QTL from population 3, and QTL from population 4.

Phenotypic selection was based on family means combined over environments for each trait in each population. Families were sorted by trait mean, and the ten highest and ten lowest families were chosen for each trait in each population.

For MAS, a selection scheme was implemented that resembled PS. Marker-assisted selection was based on the genetic effects for each of the significant QTL using a method modified from that of Stuber (Stuber and Edwards 1986; Stuber 1994). For each family within a population, marker scores (A, B or H) for markers linked to, or flanking, each of the significant QTL were substituted with additive and dominance values from preliminary QTL results as calculated by QTL Cartographer (Basten et al. 1994, 2000). If the peak of the QTL was at or near a marker, the "A" marker score was replaced by the additive effect of the "A" allele at that QTL, the "B" marker score was replaced by the additive effect of the "B" allele and the "H" marker score was replaced by the dominance deviation. If the peak of the QTL was flanked by two markers, half of the genetic effect was used for each marker such that recombination between the markers was taken into account. The sums of the genetic effects across QTL for families were sorted and used to select the ten highest and ten lowest families for each MAS criterion.

An equal number of seeds per family was bulked for each selection group. Each selection group was randomly mated (recombined) in Puerto Rico in winter 2000–2001. Pollen was bulked from at least 50 plants and was used to pollinate at least 100 ears. Equal amounts of seed were bulked from each pollinated ear to constitute a selected entry. Non-selected entries, representing the C_0 s, were reconstituted for each population by bulk-pollen random mating a sample of half of the families in that population.

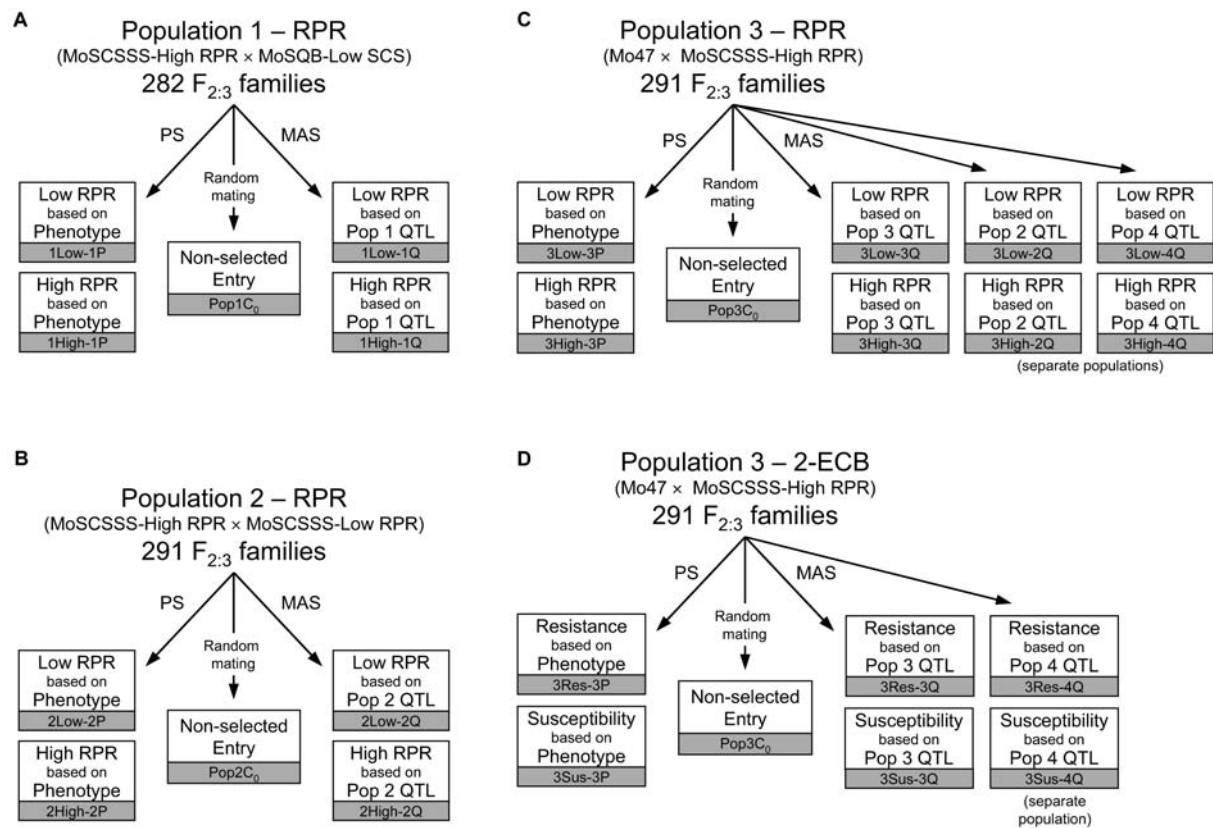


Fig. 1 Selection scheme used for phenotypic and marker-assisted selection for high and low rind penetrometer resistance (RPR) in population 1 (**A**), for high and low RPR in population 2 (**B**), for high and low RPR in population 3 using multiple populations for marker-assisted selection (**C**), and for resistance and susceptibility to second-generation European corn borer (2-ECB) in population 3

using multiple populations for marker-assisted selection (**D**). The naming convention for entries (*vertically within the bars*) was: (1) the population in which selection was conducted, (2) the trait selected for (high or low RPR, resistance or susceptibility to 2-ECB) and (3) the selection criterion (population used for selection and PS or MAS)

Phenotypic data collection

The two experiments (stalk strength and 2-ECB) were planted in summer 2001, each as a separate randomized complete block design (RCBD) experiment at four non-irrigated locations with six replications each. Locations used in this study included Hinkson Bottom, Columbia, Mo., on Freeburg silt loam; Bradford Research and Extension Center, near Columbia, Mo., on Mexico silt loam; South Farm, just east of Columbia, Mo., on Mexico silt loam and a site, in Cooper County near Tipton, Mo., on Clafork and Crestmeade silt loams. All experiments were planted as 6.7-m single-row plots spaced 0.90 m apart for a final planting density of 53,800 plants ha⁻¹. Standard cultural practices were used for fertilization and weed control. No post-emergence insecticides were used in these experiments since they were to be artificially infested with ECB larvae and evaluated for damage.

Two, two, and six duplicate entries of C₀ were added to the stalk strength experiment for populations 1, 2, and 3, respectively (Fig. 1). Three duplicate entries of C₀ for population 3, a 2-ECB-resistant check, and a 2-ECB-susceptible check were added to the 2-ECB experiment. All entries in the stalk strength experiment were evaluated for RPR, while all entries in the 2-ECB experiment were evaluated for 2-ECB damage. Rind penetrometer resistance was determined about 2 weeks after anthesis for 10 competitive plants plot⁻¹ as previously described (Flint-Garcia et al. 2003). For 2-ECB evaluation, 10 plants plot⁻¹ were artificially infested with neonate ECB larvae as previously described (Jampatong et al. 2002). Approximately 8 weeks after infestation, stalks from infested plants were split longitudinally from one node above the

primary ear to the ground and the length of the tunnels caused by ECB boring within the stalk, i.e., tunnel length (TL) per plant was visually estimated.

Data analysis

Each experiment was analyzed as a separate RCBD for each location. A combined analysis of variance using genotype means across environments was calculated for each of the experiments, and the genotype sums of squares was partitioned for each population in each experiment. Specific non-orthogonal contrasts of interest included each selection versus C₀, high versus low or resistant versus susceptible for each selection pair, and PS versus MAS for each selection criterion. The genotype × environment mean square (genotypes were fixed and environments random) was used to test for significance for genotypes and all of its partitions using SAS PROC GLM (SAS Institute 1998).

Results and discussion

Selection gain for rind penetrometer resistance

Selection for high and low RPR was effective in all three populations for both PS and MAS using QTL effects from their respective populations (Figs. 2, 3 and 4). In

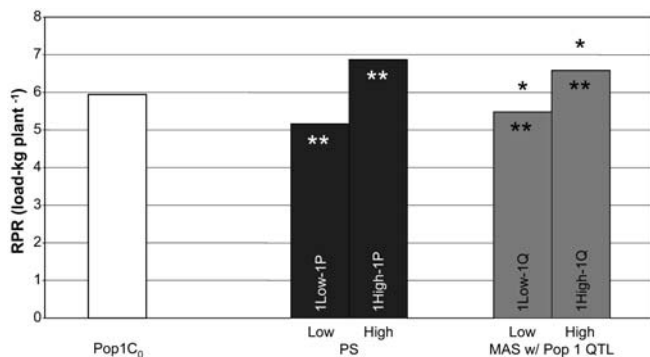


Fig. 2 Response of RPR to phenotypic (*dark bars*) versus marker-assisted (*light bars*) selection for RPR in population 1. Asterisk(s) *within bars* indicates significance of the comparison of selections versus non-selected C_0 . Asterisk(s) *above bars* indicates significance of the comparison of marker-assisted selection versus corresponding phenotypic selection. $*=P<0.05$, $**=P<0.01$

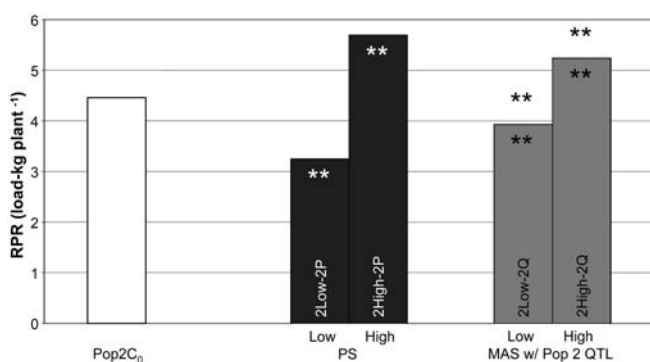


Fig. 3 Response of RPR to phenotypic (*dark bars*) versus marker-assisted (*light bars*) selection for RPR in population 2. Asterisk(s) *within bars* indicates significance of the comparison of selections versus non-selected C_0 . Asterisk(s) *above bars* indicates significance of the comparison of marker-assisted selection versus corresponding phenotypic selection. $*=P<0.05$, $**=P<0.01$

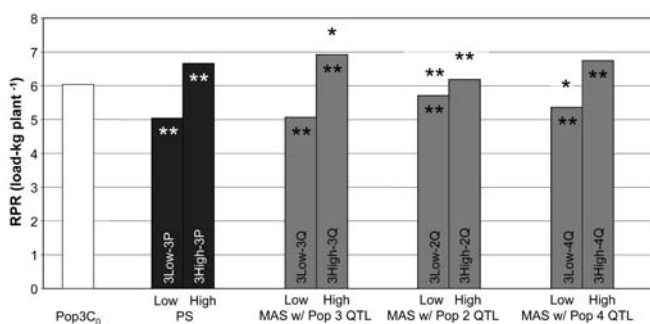


Fig. 4 Response of RPR to phenotypic (*dark bars*) versus marker-assisted (*light bars*) selection for RPR in population 3. Asterisk(s) *within bars* indicates significance of the comparison of selections versus non-selected C_0 . Asterisk(s) *above bars* indicates significance of the comparison of marker-assisted selection versus corresponding phenotypic selection. $*=P<0.05$, $**=P<0.01$

population 3, selection using QTL effects from separate populations was effective for all entries except for high RPR based on QTL from population 2 (3High-2Q). For each selection criterion, the high RPR selections were significantly different from their low RPR counterparts, regardless of whether QTL from the respective population or a separate population were used for MAS (data not shown). These results show that MAS for a single trait is generally successful as a selection tool. However, the comparisons between PS and MAS are of greater interest in this study.

Phenotypic selection for both high and low RPR in populations 1 and 2 was more effective (resulted in significantly greater gains) than MAS using QTL effects from their respective populations (Figs. 2, 3 and 4). Likewise, in population 3, PS was more effective in selecting for both high and low RPR than selection based on QTL from population 2 (3High-3P vs 3High-2Q, and 3Low-3P vs 3Low-2Q) and for low RPR based on QTL from population 4 (3Low-3P vs 3Low-4Q) (Fig. 4). Phenotypic selection for low RPR in population 3 was more effective than MAS using QTL effects from separate populations, but was not significantly different using QTL effects from the same population (3Low-3Q). However, MAS for high RPR using QTL effects from population 4 (3High-4Q) was equally effective as PS in selecting for high RPR, and the use of QTL effects from population 3 (3High-3Q) was actually more effective than PS. These results demonstrate that MAS can be just as effective as, or more effective than PS, even when using QTL effects from a separate population.

Selection gain for second-generation European corn borer

Resistance and susceptibility

Mean TL values were significantly different for the resistant and susceptible checks, indicating that infestation resulted in adequate levels of damage. The susceptible check had 2 cm more tunnel damage than any of the susceptible selections, while most of the differences between the resistant check and the resistant selections were not significant.

Selection for resistance and susceptibility to 2-ECB in population 3 was effective for both PS and MAS, with the notable exception of using QTL effects from population 3 to select for resistance (3Res-3Q) (Fig. 5). The inability of QTL from population 3 to effectively select for resistance may be explained by the fact that a model containing all four significant QTL accounted for only 16.1% of the phenotypic variation (Flint-Garcia 2001). However, mean TL values for all resistant selections were significantly lower (more resistant) than their susceptible counterparts for each selection criterion (data not shown), indicating that one cycle of MAS was able to separate C_0 into two distinct subpopulations. Mean TL values for PS for resistance and susceptibility were not significantly different from those based on QTL from either population 3

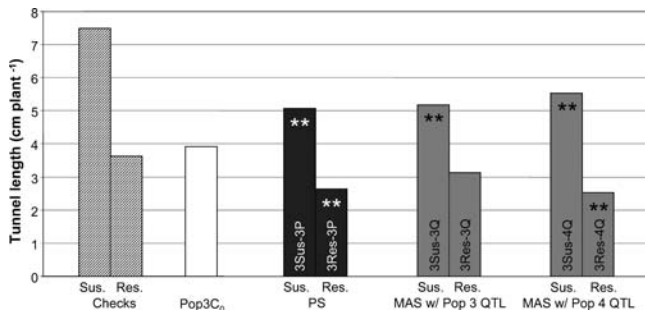


Fig. 5 Response of tunnel length to phenotypic (dark bars) versus marker-assisted (light bars) selection for European corn borer in population 3. Asterisk(s) within bars indicates significance of the comparison of selections versus non-selected C₀. There were no significant differences between phenotypic selections and marker-assisted selections. *= $P < 0.05$, **= $P < 0.01$

or 4, indicating that MAS was equally effective as PS (Fig. 5).

Populations 3 and 4 share 'Mo47' as the source of resistance to 2-ECB. It was somewhat surprising that QTL from population 4 were more effective in selection for resistance than QTL from population 3. The 2-ECB data for population 4 that were used in the original QTL analysis were obtained from three environments with three replications each (Jampatong et al. 2002), while data for the population 3 QTL analysis were based on a single environment with three replications (Flint-Garcia 2001). It is likely that the phenotypic data used in population 4 were superior to those used in population 3, resulting in better estimates of QTL positions and effects. In fact, the QTL from population 4 accounted for 57.5% of the phenotypic variation (Jampatong et al. 2002), while the QTL from population 3 accounted for only 16.1%.

Phenotypic versus marker-assisted selection

It was interesting that QTL from several populations were useful in selecting for RPR, especially in population 3 where MAS was more effective than PS for high RPR. However, for traits such as RPR, where heritability is high and phenotypic data collection is generally not very labor intensive or expensive, PS would be a more cost-effective selection method than MAS.

For 2-ECB resistance, the heritability is low to moderate (Jampatong et al. 2002), and phenotypic data collection is labor intensive and expensive. Marker-assisted selection for 2-ECB should be more cost effective than PS given accurate estimates of QTL positions and effects (Kumar 1999). Indeed, in population 3, MAS using QTL effects from population 3 was as effective as PS and more effective using QTL effects from population 4. The quality of the data used in QTL analysis varied between the two populations and led to different QTL results, even though 'Mo47' was used as the source of resistance to 2-ECB for both populations. Since the QTL detected for population 4 accounted for more of the

phenotypic variation for TL in that population and represented better estimates of the genetic effects for 2-ECB QTL, selection based on those QTL was, not surprisingly, more effective than selection based on QTL from population 3.

The results of this study support the speculation of Lande and Thompson (1990) that MAS is expected to be more useful for traits with low heritabilities. Traits that have low heritabilities require more replications of phenotypic evaluation because of environmental interactions. In the case of 2-ECB, the interaction between the physical environment, the plant, and the insect causes inconsistencies in insect damage. Considering the labor-intensive nature of infesting plants and splitting stalks to evaluate resistance, along with the large numbers of locations and replications needed for repeatability, PS for 2-ECB resistance can be prohibitively expensive. Marker-assisted selection may be able to decrease the cost and time required for screening large populations for resistance to 2-ECB. The initial time and cost of QTL analysis using high-quality phenotypic data from replicated trials in a relatively large population (300–500 families) could easily offset the cost of conducting multi-environment, replicated evaluations in multiple populations. Once a thorough QTL analysis is done for a particular source of resistance, the number of populations that can be improved by MAS using that source of resistance is unlimited.

Validation of quantitative trait loci by marker-assisted selection

Once a QTL has been identified, there are relatively few options for determining whether the QTL truly exists, or whether it has been falsely declared. The first strategy for validation of QTL is the development of NILs for the individual or combination of QTL (Yamamoto et al. 1998; Lin et al. 2000). This strategy requires multiple populations and many generations to test the QTL of a single experiment. The time required precludes routine use in applied breeding programs.

The second approach to validate a QTL is to test candidate genes, where candidate genes are identified based on coincidence between map position and involvement in biochemical, physiological, or developmental pathways related to the trait. However, because our understanding of the physiology and biochemistry underlying RPR and resistance to 2-ECB is limited, and because there is a lack of major QTL for these traits, the candidate gene approach was judged inappropriate for validating QTL for these traits.

A third and more pragmatic strategy is to conduct MAS using the QTL effects identified. By using markers to select indirectly for QTL, we can test the predicted genetic effects of the QTL by comparing to a non-selected entry. The method we used for MAS cannot test each QTL separately, but rather the sum-total effect of the QTL detected.

Using QTL effects to make selections in separate populations can also be considered to validate QTL effects. For population 3, MAS for RPR was effective when using QTL effects from population 4 in both the high and low directions of selection, and population 2 in the low RPR direction (Fig. 4). Likewise, MAS in population 3 for 2-ECB was effective when using QTL effects from population 4 for both susceptibility and resistance (Fig. 5).

We have shown that MAS for RPR and 2-ECB has been successful; whether using QTL effects identified in the population in which selection occurred, or in a separate population. These results, therefore, validate the positions and effects of QTL identified for RPR and 2-ECB.

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