Impacts of QTL × Environment Interactions on Genetic Response to Marker-Assisted Selection

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Abstract: Genotype × environment (*GE*) interaction is a common characteristic for quantitative traits, and has been a subject of great concern for breeding programs. Simulation studies were conducted to investigate the effects of *GE* interaction on genetic response to marker–assisted selection (MAS). In our study we demonstrated that MAS is generally more efficient than phenotypic selection in the presence of *GE* interaction, and this trend is more pronounced for developing broadly adaptable varieties. The utilization of different QTL information dramatically influences MAS efficiency. When MAS is based on QTLs evaluated in a single environment, the causal QTL × environment (*QE*) interactions usually reduce general response across environments, and the reduction in the cumulative general response is a function of the proportion of *QE* interactions for the trait studied. However, MAS using QTL information evaluated in multiple environments not only yields higher general response, but the general response obtained is also reasonably robust to *QE* interactions. The total response achieved by MAS in a specific environment depends largely on the total heritability of traits and is slightly subject to relative changes between general heritability and *GE* interaction heritability. Two breeding strategies, breeding experiments conducted in one environment throughout and in two environments alternately, were also examined for the implementation of marker-based selection. It was thus concluded that plant breeders should be cautious to utilize QTL information from only one environment and execute breeding studies in another.

Key words: marker–assisted selection; QTL × environment interaction; general response; total response

Genotypes in multiple environments can react differently to environmental changes. This differential response of genotypes from one environment to another is called genotype × environment (*GE*) interaction. *GE* interaction is a common characteristic for quantitative traits, and has been a subject of great concern for breeding programs[1-3]. With molecular maps and appropriate experimental designs, *GE* interaction can be further dissected into components of QTL × environment (*QE*) interaction, which are of great importance for marker-assisted selection in crop improvement [4]. Numerous cases of such interactions have been documented in recent QTL mapping studies [5-15]. A substantial proportion of QTLs identified in these experiments showed inconsistency in expression between non-stress and stress environments. *GE* interaction encountered in experiments complicates artificial selection and variety development. One challenge facing plant breeders is to take into account such *QE* interaction effects, maximizing variety adaptability and stability across environments. However, the feasible utilization of QTL information regarding *GE* interaction in crop improvement programs is a complicated issue that remains largely unexplored.

The utilization of marker-assisted selection (MAS) has received extensive attention in breeding programs to improve the efficiency of the selection for quantitative traits. Theoretical and simulation studies showed that extra genetic response through MAS can be made[16-28]. However, these studies assumed no epistasis and no *GE* interaction involved in

the improved quantitative traits. In our recent studies, epistasis was incorporated into marker-based breeding procedures and additional genetic gains and more superior genotypes were obtained from selection, indicating the importance of utilization of epistasis in crop breeding[29,30]. Incorporation of *GE* interaction into marker-assisted selection has not yet been quantified and characterized.

A primary aim of the present study is to investigate the effects of *QE* interaction on the effectiveness of MAS. In breeding practices, plant breeders usually attempt to select genotypes that are stable and that which perform well across environments[31]. On the other hand, plant breeders may aim to develop specific varieties for a given stress ecosystem. Therefore, a secondary aim of the present study is to formulate proper MAS schemes for different breeding objectives in the presence of *GE* interaction.

1 Methods and Simulations

QTL mapping experiments mainly serve as a starting point for the use of MAS in breeding programs. These experiments can be broadly divided into those conducted in a single environment and those in multiple environments. In the former case the main genetic effects of QTLs and their environmental interactions (*QE*) are confounded, while in the latter QTL effects are distinguishable[4,32,33]. We first extended our previous studies[29,30] to present breeding value as a selection index used in marker-based breeding across environments. We then designed simulation experiments to investigate the impact of *QE* on the genetic response of MAS under different breeding strategies.

1.1 Genetic model

For simplicity, we employed a cross between two inbred lines to initiate a selection, assuming each to be homozygous at all loci. Suppose that there are *n* QTLs, and denote Q_i allele at the *i*-th QTL, then each Q_i locus is bracketed by two flanking marker alleles, M_{i-} and M_{i+}. Following the genetic model described by Liu *et al.*[29], when there are *QE* interac-

tions, phenotypic value of individual *k* in environment *h* can be expressed as,

$$
\begin{aligned}
y_{hk} = \mu &+ \sum_i a_i x_{A_{ik}} + \sum_i d_i x_{D_{ik}} + \sum_{i<} \sum_j aa_{ij} x_{AA_{ijk}} \\
&+ \sum_{i<} \sum_j ad_{ij} x_{AD_{ijk}} + \sum_{i<} \sum_j da_{ij} x_{DA_{ijk}} \\
&+ \sum_{i<} \sum_j dd_{ij} x_{DD_{ijk}} + e_{E_h} + \sum_i e_{A_i E_h} x_{A_{ik}} \\
&+ \sum_i e_{D_i E_h} x_{D_{ik}} + \sum_{i<} \sum_j e_{AA_{ij}E_h} x_{AA_{ijk}} \\
&+ \sum_{i<} \sum_j e_{AD_{ij}E_h} x_{AD_{ijk}} + \sum_{i<} \sum_j e_{DA_{ij}E_h} x_{DA_{ijk}} \\
&+ \sum_{i<} \sum_j e_{DD_{ij}E_h} x_{DD_{ijk}} + \varepsilon_{hk}
\end{aligned}
$$

$$(1)$$

where μ is the population mean; a_i and d_i are the additive and dominant effects of Q_i, respectively; aa_{ij}, ad_{ij}, da_{ij} and dd_{ij} are the epistatic effects of additive × additive, additive × dominant, dominant × additive and dominant × dominant between Q_i and Q_j, respectively; e_{E_h} is the random effect of environment h (E_h), $e_{E_h} \sim N(0, \sigma^2_{e_E})$; $e_{A_i E_h}$ is the random $a_i \times E_h$ interaction effect, $e_{A_i E_h} \sim N(0, \sigma^2_{e_{A_i E}})$; $e_{D_i E_h}$ is the random $d_i \times E_h$ interaction effect, $e_{D_i E_h} \sim N(0, \sigma^2_{e_{D_i E}})$; $e_{AA_{ij}E_h}$ is the random $aa_{ij} \times E_h$ interaction effect, $e_{AA_{ij}E_h} \sim N(0, \sigma^2_{e_{AA_{ij}E}})$; $e_{AD_{ij}E_h}$ is the random $ad_{ij} \times E_h$ interaction effect, $e_{AD_{ij}E_h} \sim N(0, \sigma^2_{e_{AD_{ij}E}})$; the coefficient $x_{A_{ik}}$ and $x_{D_{ik}}$ are 1 and 0 for genotype $Q_i Q_i$, $x_{A_{ik}}$ and $x_{D_{ik}}$ are −1 and 0 for genotype $q_i q_i$, $x_{A_{ik}}$ and $x_{D_{ik}}$ are 0 and 1 for genotype $Q_i q_i$; $x_{AA_{ijk}} = x_{A_{ik}} x_{A_{jk}}$, $x_{AD_{ijk}} = x_{A_{ik}} x_{D_{jk}}$, $x_{DA_{ijk}} = x_{D_{ik}} x_{A_{jk}}$, $x_{DD_{ijk}} = x_{D_{ik}} x_{D_{jk}}$; ε_{hk} is residual effect, $\varepsilon_{hk} \sim N(0, \sigma^2_\varepsilon)$; for $i, j = 1, 2, \cdots, n$.

1.2 Estimation of breeding value

In our previous study, we recorded that the breeding value is a more proper measure than other selection indices for MAS [29]. For a genetic model with main genetic effects and *GE* effects, the total breeding value should also be partitioned as $B = B_G + B_{GE}$, where B_G is general breeding value which can be inherited over multiple environments; while B_{GE} is an interaction breeding value which can be inherited in specific environments. If we know QTL effects and the genotype

of an individual, we can write the breeding value B_G of that individual k as $\sum_i a_i x_{A_{ik}} + \sum_{i<j}\sum a a_{ij} x_{AA_{ijk}}$ and B_{GE} of individual k in environment h as $\sum_i e_{A_i E_h} x_{A_{ik}} + \sum_{i<j}\sum e_{AA_{ij} E_h} x_{AA_{ijk}}$.

In the real situation of breeding practices, the true QTL genotype of an individual is not available; only its trait phenotype and marker genotype are observable. However, probability of a particular QTL genotype conditional on its trait phenotype and marker genotype can be calculated. Therefore, the estimation of breeding value of an individual is the weighted sum of breeding value of all possible genotypes, for example., the general breeding value

$$
\begin{aligned}
\hat{B}_G &= E(B_G \mid y_k, h) \\
&= \sum_z p(z \mid y_k, h)(\sum_i a_i x_{A_{ik}} + \sum_{i<j}\sum a a_{ij} x_{A_{ijk}})
\end{aligned}
\tag{2}
$$

where the weight, $p(z \mid y_k, h)$, is the probability of a particular QTL genotype z conditional on its trait phenotype y_k and marker genotype h $p(z \mid y_k, h)$ can be calculated over several consecutive generations during the selection procedure, which was detailed in our previous study [29]. Similarly, the interaction breeding value (B_{GE}) can be estimated as

$$
\begin{aligned}
\hat{B}_{GE} &= \sum_z p(z \mid y_k, h)(\sum_i e_{A_i E_h} x_{A_{ik}} \\
&+ \sum_{i<j}\sum e_{AA_{ij} E_h} x_{AA_{ijk}}).
\end{aligned}
\tag{3}
$$

1.3 Genetic map

Simulations were conducted by using the map described in our previous study [29]. This map had 55 markers evenly spread over 5 chromosomes of length 1 Morgan, with 8 diallelic QTLs and 16 digenic epistases assigned randomly on the map. There were, however, three categories of QTLs: (i) showing genetic main effects solely, (ii) showing interaction effects solely, and (iii) a mixture of these two. The number of three categories of QTLs was 2, 2, and 4, respectively, and that of epistases was 4, 4, and 8, respectively. The recombination fraction was derived

from the map distance (d) as $r = 0.5(1 - e^{-2d})$ [34].

1.4 Generating phenotypic data

For generating phenotypic data, we require to know different source variations such as those due to main genetic effects and epistases and their environmental interactions. If there is GE interaction, the total phenotypic variance can be partitioned as,

$$
V_P = V_G + V_{GE} + V_\varepsilon
\tag{4}
$$

where v_G, v_{GE} and v_ε are the variances of genetic main effects, GE interaction effects and residual effects, respectively. The expected genotypic variance v_G in initial population (F₂) was deduced in our previous study [29]. Assuming independence of GE interaction effects within and between loci, the expected GE interaction variance v_{GE} in F₂ can be expressed as,

$$
\begin{aligned}
V_{GE} = & \frac{1}{2}\sum_i \sigma^2_{A_i E} + \frac{1}{4}\sum_i \sigma^2_{D_i E} + \frac{1}{4}\sum_{i<j}\sum \sigma^2_{AA_{ij} E} \\
& + \frac{1}{4}\sum_{i<j}\sum \delta_{ij}(2 - \delta_{ij})\sigma^2_{DD_{ij} E} + \sum_{i<j}\sum \eta_{ij}\sigma^2_{AD_{ij} E} \\
& + \sum_{i<j}\sum \eta_{ij}\sigma^2_{DA_{ij} E}
\end{aligned}
\tag{5}
$$

where $\delta_{ij} = r_{ij}^2 + (1 - r_{ij})^2$ and $\eta_{ij} = r_{ij}(1 - r_{ij})$ (r_{ij} is the recombination fraction between Q_i and Q_j). Since quantitative traits are controlled by genetic main effects and GE interaction effects, the total heritability (H^2) can be partitioned into two components: general heritability (H_G^2), which is defined as the ratio of variance of accumulated inheritable genotypic effects to the phenotypic variance, and interaction heritability (H_{GE}^2), which is defined as the ratio of variance of accumulated inheritable GE interaction effects to the phenotypic variance [35]. While generating the phenotypic data, we chose V_G and V_{GE} to yield the desired heritability, given that the phenotypic variance was fixed at 1 in all simulations. V_G and V_{GE} were, therefore, calculated as $H_G^2 V_P$ and $H_{GE}^2 V_P$, respectively. We then rescaled genetic main effects and GE interaction variances among QTL alleles by setting a given ratio of variance components (4:2:2:1:1:2 for

$V_A : V_D : V_{AA} : V_{AD} : V_{DA} : V_{DD}$ and $V_{AE} : V_{DE} : V_{AAE}$ $: V_{ADE} : V_{ADE} : V_{DDE}$) (for details see simulation section in Liu et al., 2003[29]). The phenotypic value of individual k in environment h included an additional environment effect and GE interaction effects

$$y_{kh} = \mu + E_h + G_k + GE_{kh} + \varepsilon_{kh} \qquad (6)$$

where μ is the population mean; E_h is the environment effect; G_k is the sum of all genetic main effects within and between loci [36]; GE_{kh} is the sum of QE interaction effects within and between loci in environment h; ε_{kh} is the residual effect with zero mean and known variance $(1 - H_G^2 - H_{GE}^2)V_P$. Simulations were conducted with three sets of general heritability and GE interaction heritability ($H_G^2 = 0.5$ and $H_{GE}^2 = 0.1$, $H_G^2 = 0.3$ and $H_{GE}^2 = 0.3$, and $H_G^2 = 0.1$ and $H_{GE}^2 = 0.5$).

1.5 Selection

We here focused on population improvement by MAS, which was more relevant to open-pollinated plants. In each generation of sample size N, the top 30% of individuals were selected and then mated at random to produce N offspring. Two breeding strategies were used: (i) breeding experiments conducted in one environment throughout, and (ii) breeding experiments conducted in two environments alternately. For developing the broadly adaptable genotypes, three selection methods were compared: (i) phenotypic selection (P); that is, selection was based on an individual's phenotypic value, (ii) MAS using QTL information evaluated in a single environment (Q^*); that is, selection was based on the total breeding value, and (iii) MAS using QTL information evaluated in multiple environments (Q); that is, selection was based on the general breeding value. However, for developing different genotypes adapted to a specific ecosystem, only the above selection methods P and Q^* were compared. Note that here the general response (ΔG_G) is attributed to genetic main effects, which is applicable to multiple environments, while total response (ΔG_T) is attributed to the total genetic effects, which is only applicable in specific environments. The corresponding cumulative genetic responses were, therefore, calculated as

$$\Delta G_{G(t)} = \frac{\overline{G}_{(t)} - \overline{G}_{(0)}}{\sqrt{V_{G_{(0)}}}} \qquad (7)$$

and

$$\Delta G_{T(t)} = \frac{(\overline{G}_{(t)} + \overline{GE}_{(t)}) - (\overline{G}_{(0)} + \overline{GE}_{(0)})}{\sqrt{V_{G_{(0)}} + V_{GE_{(0)}}}} \qquad (8)$$

where $\Delta G_{G(t)}$ and $\Delta G_{T(t)}$ are the cumulative general response and total response to selection at generation t ($t = 0$, standing for the initial population F$_2$), respectively; $\overline{G}_{(t)}$ and $\overline{GE}_{(t)}$ are the mean of genetic main effects and GE interaction effects of the population at generation t, respectively; $V_{G_{(0)}}$ and $V_{GE_{(0)}}$ are the genotypic variance and GE interaction variance in the F$_2$, respectively.

In this article a population of 500 individuals was used throughout. Selections were undertaken for 20 generations in total. Simulations were replicated 200 times for each case and the mean results of the 200 simulations were followed.

2 Results

2.1 Breeding experiments conducted in one environment throughout

General response and total response to phenotypic selection and MAS are given in Figs.1 and 2, respectively, when conducting selection in one environment throughout.

Simulation results show that responses to selection are achieved with a high rate at early generations but with a low rate at later generations; MAS performs considerably better than phenotypic selection in various cases. The general response to MAS using QTL information evaluated in a single environment (i.e. the method Q^*) drops noticeably with increasing GE interaction heritability; while the general response to MAS using QTL information evaluated in multiple

environments (i.e. the method Q) is reasonably robust to QE interactions for the improved trait. Phenotypic selection behaves in a similar way as that of the selection method $Q*$, but with lower response. The advantages of the selection method Q over $Q*$ and P are increasingly favored when GE interaction heritability in creases.

Fig.2 shows that, when the total heritability is fixed, cumulative total responses to both the methods P and $Q*$ are not subject to relative changes between general heritability and GE interaction heritability. This is because the total response achieved in a specific environment is largely dependent on the total heritability of the improved trait as shown in Liu et al. [29]. A comparison of Figs. 1 and 2 implicates that candidate genotypes identified by the selection method $Q*$ or P in a specific environment that perform well in one environment may perform poorly in another, and this problem is more acute when GE interaction heritability is high.

## 2. 2　Breeding experiments conducted in two environments alternately

General responses and total responses to phenotypic selection and MAS are presented in Figs. 3 and 4, respectively, when conducting selections in two environments alternately.

Plant breeders usually conduct selections in several alternate environments to speed up the development of varieties and test their performances across environments (i.e. the shuttle breeding approach). In the case of shuttle breeding schemes, the selection method $Q*$ yields a marginally higher general response, as compared with breeding experiments conducted in one environment throughout (Fig.1). This is also observed in phenotypic selection. However, the method Q produces similar results, except for the fact that the general response are slightly decreased at later generations. The advantages of the method Q over $Q*$ and P are clear whether selections are conducted in
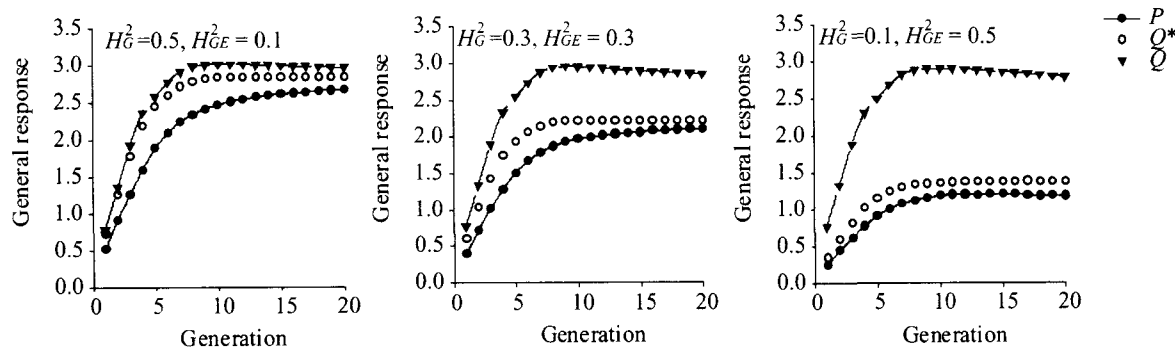
Fig. 1　**Cumulative general responses to different selection methods (P, Q^* and Q) when selections are conducted in one environment throughout**

P = phenotypic selection, Q^* = MAS using QTL information evaluated in a single environment, and Q = MAS using QTL information evaluated in multiple environments.
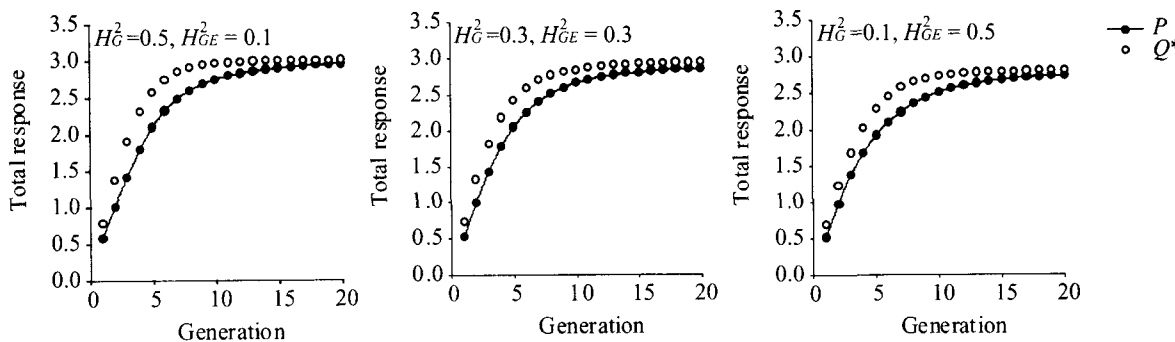
Fig. 2　**Cumulative total responses to different selection methods (P and Q^*) when selections are conducted in one environment throughout**
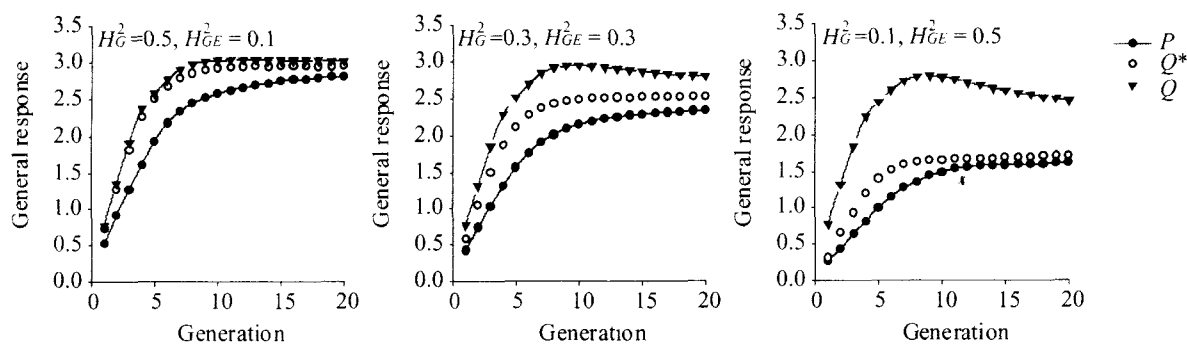
Fig. 3 Cumulative general responses to different selection methods (P, Q^* and Q) when selections are conducted in two environments alternately
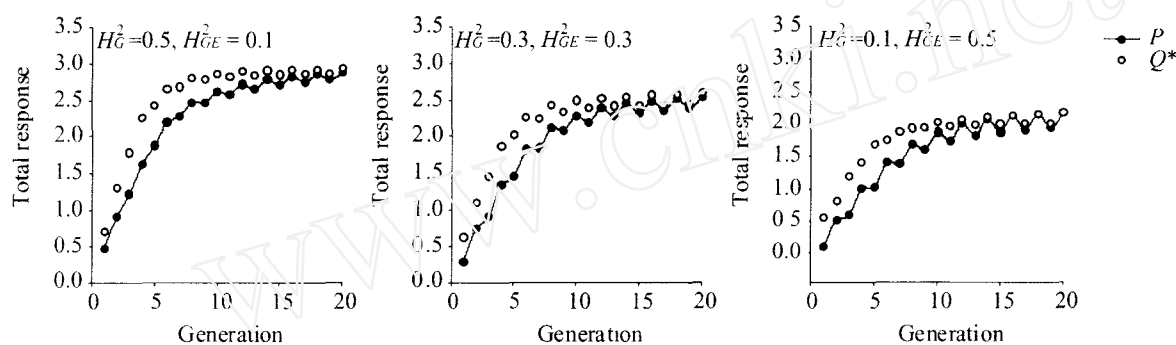

Fig. 4 Cumulative total responses to different selection methods (P and Q^*) when selections are conducted in two environments alternately

one environment throughout or in two environments alternately. This indicates that the shuttle the case of shuttle breeding schemes, the selection method Q^* yields a marginally higher general response, as compared with breeding experiments conducted in one environment throughout (Fig.1). This is also observed in phenotypic selection. However, the method Q produces similar results, except for the fact that the general response are slightly decreased at later generations. The advantages of the method Q over Q^* and P are clear whether selections are conducted in one environment throughout or in two environments alternately. This indicates that the shuttle breeding approach is an optimal choice for developing broadly adaptable varieties, since the gain from the selection method Q can be doubled per unit time.

However, in the shuttle breeding scheme, the total responses to the methods Q^* and P not only decreases considerably but also fluctuates appreciably between adjacent generations after the fifth generation, and these trends are more pronounced with lar-ger GE interaction heritability. For instance, with a GE interaction heritability of 0.5, the total response to the method Q^* is decreased after 20 generations by up to 23%, as compared with breeding experiments conducted in one environment throughout. In this case, the shuttle breeding approach also fails to speed up the development of varieties. With a GE interaction heritability of 0.5, the method Q^* reached a response of 2.73 after 10 generations when conducting breeding experiments in one environment throughout. Over the same span of time, the same method, however, reached a response of 2.16 after 20 generations when conducting breeding experiments in two environments alternately (see comparisons of Figs. 2 and 4). These results are in agreement with the breeding practice that a selection may do well in one environment, but may result in poor behavior in another environment. For traits controlled largely by GE interactions, the shuttle breeding approach is, therefore, not recommended for developing the varieties adapted for a specific region.

3 Discussion

Many studies of QTL mapping have been conducted in a fixed environment to evaluate phenotype[9]. With the knowledge gained from such experiments, significant contributions to the development of more efficient breeding strategies can be expected. However, one important question confronting plant breeders is whether results from one environment will apply to another. We found that causal *QE* interactions can usually reduce general response to MAS across environments, and the reduction in the cumulative general response is a function of the proportion of *QE* interactions involved in the improved trait. Thus, an attempt at the utilization of QTLs in breeding programs has to take into account such *QE* interactions. MAS based on those QTLs detected by analyzing mapping data of a single environment could be inadequate, and due to this situation QTL main effects and *QE* interactions could not be separated [4,33]. As a result, for developing broadly adaptable varieties, new breeding strategies based on QTL evaluation among a variety of environments will be necessary to realize the potential of MAS.

The latest QTL mapping experiments have revealed that there are three types of QTLs responsible for phenotypic variation of quantitative traits [14,15]. These include QTLs (i) showing genetic main effects which are common across environments, (ii) showing *QE* interaction effects which are dependent on a specific environment, and (iii) showing a mixture of both QTL main effects and *QE* interaction effects. We therefore concluded that the performance of a genetic entry or population across environments is mainly determined by genetic main effects of these QTLs. This assumption was partially in agreement with the conclusion of Veldboom and Lee [12], that QTLs identified for mean performance (the mean environment) could improve the performance of those breeds, which contain them, in both stress and non-stress environments. In our results, MAS using QTLs evaluated in multiple environments not only yielded higher general response across environments but, most importantly, the general response obtained was only slightly subject to *QE* interactions for the improved trait. To practical breeders these results may be an incentive to attempt to separate QTL genetic main effects from their *QE* interactions as the former represents the mean performance in various environments. However, the method *Q* gives higher general response but at the expense of lower total response; both methods *Q** and *P* usually work better than the method *Q* in a specific environment (results not shown). These results are in agreement with a regularity for the broadly adaptable varieties to have stable yields in various environments but at a lower level than narrowly adaptable ones, which perform exceedingly well in favorable conditions but poorly in unfavorable ones [37]. Another implication from these results is that, for breeding different varieties adapted to specific ecosystems, MAS should be based on both QTL main genetic effects in various environments and *QE* interactions attributed to specific environments; breeding experiments are conducted in one environment throughout, maximizing the adaptation of varieties in that specific environment.

Plant breeders usually conduct selections in alternate environments to speed up the development of varieties and test their performances across environments. We showed that even when breeding experiments are conducted in alternate environments, the method *Q* performs comparatively better than *Q** or *P*. The higher the *GE* interaction heritability, the greater the cumulative superiorities of *Q* over *Q** and *P*. These results are confident for breeders for the fact that when MAS use QTL information evaluated in multiple environments, considerable costs could be saved by eliding multi-environment trials in assessing the performance of experimental materials across environments. It should be noted, however, that to breed different varieties for specific regions, MAS based on those QTLs evaluated in a single environment and breeding experiments conducted in that environment throughout, is an optimal choice. This is because the shuttle breeding approach usually causes considerable reduction in the total response achieved in a specific environment.

In our previous study [29], we proposed a proper

strategy to optimize the implementation of MAS. It consists of two phases: (i) QTL evaluation with a large population and (ii) marker-based selection with a small population. We here add another: (iii) for developing the broadly adaptable varieties, QTL evaluation must be conducted over several environments and subsequent selection performed on the general breeding values of these QTLs within an optional environment. However, for traits less sensitive to environment, this is usually not the case, however.

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QTL× 环境互作对标记辅助选择响应的影响

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摘 要： 基因型 × 环境互作是植物数量性状的普通属性和遗传育种改良的关注重点。采用Monte Carlo 模拟方法研究了基因型 × 环境互作对标记辅助选择(Marker-assisted selection，简称MAS)响应的影响，揭示了育种上利用QTL(Quantitative trait locus，简称QTL)应当同时考虑其环境互作效应。存在基因型 × 环境互作下，MAS比普通表型选择更有效。特别以选育广适应性的品种为目标，MAS的优越性更明显。基于单个环境QTLs 的MAS，QTL× 环境互作效应通常降低了一般选择响应，一般选择响应累积量的降低程度与改良性状的QTL × 环境互作效应大小相关。基于多个环境QTLs的MAS，不但产生较高的一般选择响应，而且获得的一般选择响应不受其QTL× 环境互作效应大小的影响。但在某一特定环境下获得的总体选择响应仅与改良性状的总遗传率大小有关，普通遗传率和基因型与环境互作遗传率的相对变化对其影响很小。还比较研究了单地和穿梭选择对MAS遗传响应的影响。植物育种者应谨慎将某一环境的QTL 信息用于实施另一环境的育种研究。

关键词： 标记辅助选择；QTL× 环境互作效应；一般选择响应；总体选择响应

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