基于环境互作的加性-显性-加加上位性模型的
多环境指数选择

张文英[1,2],徐海明[1],朱 军[1*]

(1. 浙江大学生物信息学研究所,浙江 杭州 310029; 2. 长江大学农学系,湖北 荆州 434025)

摘要:适应性和稳定性是优良品种所必须具备的基本条件。在多个环境下对多个性状进行选择一直是一个悬而未决的难题。基于加性-显性-加加互作以及它们和环境互作的遗传模型,本文提出了两类选择指数:普通选择指数和考虑基因型与环境互作的选择指数(环境互作选择指数)。其中普通选择指数可用于具有广泛适应性品种的选择,环境互作选择指数则可用于具有特定环境适应性的基因型的选择。对于自花授粉作物,本文提出了两类育种值,即普通育种值和基因型与环境互作育种值。其中,普通育种值包括上位性效应和加加上位性效应,基因型与环境互作育种值包括加性、加加上位性与环境的互作效应。应用混合线性模型估算选择指数构建中涉及的方差-协方差分量。以一组陆地棉双列杂交设计试验作为实例,演示了所提出的选择指数的构建过程。本文提出的指数选择方法可望为多环境下多个性状同步选择提供一条有效的途径。

关键词:棉花;指数选择;加性 - 显性 - 加加上位性模型;基因型与环境互作;混合线性模型

Index Selection in Multi-environments Based on an Additive-dominance and Additive × Additive Model with Environment Interaction

ZHANG Wen-ying[1,2], XU Hai-ming[1], ZHU Jun[1*]

(1. *Institute of Bioinformatics, Zhejiang University, Hangzhou, Zhejiang* 310029, *China*; 2. *Department of Agronomy, Yangtze University, Jingzhou, Hubei* 434025, *China*)

Abstract: Adaptability and stability are very important characteristics of elite cultivars. Selection upon multiple traits in various environments is a pendent item. Based on an additive, dominance and additive × additive (AA) model with environment interaction, two types of selection indices, general index and index involving in genotype by environment interaction (GE interaction index) were developed. The general selection index can be utilized for selecting cultivars with a wide adaptation potential, while the GE interaction selection index can be adopted to select lines that are adapted to specific environments. For self-fertilizing crops, two kinds of breeding values, general breeding value and breeding value related to genotype by environment interaction (GE interaction breeding value) were proposed. The first one consists of AA epistatic effects in addition to additive effect. The second is comprised of effects of additive × environment interaction and AA × environment interaction. Mixed linear model approaches were employed to estimate variance-covariance components of traits involved in the selection index. Data from a diallel cross of *Gossypium hirsutum* L. were analyzed as a working example for the construction of selection indices by using the newly developed methodology.

Key words: cotton; index selection; additive-dominance-epistasis model; genotype by environment interaction; mixed linear model approach

Stability is a crucial property of a variety, which relates to genotype × environment (GE) interaction in the context of quantitative genetics. Evidences from quantitative trait locus (QTL) mapping have shown that there was a portion of identified QTLs exhibiting significant GE interactions [1-3]. Some environment-related QTLs have opposite effects in different environments while some are merely particularly expressed in certain environments[4-5]. These studies revealed the genetic basis for the instability of trait performance and the effects of GE interaction.

Up to now, selection on multiple traits simultaneously over multi-environment is still a constraint to the plant breeders. Wright [6] argued that the only solution is to select a different strain for every environment. Hammond [7], however, advised that selection should be conducted under different environmental conditions. Falconer [8] suggested that genotypic performances in two environments could be treated as two genetically correlated characters. Following Falconer's theory, James [9] developed a statistical method of index selection for animal traits in two environments. Later, Van Sanford et al [10] performed index selection on genetic correlations of cultivar performance based on the genetic correlations between primary locations and the target environments. More recently, Atlin et al [11] studied the selection response of genotypic value in a large region and constituent sub-regions. Although selection indices were adopted in all of these studies, the essential issue is single-trait improvement in varied environments, which does not indeed exert the predominance of index selection in the aspect of multi-trait improvement.

On the other hand, the classic selection index proposed by Smith[12] and Hazel[13] and a series of extensions are actually specific selection indices, which are constructed for each population/environment. Normally, there are two obvious limitations of specific index selection: (a) obtaining reliable parameter estimates from the limited evaluation of the materials involved, and (b) the laborious task of constructing an index for each population in each generation[14-15]. To solve these problems, Hanson and Johnson[14] modified specific selection index theory by combining parameter information from various experiments to a general or an average selection index. Furthermore, the Smith-Hazel index and its various modifications mainly focused on the utilization of additive genetic effects for the improvement of economically important traits.

Based on mixed linear model approaches, Zhu[16-17] developed a statistical technique and software to analyze an additive-dominance-epistasis (ADE) model with GE interaction effects. This technique facilitates the estimation of variance-covariance components, heritability and correlation coefficients, which provide theoretic and technical support for the construction of selection indices on several traits in multi-environments.

The objective of the present study was to extend the traditional selection index to achieve selection on multiple traits in different environments, and to satisfy the requirement of selection for specific and wide adaptation, respectively, in breeding programs. An example of the application of this methodology is also given.

1　Materials and Methods

1.1　Genetic model

Zhu[16-17] proposed an additive, dominance and additive × additive model (ADAA model) with GE interaction effect using diallel mating design. When genetic experiments are carried out in a randomized complete block design, a linear model for the genetic entry of the k-th type of generation derived from parent i and j in the l-th block within the h-th environment can be written as

$$y_{hijkl} = \mu + G_{ijk} + E_h + GE_{hijk} + e_{hijil} \qquad (1)$$

where μ= population mean, G_{ijk}= total genetic main effect, E_h= environment effect, GE_{hijk}= GE interaction

effect, and e_{ijk} = residual effect, ~ $(0, \sigma_e^2)$, $k = 0, 1, 2$ for parents, F_1 and F_2, respectively.

Following the definition of epistasis by Cockerham[18], when additive × dominance and dominance × dominance epistatic effects are ignored, G_{ijk} in the ADAA model can be partitioned into

$$G_{ijk} = \sum_i \alpha_i A_i + \sum_i \sum_{j \geqslant i} \delta_{ij} D_{ij} + (\sum_i \alpha_i A_i)^2.$$

Where α_i is the coefficient of the additive effect, $\sum_i \alpha_i = 2$; δ_{ij} is the coefficient of the donimance effect, $\sum_i \sum_{j \geqslant i} \delta_{ij} = 1$, $\alpha_i = 2\delta_{ij} + \sum_{j \neq i} \delta_{ij}$.

And GE_{hijk} in formula (1) can be partitioned into

$$GE_{hijk} = \sum_h \sum_i \alpha_{hi} A E_{hi} + \sum_h \sum_i \sum_{j \geq i} \beta_{hij} DE_{hij} + \sum_h (\sum_i \alpha_{hi} A E_{hi})^2.$$

According to formula (1), the genetic main effect and the GE interaction effect of various entries such as parents, F_1s, F_2s, BC_1s, BC_2s can be expressed.

Under Zhu's model [17], the phenotypic variance (V_p) can be partitioned into several components as

$$V_p = V_G + V_{GE} + V_e$$
$$= V_A + V_D + V_{AA} + V_{AE} + V_{DE} + V_{AAE} + V_e.$$

Where V_G = genetic main variance, V_{GE} = GE interaction variance, V_e = residual variance, V_A = additive genetic variance, V_D = dominance genetic variance, V_{AA} = additive × additive (AA) epistatic variance, V_{AE} = additive × environment interaction variance, V_{DE} = dominance × environment interaction variance, and V_{AAE} = AA epistasis × environment interaction variance.

Also, the total heritability in narrow sense can be partitioned into various components:

$$h^2 = h_G^2 + h_{GE}^2$$
$$= (h_A^2 + h_{AA}^2) + (h_{AE}^2 + h_{AAE}^2).$$

Where h_G^2 is the general heritability in narrow sense, $h_G^2 = V_G / V_p$; h_{GE}^2 is the interaction heritability in narrow sense, $h_{GE}^2 = V_{GE} / V_p$; h_A^2 is the additive heritability, $h_A^2 = V_A / V_p$; h_{AA}^2 is the AA epistatic heritability, $h_{AA}^2 = V_{AA} / V_p$; h_{AE}^2 is the additive × environment interaction heritability, $h_{AE}^2 = V_{AE} / V_p$; h_{AAE}^2 is the AA epistasis × environment interaction heritability, $h_{AAE}^2 = V_{AAE} / V_p$.

Likewise, the phenotypic covariance (C_p) can be partitioned as:

$$C_p = C_G + C_{GE} + C_e$$
$$= C_A + C_D + C_{AA} + C_{AE} + C_{DE} + C_{AAE} + C_e.$$

To estimate the variance-covariance components, MINQUE (0/1) method[16] was applied.

1.2 Selection index approach

For the purpose of illustration, the Smith-Hazel index is introduced in the present study. The construction of a selection index mainly involves the calculation of the phenotypic variance-covariances of the information traits, the genetic variance-covariances of the objective traits, and the genetic covariances between the phenotypic values of the information traits and the breeding values of the objective traits. Among these procedures, determination of breeding value is a crucial step for the establishment of selection indices. During multi-environment breeding programs, additive, additive × additive epistatic effects and their interaction with the environment of an agronomic trait can be fixed through artificial selection in a specific environment. Thus, we can write the breeding value (B) of an individual as

$$B = B_G + B_{GE} = (A + AA) + (AE + AAE).$$

Where B_G is the general breeding value, and B_{GE} is the GE interaction breeding value. These two types of breeding value should be utilized in different conditions. Value of B_G can be utilized in the selection procedures conducted in various environ-

ments, whereas B can be applied in the selection procedures conducted in a specific environment.

With respect to multi-environment trails, we construct two types of selection indices. One is the general selection index (I_G) for evaluation conducted in multiple environments, and another is the index involving in genotype by environment interaction (GE interaction index, I_l) for selection conducted in a specific environment. Accordingly, B_G is used for the construction of the general index and both B_G and B_{GE} are employed in the construction of the GE interaction index.

The covariance between phenotypic trait x_i and breeding value B_j in h-th environment can be written as

$$C_B = C(x_i, B_j) \tag{2}$$
$$= C(G_i, B_j) + C(E_{hi}, B_j) + C(GE_{hi}, B_j) + C(e_i, B_j).$$

It is generally assumed that there is no covariance between E_{hi} and B_j, e_i and $\mathbf{B_j}$. Then $C(E_{hi}, B_j)$ =0, $C(e_i, B_j) = 0$. Thus, formula (2) can be expressed as

$$C_B = C(G_i, B_j) + C(GE_{hi}, B_j)$$
$$= C[(A_i + D_i + AA_i), (A_j + AA_j + AE_j + AAE_j)]$$
$$+ C[AE_i + DE_i + AAE_i), (A_j + AA_j + AE_j + AAE_j)].$$

Under the assumption that there is no covariance between GE interaction effects and main genetic effects, we can further write formula (2) as

$$C_B = C(A_i, A_j) + C(AA_i, AA_j) + C(AE_i, AE_j) + C(AAE_i, AAE_j)$$
$$= (C_A + C_{AA}) + (C_{AE} + C_{AAE}) \tag{3}$$
$$= C_{B_G} + C_{B_{GE}}$$

Where C_{B_G} is the covariance between phenotypic trait x_i and general breeding value B_G, and $C_{B_{GE}}$ is the covariance between phenotypic trait x_i and GE interaction breeding value C_{B_G}.

When $i = j$, the variance of breeding value B_j is

$$V_B = (V_A + V_{AA}) + (V_{AE} + V_{AAE})$$
$$= V_{B_G} + V_{B_{GE}}. \tag{4}$$

Where V_{B_G} is the genetic variance of general breeding value, and $V_{B_{GE}}$ is the genetic variance of GE interaction breeding value.

In formula (3) and (4), the first part of the right side of the equal mark is related to the main genetic effect, and the second one is related to the GE interaction effect. Then, general index and GE interaction index can be constructed on the basis of the estimation of phenotypic and genotypic variance-covariances illustrated above.

The predicted response to index selection can be calculated following Wricke and Weber[19]:

$$R = i \cdot [(b^T Pb)/w^T Gw)]^{1/2}.$$

Where i is the selection intensity, b is the vector of index coefficients, P is the matrix of phenotypic variance-covariance of information traits, w is the vector of relative economic weight of information traits, and G is the variance-covariance matrix of breeding values of primary traits.

The selection response to index selection for single trait j is:

$$R_j = i \cdot [(b^T c_j)/(b^T Pb) V_{B_j}]^{1/2}.$$

Where c_j is the j-th column of genetic covariance matrix C.

1.3 A working example

Data of a modified diallel cross with parents and F_1s of upland cotton (*Gossypium hirsutum* L.) were used as an example to illustrate the application of the general index and the GE interaction index presented in this study. The experimental germplasm comprised ten elite domestic cultivars and lines: (1) A226, (2) A160, (3) A17, (4) Lumian 6 (LM6), (5) CCRI 12, (6) CCRI 13, (7) Xuzhou 184 (XZ 184), (8) Shimian 2 (SM 2), (9) 4305, (10) 4318. Among these materials, (1) ~ (6) were treated as female parents and the other four genotypes were selected as male parents, from which 20 F_1's and F_2's crosses were produced in 2003 and 2004, respectively, by adding seed generation in Hainan Island, China. The 20 F_1s and 20 F_2s along with 10 parents were grown in a randomized complete block design consisting of three replications in the experimental station of Zhejiang University in 2004 and 2005. Data

were recorded on lint yield (LY, kg·hm⁻²), boll number (BN), boll weight (BW, g), and lint percentage (LP, %). In this case study, for simplicity, the selection fraction is fixed as $\alpha = 0.05$, with $i = 2.063$ as the selection intensity, and equal economic weights were used for all the traits. In the index, all the four yield traits acted as both objective traits and information traits, and the matrix C was identical with matrix G. The data were mainly analyzed on an IBM compatible PC by programs written in C language.

2　Results and Analysis

In the first analysis, we estimated the covariance components of the four yield traits. The covariance to be used in the matrix C and G was combined (Table 1). Two situations were considered, one was the general genetic effects expresses in multiple environments, and the other was the *GE* interaction effect particularly expresses in a given environment. The value of C_{BG} was used to construct the general index (I_G) and C_{BGE} was used to construct the interaction selection index (I_I). Phenotypic covariances between the information traits were also estimated.

In the second analysis, we estimated the genetic variance components of the four yield traits. Then we combined the variances which should be used in the matrix C and G (Table 2). Value of V_{BG} was applied to calculate the special index, and V_{BGE} was employed to calculate the interaction selection index. It turned out that lint percentage had the greatest general genetic variance among the four yield traits. Thus it was easy to select varieties with stable lint percentage in different environments. On the other hand, lint yield had the smallest general variance but the largest interaction genetic variance. It indicated that lint yield was prone to be hereditarily influenced by environments. And it was more difficult to select superior lines with stable lint yield over various environments. Accordingly, we estimated the phenotypic variance of the four yield traits.

Table 1　Phenotypic and genetic covariance between yield traits

Trait	Parameter	Boll number	Boll weight	Lint percentage
lint yield	C_{BG}	-2.383	-2.094	6.318
	$C_{BG} + C_{BGE}$	-5.454	-2.242	4.881
	C_p	35.651	4.580	22.519
boll number	C_{BG}		-0.152	0.707
	$C_{BG} + C_{BGE}$		-0.103	-0.046
	C_p		0.071	2.756
boll weight	C_{BG}			-0.160
	$C_{BG} + C_{BGE}$			-0.169
	C_p			-0.123

Note: C_{BG} is the covariance between phenotypic value of information trait and general breeding value, $C_{BG} = C_A + C_{AA}$, C_A is the additive covariance, C_{AA} is the additive × additive (AA) epistatic covariance; C_{BGE} is the covariance between phenotypic trait and genotype × environment interaction breeding value, $C_{BGE} = C_{AE} + C_{AAE}$, C_{AE} is the additive × environment interaction covariance, C_{AAE} is the AA epistasis ×environment interaction covariance.

Table 2　Phenotypic and genetic variance of yield traits

Parameter	Lint Yield	Boll number	Boll weight	Lint percentage
V_{BG}	0.002	0.853	0.004	5.627
$V_{BG} + V_{BGE}$	14.249	0.853	0.030	5.660
V_p	574.326	11.409	0.253	10.637

Note: V_{BG} is the genetic variance of general breeding value, $V_{BG} = V_A + V_{AA}$, V_A is additive variance, V_{AA} is additive × additive (AA) epistatic variance, V_{BGE} is the variance of genotype × environment interaction breeding value, $V_{BGE} = V_{AE} + V_{AAE}$, V_{AE} is additive × environment interaction variance, V_{AAE} is the AA × environment interaction variance.

In this example, for simplification, we assumed that the four objective traits had equal economic values for each phenotypic standard deviation increase. The general index (I_G) is constructed to be utilized in multiple environments. The phenotypic variance-covariance matrix (P) is:

$$P = \begin{bmatrix} 574.326 & 35.651 & 4.580 & 22.519 \\ 35.651 & 11.409 & 0.071 & 2.756 \\ 4.580 & 0.071 & 0.253 & -0.123 \\ 22.519 & 2.756 & -0.123 & 10.637 \end{bmatrix}$$

The genetic variance-covariance matrix C is:

$$G = C = \begin{bmatrix} 0.002 & -2.383 & -2.094 & 6.318 \\ -2.383 & 0.853 & -0.152 & 0.707 \\ -2.094 & -0.152 & 0.004 & -0.160 \\ 6.318 & 0.707 & -0.160 & 5.627 \end{bmatrix}$$

Here, because there were only objective traits, i.e. four yield traits served as information traits, matrix C was identical with the genetic variance-covariance matrix G. The general index was $I_G = 0.076x_{LY} - 0.507x_{BN} - 10.229x_{BW} + 1.027x_{LP}$. The predicted total response was 3.843 while the single response of lint yield, boll number, boll weight, and lint percentage were 217.788, 0.604, -1.519, and 1.063, respectively.

The second index, namely, interaction selection index, was constructed to be applied in a specified environment. In this circumstance, matrix P was as before. The matrix G (or C) obtained was:

$$G = C = \begin{bmatrix} 14.249 & -5.454 & -2.242 & 4.881 \\ -5.454 & 0.853 & -0.103 & -0.046 \\ -2.242 & -0.103 & 0.030 & -0.169 \\ 4.881 & -0.046 & -0.169 & 5.660 \end{bmatrix}$$

The GE interaction index was $I_I = 0.144x_{LY} - 0.983x_{BN} - 11.768x_{BW} + 0.784x_{LP}$. The predicted total response was 3.576 and the single response of lint yield, boll number, boll weight, and lint percentage were 3.112, -0.151, -1.275, and 0.942, respectively.

3 Discussion

The breeding value is the genetic value which should be transmitted to the progenies and can be utilized by breeders and growers. Traditionally, additive genetic effect is referred to as breeding value. Accordingly, the components in the matrix C for calculating index coefficient are additive variance-covariances. In numerous studies, total genetic variances rather than additive genetic variances were used in index selection[11, 14, 20-21]. These studies, in principle, have been inconsistent with the basic rule of index selection. In reality, the type of breeding value used in index selection depends on the type of variety[19]. For cross-fertilized crops, when experiments are conducted in a single environment, only additive genetic effect can be fixed in the segregating generations. For self-pollinating species, however, additive together with AA epistatic effects can be utilized. For cloned varieties, the whole genotypic value can be exploited. Studies[22-24] have showed that selection response should last longer and greater in the presence of epistatic effect than only under additive gene action. Under this circumstance, for self-pollinating crops we propose to refer to breeding value as the combination of additive and AA epistatic effects. When breeding experiments are carried out in multiple environments, the GE interaction effect should be taken into consideration as a contribution to breeding value, too.

GE interaction effect leads to varied performances across environments. In experiments related to plants and animals, GE interaction generally consists of genotype × location (GL) interaction and genotype × year (GY) interaction. Many reporters[25-27] claimed that GL interaction was more useful than GY in depicting adaptation patterns, because year-to-year environmental variation is not known in advance. On the other hand, the notable influence of year-to-year fluctuation in climate on agricultural production due to factors such as the El Nino cannot be overlooked, either. Actual measurements over both locations and years may be the only accurate criterion for reliable evaluation of genotypes. In the present study, we used two-year cotton data as an

example to demonstrate how to conduct selection on multivariate traits in multi-environments. Although the data were limited to two years, it could also represent, to some degree, two distinct climatic conditions. The year 2005 was rainy and chilling, which significantly influenced the growth and development of cotton bolls. As a result, the first average harvest percentage was only 28.76%, while being 56.29% in 2004 due to its relatively normal climate.

According to Hanson and Johnson[14], Caldwell and Weber[15], a general index is constructed by making use of parameter estimates from some unrelated populations; an average index is constructed by combining parameter information from given studies; and each specific index is constructed by estimate from a particular population. The general index is not easy to handle because usually the actual relationship among the populations is not completely known. In contrast to non-specific index selection, specific index selection, as a whole, exhibited the best performance. However, either gen eral or average index were reasonable substitutes for the specific index[14]. Byth et al[28] examined yield advance in two populations over three environments. The results showed that for each population, specific indices had the greatest predicted genetic advance. For estimates, over multiple environments, however, specific indices were less efficient for actual yield advance than general indices. In the present study, we propose two types of selection indices, general index and GE interaction index. General index refers to the selection index constructed by utilizing the main genetic breeding value. GE interaction index, however, is constructed by using the combined information of the main genetic breeding value and the interaction breeding value. The general index defined in the present study, to a certain extent, is similar to the general index defined by Hanson and Johnson[14]. However, the GE interaction index is a new definition. Most of parent materials

used in the previous case study are cultivars or lines in China, which could not be excluded as unrelated population. Therefore, the selection indices deduced from these genetic entries only can be treated as average index according to the module of Hanson and Johnson[14], Caldwell and Weber[15]. These indices, in some degree, can be used as reference in the cotton breeding program.

Diverse selection strategies should be adopted depending on different breeding objectives. In most cases, plant and animal breeders make efforts to improve overall performance in a range of diverse environments[29]. Under these conditions, much attention should be paid to selecting the general genetic effects. On the other hand, some plant breeders aim at developing specific varieties for a given stress ecosystem[30]. For instance, cotton varieties that can tolerate saline-alkaline and drought stress are in demand in the desert regions. Then the specific genotype by location interaction component can be used for selection in addition to the main effects of genotypes.

In practice, selection and evaluation programs for new lines are mainly carried out at experimental stations. Thus, it is important for the breeders to understand the relationship between primary testing sites and target environments[31-33]. However, most of these studies focused on the improvement of a single trait, such as yield. The theory of correlated selection response proposed by Falconer[8] was commonly used as indirect selection on one trait in nursery environments to the target environments. Falconer's theory was further combined with the method of index selection to preliminarily test the breeding lines at primary testing locations[9-10]. However, Falconer's method can only be applied to select superior genotypes for a single trait. The methodology presented in this study can be used to resolve this problem. The general index can be used to select superior genotypes that should perform well in multiple environments. Elite genotypes se-

lected in one environment (especially for location) may safely be used for cultivation in related environments. Besides, the interaction selection index can be employed to select specific varieties for particular ecosystems. In this situation, only one specific goal will be achieved. The lines improved at the testing locations can only be adopted locally, and cannot be introduced into other locations.

In traditional breeding programs, the breeders take the phenotypic information of individuals for selection instead of genotypes because of their non-availability. One of the shortcomings of this procedure is the low efficiency. The successful development of molecular markers provides the possibility of direct selection upon genotypes through the strategy known as marker-assisted selection (MAS), which is especially effective for the selection in the early generations [34]. To maximize the rate of improvement quantitative traits, Lande and Thompson[35] described a selection index combining molecular and phenotypic information, which only focused on one-trait improvement. Later, in common bean (*Phaseolus vulgaris* L.), Tar'an et al[36] developed a procedure integrated QTL-based index involving in several traits and genetic distance to identify lines that retain important QTLs and have desired genetic background. More recently, a model was illustrated to formulate selection index methods together with MAS covers both single trait selection and multi-trait selection[37]. However, all those studies regard additive effect as breeding value and did not place the ranges on multiple environments. The methodology proposed in this study can be expanded to the situation of incorporation of index selection theory and QTL by environment interaction (QEI) in multiple environments, which is under study.

In application, the selection indices proposed in this study can be operated in two steps. In the first step, the calculation of parameters such as phenotypic and genetic variance-covariance can be achieved by the Quantitative Genetic Analysis (QGA) software package developed by Dr. Zhu Jun's group. QGA is freely released and available from webpage http://ibi.zju.edu.cn/software/. In the second step, the selection indices construction can be fulfilled by some matrix operations in statistical software such as Microsoft ® Office Excel ® or MATLAB ®.

4 Conclusion

In the present study, two types of selection indices, general index and GE interaction index were proposed. Two kinds of breeding values were developed for the construction of the corresponding selection index. Breeders can make use of different type of index in their selection practice according to various breeding purpose in multiple selection surroundings. It is practical to perform the calculation and analysis follow the methodology presented in this study.

References:

[1] JANSEN R C, Van Ooijen J W, Stam P, et al. Genotype-by-environment interaction in genetic mapping of multiple quantitative trait loci[J]. Theor Appl Genet, 1995, 91: 33-37.

[2] STRATTON D A. Reaction norm functions and QTL-environment interaction for flower time in *Arabidopsis thaliana* [J]. Heredity, 1998, 81: 144-155.

[3] UNGERER M C, Halldorsdottir S S, Purugganan M D, et al. Genotype-environment interactions at quantitative trait loci affecting inflorescence development in *Arabidopsis thaliana* [J]. Genetics, 2003, 165: 353-365.

[4] LI Z K, Yu S B, Lafitte H R, et al. QTL × environment interactions in rice. I. Heading date and plant height [J]. Theor Appl Genet, 2003, 108: 141-153.

[5] PATERSON A H, Saranga Y, Menz M, et al. QTL analysis of genotype × environment interactions affecting cotton fiber quality[J]. Theor Appl Genet, 2003, 106: 384-396.

[6] WRIGHT S. Genetic principles governing the rate of progress of livestock breeding [C]//Proc Amer Sco Anim Prod 32nd Ann Meet.1939:18-26.

[7] HAMMOND J. Animal breeding in relation to nutrition and environmental conditions[J]. Biol Rev, 1947, 22: 195-213.

[8] FALCONER D S. The problem of environment and selection[J]. Amer Nat, 1952, 86: 293-298.

[9] JAMES J W. Selection in two environments [J]. Heredity, 1961, 16: 145-152.

[10] VAN SANFORD D A, Pfeiffer T W, Cornelius P L. Selection index based on genetic correlations among environments [J]. Crop Sci, 1993, 33: 1244-1248.

[11] ATLIN G N, Baker R J, McRae K B, et al. Selection response in subdivided target regions[J]. Crop Sci, 2000, 40: 7-13.

[12] SMITH H F. A discriminant function for plant selection[J]. Ann Eugen, 1936, 7: 240-250.

[13] HAZEL L N. The genetic basis for constructing indexes[J]. Genetics, 1943, 28: 476-490.

[14] HANSON W D, Johnson H W. Methods for calculating and evaluating a general selection index obtained by pooling information from two or more experiments [J]. Genetics, 1957, 42: 421-432.

[15] CALDWELL B E, Weber C R. General, average, and specific selection indices for yield in F_4 and F_5 soybean populations[J]. Crop Sci, 1965, 5: 223-226.

[16] ZHU Jun. General genetic models and new analysis methods for quantitative traits[J]. J Zhejiang Agr Univ, 1994, 20(6): 551-559.

[17] ZHU J. Diallel analysis for additive-dominance-epistasis model with genotype by environment interaction effects [M]//Kang M S. Handbook of Formulas and Software for Plant Geneticists and Breeders. New York: Food Products Press, 2003:51-66.

[18] COCKERHAM C C. An extension of the concept of partitioning hereditary variance for analysis of covariances among relatives when epistasis is present[J]. Genetics, 1954, 39: 859-882.

[19] WRICKE G, Weber W E. Quantitative genetics and selection in plant breeding[M]. Berlin: Walter de Gruyter, 1986:338-346.

[20] ZAVALA-GARCIA F, Bramel-Cox P J, Eastin J D, et al. Increasing the efficiency of crop selection for unpredictable environments[J]. Crop Sci, 1992, 32: 51-57.

[21] XIE C, Mosjidis J A. Selection of stable cultivars using phenotypic variances[J]. Crop Sci, 1996, 36: 572-576.

[22] JANNINK J L. Selection dynamics and limits under additive × additive epistasis gene action[J]. Crop Sci, 2003, 43: 489-497.

[23] LIU Peng-yuan, Zhu Jun, Lou Xiang-yang, et al. A method for marker-assisted selection based on QTLs with epistatic effects [J]. Genetica, 2003, 119: 75-86.

[24] WANG Jian-kang, Ginkel M V, Trethowan R, et al. Simulating the effects of dominance and epistasis on selection response in the CIMMYT wheat breeding program using QuCim [J]. Crop Sci, 2004, 44: 2006-2018.

[25] LIN C S, Binns M R. A method for analyzing cultivar × location × year experiments: a new stability parameter [J]. Theor Appl Genet, 1988, 76: 425-430.

[26] PIEPHO H P. Methods for comparing the yield stability of cropping systems - a review[J]. J Agron Crop Sci, 1998, 180: 193- 213.

[27] ANNICCHIARICO P. Genotype × environment interactions: challenges and opportunities for plant breeding and cultivar recommendations [M] // Plant Production and Production Paper 174. Rome: FAO, 2002:6-20.

[28] BYTH D E, Caldwell B E, Weber C R. Specific and non-specific index selection in soybeans, *Glycine max* L. (Merrill) [J]. Crop Sci, 1969, 9: 702-705.

[29] ROSIELLE A A, Hamblin J. Theoretical aspects of selection for yield in stress and non-stress environments[J]. Crop Sci, 1981, 21: 943-946.

[30] YADAV O P, Bhatnagar S K. Evaluation of indices for identification of pearl millet cultivars adapted to stress and non-stress conditions[J]. Field Crop Res, 2001, 70: 201-208.

[31] WOLDEYESUS S, Gretzmacher R, Edelbauer A. Environment of selection for grain yield in low fertilizer input barley[J]. Field Crop Res, 2002, 74: 151-162.

[32] CASLER M D, Barker R E, Brummer E C, et al. Selection for orchardgrass seed yield in target vs. nontarget environments[J]. Crop Sci, 2003, 43: 532-538.

[33] GUILLEN-PORTAL F R, Russell W K, Eskridge K M, et al. Selection environments for maize in the U.S. Western High Plains [J]. Crop Sci, 2004, 44: 1519-1526.

[34] XU Yun-bi, Crouch J H. Marker-assisted selection in plant breeding: from publications to practice [J]. Crop Sci, 2008, 48: 391- 407.

[35] LANDE R, Thompson R. Efficiency of marker-assisted selection in the improvement of quantitative traits[J]. Genetics, 1990, 124: 743-756.

[36] TAR'AN B, Michaels T E, Pauls K P. Marker-assisted selection for complex trait in common bean (*Phaseolus vulgaris* L.) using QTL-based index[J]. Euphytica, 2003, 130: 423-432.

[37] DEKKERS J C M. Prediction of response to marker-assisted and genomic selection using selection index theory[J]. J Anim Breed Genet, 2007, 124: 331-341.　●