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Genetic investigation of contributions of embryo and endosperm genes to malt Kolbach index, alpha-amylase activity and wort nitrogen content in barley

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Abstract A genetic model is proposed for the analysis of embryo and endosperm effects as well as GE interaction effects. An investigation of three malting quality traits in grains of seven parents and their F_2s was undertaken in a half-diallel cross of barley (*Hordeum distichum* L.) over 2 years. The results indicated that the malt Kolbach index (KI), alpha-amylase activity (αAA) and wort soluble nitrogen (Wort-N) are controlled by both embryo genetic effects and endosperm genetic effects. Variance of the endosperm additive effects was obviously larger than that of the embryo additive effects. In the contribution of the embryo genetic effects to variation in malt αAA and Wort-N, the dominance effects were considerably larger than the additive effects. The endosperm dominance effects constituted a major part of the total genetic effect on the KI. Significant endosperm GE interactions were also detected in the malt traits concerned. Endosperm general heritability (h_e^2) tended to be larger than interaction heritability (h_{oE}^2 or h_{eE}^2) for all the traits. Endosperm heterosis was observed to be significantly positive for αAA but negative for Wort-N in the F_2 seed generation. Prediction of main gene effects for seven parents showed that 'Ganmu 2' and 'Supi1' were suitable parental varieties for malt αAA and Wort-N improvement. Our genetic model for malting quality traits and its application in breeding are discussed.

Key words Two-rowed barley · Embryo and endosperm effects · Kolbach index · Alpha-amylase · Wort-N · GE interaction

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Introduction

Malt Kolbach index (KI), alpha-amylase activity (αAA) and wort soluble nitrogen (Wort-N) content are important quality factors in malting barley (Cook 1962). During germination of the barley grain, the germinating embryo secretes gibberellin (GA_3) into triploid cells of the aleurone layer, and this GA_3 subsequently induces the synthesis of hydrolytic enzymes which catalyze the break-down of the cell walls and reserves of endosperm tissues for the developing embryo or malt extracts as beer raw materials (Ranki 1990). All of the KI, αAA and Wort-N is produced during malting. Therefore, the expression of malt traits may not only be controlled by two sets of genetic systems, i.e. triploid endosperm and diploid germinating embryo, but it may also be influenced by environmental factors (Harris and Banasik 1952; Haytyer and Riggs 1973; Rutger et al. 1966). Accordingly, more understanding of the inheritance of malt traits might promote an improvement in malting barley quality.

The inheritance of barley malt traits such as enzyme activity, diastatic power, Wort-N and KI has been studied by many researchers (Baker et al. 1968; Greenberg 1977; Hayter and Riggs 1978; Hockett et al. 1993; Kaeppler and Rasmusson 1991; Rutger et al. 1966). However, most of these findings were obtained using the diploid genetic models proposed by Hayman (1954), and the effects of triploid endosperm and embryo genes on malt traits were not considered simultaneously. Up to now, little is known about the contribution of genetic variation of the embryo to malting quality. One of the principal problems in genetic investigations of malting barley is the difficulty in separating embryo effects and endosperm effects from total genetic effects in the various malting quality characteristics concerned. Cockerham (1980) proposed a methodology for constructing general genetic models. In recent years, Mo (1988), Bogyo et al. (1988), Foolad et al. (1992) and Pooni et al. (1992) have all independently presented

genetic models for the analysis of quantitative traits of endosperm. Zhu and Weir (1994a,b) proposed diploid seed (or embryo) models and triploid endosperm models for the analysis of seed (or endosperm) genetic effects, cytoplasmic effects and maternal genetic effects, and they developed related statistical methods (Zhu 1992,1993; Zhu and Weir 1996). These techniques have made it possible to study complex malting quality traits.

In the investigation reported here, a genetic model was developed for malting quality traits controlled by germinating embryo (designated as "embryo" for short in the paper) genes and endosperm genes as well as their environmental interactions. Appropriate procedures are suggested for an unbiased estimation of variance and covariance components and their sampling variances, and for prediction of genetic effects for the genetic models. These models and methods were applied in an investigation of the inheritance of the KI, αAA and Wort-N in seven varieties and their F_2s in a half-diallel cross of two-rowed barley.

Materials and methods

A 7×7 half-diallel cross, not including reciprocals, was made using varieties which differed widely in malt KI, αAA and Wort-N. All of these parents were two-rowed barley cultivars (*Hordeum distichum*L.): 'Ganmu 2' (P_1); 'Supi 1' (P_2); 'Qianzhe 1' (P_3); 'Zhenong 3' (P_4); 'Zhipi' (P_5); 'S-096' (P_6) and 'RisΦ 1508' (P_7). All of the entries were grown in a randomized complete block experiment with three replications at the Zhejiang Agricultural University in 1992 and 1995, respectively. In the following years, the parental seeds and F_2 seeds from F_1 plants from all three blocks in each year were bulked to obtain samples for malting. Malting quality traits were determined at the Laboratory of Malting Barley Quality, Chinese Academy of Agricultural Sciences according to the methods specified by the European Brewery Convention (EBC methods) (Guan 1985). The Kolbach index was determined by dividing the soluble nitrogen content by total malt nitrogen content. Malt and wort nitrogen (mg/100 g) were determined by the Kjeldahl method. All the results were on a dry-weight base. Each sample for one trait was examined three times in both 1993 and 1996. In the statistical analysis, three sets of the data of each sample were treated as replications. The means of these three malt traits over 2 years are shown in Table 1.

Genetic models and methodology

When a malt quantitative trait of a cereal crop is controlled by both embryo nuclear genes and endosperm nuclear genes, its total genetic effect (*G*) should include the embryo genetic effect (*Go*) and endosperm genetic effect (*Ge*). If we only consider the additive-dominance model throughout, the *Go* can be further partitioned into embryo additive (*Ao*) and embryo dominance (*Do*) genetic components, whereas the *Ge* can also be partitioned into endosperm additive (*Ae*) and endosperm dominance (*De*) genetic components.

For genetic experiments conducted in several environments, an interaction between each of the above genetic effects and environmental effects (*E*) may result in the inheritance of malt traits. Under the assumptions of (1) no paternal and maternal effects, (2) no epistatic interaction, (3) no high-order dominance interaction, (4) no correlation between embryo and endosperm effects and (5) no cytoplasmic effects, the genetic model can be written as a mixed linear model. The phenotypic mean of the *k*-th type of genetic entry (y_{hijkr}) from parent $i \times$ parent j ($i = j$ for inbred line) in the *r*-th block within

Table 1 Average values for malt Kolbach index (KI), alpha-amylase activity (αAA) and wort-N (mg/100 g dry-weight) for seven parental varieties and their F_2s over 2 years

Variety	Trait	Variety						
		P_1	P_2	P_3	P_4	P_5	P_6	P_7
	Wort-N	786.3	776.3↓[a]	725.5↓	749.0↓	826.7↑	734.2↓	743.7↓
P_1	KI	46.5	46.5	42.4	45.1	45.1	46.4	48.1
	αAA	66.2	87.0↑	63.1	76.4↑	76.4↑	76.1↑	80.7↑
	Wort-N		813.2	690.2↓	741.8↓	654.5↓	694.3↓	687.2↓
P_2	KI		44.6	42.3	42.8↓	37.6	44.9↑	45.0
	αAA		49.9	73.0↑	75.3↑	62.8↑	67.9↑	83.9↑
	Wort-N			749.7	675.3↓	705.2	662.5↓	676.7↓
P_3	KI			40.1	41.8	37.1	44.9↑	44.2
	αAA			49.6	59.0	56.1↑	65.6↑	57.0↑
	Wort-N				810.3	630.5↓	702.5↓	696.3↓
P_4	KI				44.3	38.8	46.5↑	46.7
	αAA				60.1	41.3↓	58.2	66.9
	Wort-N					695.8	664.8↓	678.8↓
P_5	KI					34.1	41.0	42.0
	αAA					52.8	53.5	58.8
	Wort-N						814.5	660.8↓
P_6	KI						44.6	44.4↓
	αAA						57.9	80.0
	Wort-N							804.2
P_7	KI							49.7
	αAA							80.6

Note: Figures in diagonal are parental means, while those in non-diagonal are F_2 means
[a] ↑indicates that the average value in F_2 seeds is higher than that of the high-parent; ↓indicates that the average value in F_2 seeds is lower than that of the low-parent

the h-th environment is expressed as

$$y_{hijkr} = \mu + E_h + G_{ijk} + GE_{hijk} + B_{r(h)} + \varepsilon_{hijkr}$$

where μ is the constant population mean; E_h is the environmental effect; $B_{r(h)}$ is the block effect of the r-th randomly complete block within the h-th environment; GE_{hijk} is the $G_{ijk} \times E_h$ interaction effect; ε_{hijkr} is the residual error.

If the experiment is designed in replications but not in a randomized complete block, the block effect B_r should be dropped. The components of the total genetic effect G_{ijk} and the total$G \times E$ interaction GE_{hijk} depend on the specific genetic entry.

For inbred line P_i $(k = 0)$,

$$G_{ii0} = 2Ao_i + Do_{ii} + 3Ae_i + 3De_{ii}$$

$$GE_{hii0} = 2AoE_{hi} + DoE_{hii} + 3AeE_{hi} + 3DeE_{hii}$$

For F_{1ij} from maternal $\mathrm{P}_i \times$ paternal P_j $(k = 1)$,

$$G_{ij1} = Ao_i + Ao_j + Do_{ij} + 2Ae_i + Ae_j + De_{ii} + 2De_{ij}$$

$$GE_{hij1} = AoE_{hi} + AoE_{hj} + DoE_{hij} + 2AeE_{hi} + AeE_{hj} + DeE_{hii} + 2DeE_{hij}$$

For F_{2ij} obtained from F_{1ij}s self-pollinating $(k = 2)$,

$$G_{ij2} = Ao_i + Ao_j + 0.25Do_{ii} + 0.25Do_{jj} + 0.5Do_{ij} + 1.5Ae_i + 1.5Ae_j + De_{ii} + De_{jj} + De_{ij}$$

$$GE_{hij2} = AoE_{hi} + AoE_{hj} + 0.25DoE_{hii} + 0.25DoE_{hjj} + 0.5DoE_{hij} + 1.5AeE_{hi} + 1.5AeE_{hj} + DeE_{hii} + DeE_{hjj} + DeE_{hij}$$

For BC_j from maternal $F_{1ij} \times$ paternal P_j $(k = 3)$,

$$G_{ij3} = 0.5Ao_i + 1.5Ao_j + 0.5Do_{jj} + 0.5Do_{ij} + Ae_i + 2Ae_j + 0.5De_{ii} + 1.5De_{jj} + De_{ij}$$

$$GE_{hij3} = 0.5AoE_{hi} + 1.5AoE_{hj} + 0.5DoE_{hjj} + 0.5DoE_{hij} + AeE_{hi} + 2AeE_{hj} + 0.5DeE_{hii} + 1.5DeE_{hjj} + DeE_{hij}$$

For BC_i from maternal $F_{1ij} \times$ paternal P_i $(k = 4)$,

$$G_{ij4} = 1.5Ao_i + 0.5Ao_j + 0.5Do_{ii} + 0.5Do_{ij} + 2Ae_i + Ae_j + 1.5De_{ii} + 0.5De_{jj} + De_{ij}$$

$$GE_{hij4} = 1.5AoE_{hi} + 0.5AoE_{hj} + 0.5DoE_{hii} + 0.5DoE_{hij} + 2AeE_{hi} + AeE_{hj} + 1.5DeE_{hii} + 0.5DeE_{hjj} + DeE_{hij}$$

If the inbred parents are randomly sampled from a reference population, each of the above genetic effects is a random effect. Ao_i (or Ao_j) is the cumulative additive effect of embryo genes from line i (or line j), Ao_i (or Ao_j) $\sim (0, \sigma^2_{Ao})$; Do_{ii} (or Do_{jj} or Do_{ij}) is the cumulative dominance effect of embryo genes from line $i \times$ line j $(i \leqslant j)$, Do_{ii} (or Do_{jj} or Do_{ij}) $\sim (0, \sigma^2_{Do})$; Ae_i (or Ae_j) is the cumulative additive effect of endosperm genes, Ae_i (or Ae_j) $\sim (0, \sigma^2_{Ae})$; De_{ii} (or De_{jj} or De_{ij}) is the cumulative dominance effect of endosperm genes from line $i \times$ line j $(i \leqslant j)$, De_{ii} (or De_{jj} or De_{ij}) $\sim (0, \sigma^2_{De})$; AoE_{hi} (or AoE_{hj}) is the Ao_i (or Ao_j) $\times E_h$ interaction effect, AoE_{hi} (or AoE_{hj}) $\sim (0, \sigma^2_{AoE})$; DoE_{hii} (or DoE_{hjj} or DoE_{hij}) is the Do_{ii} (or Do_{jj} or Do_{ij}) $\times E_h$ interaction effect, DoE_{hii} (or DoE_{hjj} or DoE_{hij}) $\sim (0, \sigma^2_{DoE})$; AeE_{hi} (or AeE_{hj}) is the Ae_i (or Ae_j) $\times E_h$ interaction effect, AeE_{hi} (or AeE_{hj}) $\sim (0, \sigma^2_{AeE})$; DeE_{hii} (or DeE_{hjj} or DeE_{hij}) is the De_{ii} (or De_{jj} or De_{ij}) $\times E_h$ interaction effect, DeE_{hii} (or DeE_{hjj} or DeE_{hij}) $\sim (0, \sigma^2_{DeE})$.

As a result, the phenotypic variance (V_P) for the genetic model of the malt trait can be partitioned as

$$\begin{aligned} V_P &= V_{Go} + V_{Ge} + V_{GoE} + V_{GeE} + V_\varepsilon \\ &= (V_{Ao} + V_{Do}) + (V_{Ae} + V_{De}) + (V_{AoE} + V_{DoE}) \\ &\quad + (V_{AeE} + V_{DeE}) + V_\varepsilon \end{aligned}$$

where V_{Go} is the embryo genetic variance with components of additive variance V_{Ao} and domiance variance V_{Do}; V_{Ge} is the endosperm genetic variance with components of endosperm additive variance V_{Ae} and endosperm domiance variance V_{De}; V_{GoE} is the $Go \times E_h$ interaction variance with components of $Ao \times E$ interaction variance V_{AoE} and $Do \times E$ interaction variance V_{DoE}; V_{GeE} is the $Ge \times E$ interaction variance including components of $Ae \times E$ interaction variance V_{AeE} and $De \times E$ interaction variance V_{DeE}; and V_ε is the residual variance.

Variance components are different in different generations (F_1, F_2, BC_i and BC_j). Thus, the phenotypic variance should be calculated separately for each generation

$$\begin{aligned} V_P(F_1) &= (2\sigma^2_{Ao} + \sigma^2_{Do}) + (5\sigma^2_{Ae} + 5\sigma^2_{De}) + (2\sigma^2_{AoE} + \sigma^2_{DoE}) \\ &\quad + (5\sigma^2_{AeE} + 5\sigma^2_{DeE}) + \sigma^2_\varepsilon \end{aligned}$$

$$\begin{aligned} V_P(F_2) &= (2\sigma^2_{Ao} + \tfrac{3}{8}\sigma^2_{Do}) + (4\tfrac{1}{2}\sigma^2_{Ae} + 3\sigma^2_{De}) + (2\sigma^2_{AoE} + \tfrac{3}{8}\sigma^2_{DoE}) \\ &\quad + (4\tfrac{1}{2}\sigma^2_{AeE} + 3\sigma^2_{DeE}) + \sigma^2_\varepsilon \end{aligned}$$

$$\begin{aligned} V_P(BC_i) = V_P(BC_j) &= (2\tfrac{1}{2}\sigma^2_{Ao} + \tfrac{1}{2}\sigma^2_{Do}) + (5\sigma^2_{Ae} + 3\tfrac{1}{2}\sigma^2_{De}) \\ &\quad + (2\tfrac{1}{2}\sigma^2_{AoE} + \tfrac{1}{2}\sigma^2_{DoE}) + (5\sigma^2_{Ae} + 3\tfrac{1}{2}\sigma^2_{De}) + \sigma^2_\varepsilon \end{aligned}$$

Although five generations of the models are listed above, it is generally not necessary to include all of the generations in a genetic experiment if a diallel mating design is used. There are several types of experiments for choice: (I) P, F_1, F_2; (II) P, BC_i (or BC_j), F_2.

When GE interaction exists, the total heritability in the narrow sense (h^2) can be partitioned into embryo general heritability (h^2_o), endosperm general heritability (h^2_e), embryo interaction heritability (h^2_{oE}) and endosperm interaction heritability (h^2_{eE}). The total heritability is obtained as

$$\begin{aligned} h^2 &= h^2_o + h^2_e + h^2_{oE} + h^2_{eE} \\ &= V_{Ao}/V_P + V_{Ae}/V_P + V_{AoE}/V_P + V_{AeE}/V_P \end{aligned}$$

A minimum norm quadratic unbiased estimation [MINQUE(1)] method setting 1 for all the prior variances can be used to obtain unbiased estimates of variance components in the above mixed linear models for each trait (Zhu and Weir 1996). A linear adjusted unbiased prediction (AUP) method is applicable to predicting the random genetic effects (Zhu 1993). The jackknife procedure is appropriate for estimating the sampling variances of estimated variances and of predicted genetic effects (Miller 1974; Zhu and Weir 1994a). A t-test following jackknifing can be employed to detect the significance of variances (Zhu 1993).

Results

Phenotypic values of parental varieties and their F_2s

The phenotypic values of the seven varieties differed significantly for all the malt traits studied (Table 1). As expected, 'Ganmu 2' (P_1) and 'Zhenongda 3' (P_4), the two malting varieties, had the most desirable quality. They were high in all three traits. 'Supi 1' (P_2) and 'Qinzhe 1' (P_3) were low in αAA, although both of them

are malting varieties and P_2 had high values of the Wort-N and KI. 'Zhipi' had naturally poor malting quality since it is a nutritional variety. Surprisingly, 'S-096' (P_6) and 'RisΦ 1508' (P_7) were quite high for all the characteristics measured although they are both nutritional varieties.

The F_2 progenies were apparently different from the parental varieties for the malt KI, αAA and Wort-N. The F_2 offspring were all lower than the low-parent in Wort-N with two exceptions, the "$P_1 \times P_5$" cross was higher than the high-parent, and the "$P_3 \times P_5$" cross was lower than the mid-parents. For KI, the mean of the F_2 progenies was generally intermediate between that of their parental varieties. Of the 21 F_2hybrids, half were higher than the high-parent for αAA and the rest were intermediate between the parents. It was suggested that gene expression may be different in the inheritance of αAA, KI and Wort-N. In addition, a genotype × environment (GE) interaction might exist because the phenotypic means fluctuate during the 2 years.

Estimation of genetic variance components

Estimation of genetic variance components indicated that variances in embryo additive effects (V_{Ao}) and endosperm additive effects (V_{Ae}) were significant for malt αAA, KI and Wort-N values (Table 2). The contribution of the latter to genetic variation was a great deal larger than that of the former. Embryo dominance variance (V_{Do}), however, was most important for both Wort-N and αAA, while endosperm dominance variance (V_{De}) was most important for KI. For these three malt traits, significant variance of an interaction between the embryo gene (additive and dominance) effects and environmental effects was found, but no interaction variance of the endosperm gene effects and environmental effects was detected.

Endosperm general heritabilities (h_o^2) of the αAA, KI and Wort-N were 4.6%, 29.2% and 21.9%, respectively, which were much higher than embryo general heritabilities (h_{en}^2) (0.9%, 5.8% and 4.3%, respectively). Interaction heritability (h_{oE}^2 or h_{enE}^2) of these traits was very low.

Prediction of gene effects

Since the breeding value of an inbred variety can be generally evaluated by endosperm and embryo additive effects, predicted additive effects of the seven parents and their standard errors are listed in Table 3 for αAA, KI and Wort-N. There were highly significantly positive embryo and endosperm additive effects on the Wort-N of 'Ganmu 2' (Ao_1 and Ae_1) and on the αAA of 'Ganmu 2' (Ao_1 and Ae_1) and 'Supi 1' (Ao_2 and Ae_2) among the seven parental varieties. We concluded that 'Ganmu 2' might be more superior to other varieties for increasing Wort-N content and malt αAA in the malting quality breeding program and that 'Supi 1' might also be a suitable parent for increasing the αAA. None of predicted values of embryo and endosperm additive effects for KI was significantly different from zero because of a very small ratio of variance of these effects to the phenotypic variance (see Table 2).

The predicted dominance effects for those traits with significant variances (Table 4) showed that the highest predicted values of the embryo dominance effect on Wort-N was Do_{15}, which could be, besides Ao_1 and Ae_1 with the highest positive values, another main cause for the highest Wort-N content observed in the malt of F_2 seeds from cross $P_1 \times P_5$ (see Table 1). The embryo dominance effect on the Wort-N was significantly negative in most crosses. This led to lower phenotypic values in most crosses of the F_2 generation than those of their low-parent. Do_{1j} and Do_{2j} ($j = 1, 2, \ldots, 7$) were

Table 2 Components of genetic variance of malt Kolbach index (KI), alpha-amylase activity (αAA) and wort-N

Parameter	KI Estimate ± SE	Wort-N Estimate ± SE	αAA Estimate ± SE
V_{Ao}	0.448* ± 0.220	721.212** ± 155.822	64.518** ± 6.442
V_{Do}	0.000 ± 0.000	8 609.050** ± 781.993	443.341** ± 39.798
V_{Ae}	2.280* ± 1.120	3 647.010** ± 786.963	326.433** ± 32.630
V_{De}	17.620** ± 3.223	0.000 ± 0.000	0.000 ± 0.000
V_{AoE}	1.885** ± 0.322	243.416* ± 86.381	36.189* ± 13.135
V_{DoE}	27.484** ± 2.292	3 325.230** ± 737.767	234.621** ± 69.174
V_{AeE}	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000
V_{DeE}	0.000 ± 0.000	0.000 ± 0.00	0.000 ± 0.000
V_{ε}	0.225** ± 0.067	86.535* ± 31.081	14.103* ± 5.924
V_P	49.943** ± 3.937	16 632.500 ± 2398.180	1 119.200** ± 95.528
h_o^2	0.009^+ ± 0.006	0.043** ± 0.003	0.058** ± 0.006
h_e^2	0.046^+ ± 0.030	0.219** ± 0.017	0.292** ± 0.028
h_{oE}^2	0.038** ± 0.005	0.015** ± 0.004	0.032* ± 0.010
h_{eE}^2	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000

$^+P \leqslant 0.10$, $*P \leqslant 0.05$, $**P \leqslant 0.01$

Table 3 Predictions of gene additive effects of parents for malt Kolbach index (KI), alpha-amylase activity (αAA) and wort-N

Parameter	KI Estimate ± SE	Wort-N Estimate ± SE	αAA Estimate ± SE
Germinating embryo			
Ao_1	0.541 ± 0.325	40.999** ± 4.537	5.467** ± 1.050
Ao_2	− 0.164 ± 0.091	− 0.720 ± 2.039	8.293** ± 0.395
Ao_3	− 0.304 ± 0.165	− 7.157** ± 1.308	− 2.635** ± 0.329
Ao_4	− 0.014 ± 0.021	− 6.492** ± 1.105	− 3.532** ± 0.289
Ao_5	− 0.631 ± 0.381	2.110 ± 1.371	− 8.801** ± 0.579
Ao_6	0.353 ± 0.156	− 16.459** ± 2.062	0.192 ± 0.712
Ao_7	0.219 ± 0.133	− 12.289** ± 0.885	1.014 ± 0.737
Endosperm			
Ae_1	0.816 ± 0.489	61.464** ± 6.789	8.198** ± 1.574
Ae_2	− 0.248 ± 0.137	− 1.076 ± 3.059	12.437** ± 0.593
Ae_3	− 0.458 ± 0.248	− 10.723** ± 1.961	− 3.951** ± 0.494
Ae_4	− 0.021 ± 0.032	− 9.740** ± 1.656	− 5.297** ± 0.433
Ae_5	− 0.952 ± 0.574	3.163 ± 2.057	− 13.198** ± 0.869
Ae_6	0.533 ± 0.236	− 24.671** ± 3.087	0.289 ± 1.068
Ae_7	0.331 ± 0.200	− 18.427** ± 1.325	1.520 ± 1.106

*$P \leqslant 0.05$, **$P \leqslant 0.01$

Table 4 Predictions of gene dominance effects of seven parents and their F_2s for malt Kolbach index (KI), alpha-amylase activity (αAA) and wort-N in barley

Embryo dominance effect			Endosperm dominance effect	
Parameter	Wort-N Estimate ± SE	αAA Estimate ± SE	Parameter	KI Estimate ± SE
Do_{11}	− 19.106 ± 23.667	− 45.841** ± 6.911	De_{11}	− 1.064$^+$ ± 0.660
Do_{22}	217.489** ± 27.841	− 87.184** ± 3.892	De_{22}	1.571$^+$ ± 0.667
Do_{33}	180.804** ± 6.360	− 22.606** ± 4.543	De_{33}	− 0.783 ± 0.349
Do_{44}	243.123** ± 9.233	− 1.438 ± 2.446	De_{44}	0.457** ± 0.429
Do_{55}	76.402** ± 8.745	19.096** ± 2.588	De_{55}	− 2.994** ± 0.452
Do_{66}	297.168** ± 16.457	− 26.953** ± 6.388	De_{66}	− 1.096** ± 0.180
Do_{77}	265.441** ± 7.818	2.297 ± 6.243	De_{77}	2.943* ± 0.542
Do_{12}	44.393$^+$ ± 20.450	63.548** ± 11.304	De_{12}	2.025** ± 0.733
Do_{13}	− 35.931 ± 20.802	− 10.319$^+$ ± 4.449	De_{13}	− 2.688 ± 0.650
Do_{14}	− 24.989 ± 13.366	33.995** ± 7.079	De_{14}	− 0.807** ± 0.937
Do_{15}	308.955** ± 19.204	− 6.452 ± 5.520	De_{15}	7.050** ± 0.516
Do_{16}	− 53.360** ± 4.957	26.303* ± 8.095	De_{16}	0.484 ± 0.107
Do_{17}	− 23.472 ± 17.936	12.891$^+$ ± 5.852	De_{17}	0.996 ± 0.666
Do_{23}	− 83.895** ± 13.820	46.876** ± 4.596	De_{23}	0.389** ± 0.425
Do_{24}	13.107 ± 8.508	44.416** ± 4.404	De_{24}	− 2.106** ± .0.354
Do_{25}	− 158.928** ± 14.675	14.105$^+$ ± 6.968	De_{25}	− 4.000 ± 0.480
Do_{26}	− 116.222** ± 16.999	6.761 ± 6.554	De_{26}	0.801* ± 0.457
Do_{27}	− 136.610** ± 15.350	41.708** ± 4.736	De_{27}	− 1.748 ± 0.642
Do_{34}	− 114.574** ± 19.665	2.853 ± 4.082	De_{34}	− 0.685** ± 0.721
Do_{35}	72.193** ± 3.934	13.170$^+$ ± 5.403	De_{35}	− 1.827** ± 0.344
Do_{36}	− 137.563** ± 15.923	24.152* ± 7.487	De_{36}	3.888 ± 0.352
Do_{37}	− 92.729** ± 4.887	− 45.168** ± 1.696	De_{37}	− 0.192** ± 0.590
Do_{45}	− 217.922** ± 11.124	− 61.573** ± 8.421	De_{45}	− 1.983** ± 0.304
Do_{46}	− 76.190** ± 11.277	− 19.477 ± 10.791	De_{46}	3.426** ± 0.624
Do_{47}	− 93.817** ± 9.515	− 15.659$^+$ ± 6.672	De_{47}	1.194** ± 0.238
Do_{56}	− 96.340** ± 4.191	− 16.398* ± 4.547	De_{56}	0.962 ± 0.197
Do_{57}	− 51.546** ± 10.054	− 26.722** ± 2.148	De_{57}	0.162** ± 0.257
Do_{67}	− 185.907** ± 13.637	33.615** ± 5.763	De_{67}	− 4.377 ± 0.292
Δ_o	− 3.146** ± 0.092	1.788** ± 0.094	Δe	0.151 ± 0.298

$^+P \leqslant 0.10$, *$P \leqslant 0.05$, **$P \leqslant 0.01$

significantly positive values in most instances, indicating that 'Ganmu 2' (P_1) and 'Supi 1' (P_2) might be good candidates for parents of a hybrid with a high soluble nitrogen content in worts due to the embryo over-dominance effects. Moreover, the highest De_{15} for KI showed that the "$P_1 \times P_5$" cross could give a superior hybrid with a high solubility of the malt protein under the control of endosperm gene dominance effects. Also, significant endosperm dominance effects were obtained in the F_2 generation involving parent 6.

Heterosis for malt attributes can be measured by the average of the homozygous dominance effects. A significant positive value of $\hat{\Delta}_O = (-\sum_i \hat{D}o_{ii}/\sqrt{p\hat{\sigma}^2_{Do}})$ (or $\hat{\Delta}e = (-\sum_i \hat{D}e_{ii}/\sqrt{p\hat{\sigma}^2_{Den}})$) indicates positive heterosis of the embryo (or endosperm), and the reverse is true for negative heterosis (Zhu 1993). The Δ_o value was negative for Wort-N (-3.146**) and positive for the αAA (1.788**). Thus, negative heterosis for Wort-N and positive heterosis for αAA were expected for the malt of F_2 grains on F_1 plants. This may explain the phenomenon that an increase in αAA and a decrease in Wort-N were significant for most of the F_2 progenies as compared to the homozygous parental varieties.

Discussion

Since malt is a product derived from barley grains which are germinated for a limited period of time and then dried and lightly cooked (Cook 1962), genetic control of the malt trait is different from that of either a plant trait or a kernel quality trait. Thus, the standard diploid genetic models can not be applied to barley malt characteristics. The genetic models with two sets of genetic systems and GE interaction along with the analytical methods presented here for malting quality traits can be used not only for balanced data with no missing crosses, but also for unbalanced data with missing crosses. Although, in general, three generations are needed for applying the genetic analysis by using the embryo–endosperm models, we only included two generations (Ps and F_2s) and treated F_1s as missing generations in the present study.

The models are also applicable to genetic research on seed or seedling traits of cereal crops other than barley malts. The results of the working data for malt αAA, KI and Wort-N showed that the genetic parameters included in the model could explain the real genetic features of the malt traits.

Malt αAA, KI and Wort-N have been reported to be influenced to some extent by the environment (Hater and Riggs 1973; Arend et al. 1995; Rutger et al. 1966). Several studies have revealed that cytoplasmic effects have very little influence on malting quality traits in barley (Kaeppler and Rasmusson 1991; Lee 1987). Few studies, however, have examined the embryo gene effect on the inheritance of malting quality. In the present study, it was observed that the malt quality traits under consideration were clearly controlled by the embryo genetic effects as well as the endosperm genetic effects. The effects of embryo genes were presented mainly by the dominance effects and $Do \times E$ interaction, and the contribution of the embryo additive effects to variation of the malt traits was relatively small in comparison with that of other genetic components concerned. In addition, significant genotype × environment interaction was also observed for these three traits. This finding is in agreement with that of Lee et al. (1987). In their study, GE interactions involving years generally were greater than those involving planting dates.

Until now, only a few studies on the heterosis of malt quality traits in barley have been reported, but no significant heterosis was found in most of the malt traits of F_2 seeds (on F_1 plants) (Rasmussion et al. 1966; Kaeppler and Rasmusson 1991). Unlike the previous findings reported, the present study showed significant positive embryo heterosis over the high-parent for the αAA and significant negative embryo heterosis below the low-parent for Wort-N in the F_2 seed generation. A possible explanation for the discrepancy may lie in the great difference in genetic backgrounds among the varieties chosen in our study.

Generally, malting barley breeding programs emphasize conducting crosses among adapted elite germplasm or varieties. In the present study, although 'S-095' and 'RisΦ 1508' were very high in αAA, KI and Wort-N, they were not desirable parental varieties in malting quality because these two varieties had very low values of endosperm and embryo additive effects.

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