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Genetic effects of embryo and endosperm for four malting quality traits of barley

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Summary

Seed of seven cultivars of two-rowed barley (*Hordeum Vulgare* L.) and F_2 seed from a half-diallel set of crosses among the cultivars were malted in two years to obtain data on diastatic power (DP), alpha-amylase activity (αAA), beta-amylase activity (βAA) and malt nitrogen (N) content. Embryo and endosperm genetic effects on the traits were studied by using a genetic model including genotype × environment interaction for malting quality characters. Variation of the four malting quality traits was affected by gentic effects and environmental interaction. Performance of DP and βAA was mainly controlled not only by endosperm dominance effects but also by embryo genotype × environment interaction and endosperm dominance × environment interaction. Variation of αAA and malt N content was controlled by both embryo and endosperm genetic effects, but the embryo dominance and endosperm additive effects contributed a major part to the total genetic effects. Significant interaction variances (embryo additive × environment and dominance × environment and endosperm dominance × environment) were also observed for αAA and malt N content. Diastatic power was related positively to βAA. Malt N content was associated positively with DP, largely because of the relationship between malt N and βAA. No obvious phenotype association between DP and αAA was found. General narrow-sense heritabilities of αAA and malt N content were 26.1% and 27.8%, respectively.

Abbreviations: DP, diastatic power; αAA, alpha-amylase activity; βAA, beta-amylase activity

Introduction

Barley malt, the main raw ingredient for production of beer, contains many starch-degrading enzymes (Cook, 1962). Activity of the enzymes is considered to be an important quality characteristic for malting and brewing (Arends et al., 1995). To a large extent, diastatic power (DP) is a measure of activity of the several amylolytic enzymes (Enari et al. 1969; Hayter & Riggs, 1973) and has a close correlation with alpha-amylase activity (αAA), beta-amlyse activity (βAA) and malt nitrogen (N) content (Arends et al., 1995; Baker et al., 1968; Den Hartog & Lambert, 1953; His & Lambert, 1954; Rasmusson & Glass, 1965, 1967; Rutger et al., 1967). Barley cultivars with a high DP have a superior beer quality and yield in malting and brewing process (Cook, 1962; Guan, 1985; Zhu et al., 1991). Accordingly, improvement in DP and associated malting traits is a critical goal of barley quality breeding programs.

Up to now, only a few studies on the inheritance of malting quality in barley have been reported. DP has been reported to be determined by a complex interaction of genetic and environmental factors (Arends et al., 1995; Foster et al., 1967; Hayter & Riggs, 1973). Hayter & Riggs (1978) found that an additive-dominance model could be used to analyze the DP and αAA, but Zhu et al. (1991) observed the presence of non-allelic interactions for DP. Some studies have shown that on most of malting quality traits in barley, there were no significant cytoplasmic effects

(Kaeppler & Rasmusson, 1991; Lee et al., 1987) and maternal effects (Greenberg, 1977; Hayter & Riggs, 1978), but there was a certain environmental influence (Arends et al., 1995; Greenberg, 1977; Rutger et al., 1966). Most of these studies, however, were conducted on the base of the standard diploid model and generally have not taken into consideration the different actions of embryo and endosperm genes on malt traits during seed development, malting and brewing processes. One of the principal problems in the genetic study of barley malting quality is the difficulty in separating the embryo effects and endosperm effects from the total genetic variation in the various malt traits concerned. In recent years, some authors have proposed several diploid seed models and triploid endosperm models (Bogyo et al., 1988; Foolad & Jones, 1992; Mo, 1988; Zhu, 1992; Zhu & Xu, 1994; Zhu & Weir, 1994a,b) and related statistical methods (Zhu, 1992; Zhu & Weir, 1994a; Zhu & Weir, 1996). These techniques and procedures have made it possible for genetic study of complex malting quality characters.

The maternal and endosperm effects on variation of grain nutritional quality in barley were analyzed in the previous papers using a diallel cross of seven barley varieties (Xu et al., 1996; Yan et al., 1997). In this study, the same entries were further studied on some malting quality traits in barley. A modified genetic model including embryo effects, endosperm effects and GE interaction effects was used to investigate the genetic control of DP, αAA, βAA and malt nitrogen content and to determine the relationship among the traits.

Materials and methods

Materials

A 7 × 7 half-diallel cross, not including reciprocals, was made using two-rowed barley cultivars which were a typical sample from malting barley population. These parents were 'Ganmu 2' (P_1); 'Supi 1' (P_2); 'Qianzhe 1' (P_3); 'Zhenong 3' (P_4); 'Zhipi' (P_5); 'S-096' (P_6) and 'RisΦ1508' (P_7).

Experiments in the field

The crosses were made in the spring of 1992. Parents and the F_1's were grown at the experimental farm of Zhejiang Agricultural University during the winter of 1992/1993. A randomized comple-block design with three replications was used. Experimental plots were four rows for parents but one row for F_1 progenies. A plot was 120 cm long, spaced 30 cm apart with 40 seeds in each row. These cultivars were crossed again in the spring of 1995 in the same way as in 1992. The design and cultivation were the same in 1995/1996 as in 1992/1993, with the exception of two rows for parents and 50 seeds in each row. Seeds of each parent or F_2 seeds on F_1 plants of each cross from all three blocks in each year were bulked to obtain sufficient samples for malting.

Malting quality determination

Malting quality analysis was conducted at the Laboratory of Malting Barley Quality, Chinese Academy of Agricultural Sciences. The analytical procedures used for DP, αAA, and βAA were those of the European Brewery Convention (EBC methods) (Quan, 1985). Malt nitrogen content (%) was determined by the Kjeldahl method. All the results were on a dry-weight base. Three samples were sampled at random and independently from each malt mixture of 3 experimental replicates in the field for malting quality determination in both 1993 and 1996. In the statistical analysis, 1) data from two years were put together for joint analyses; 2) data of these three samples of each entry were treated as replications for each cross or parent to estimate sampling errors; and 3) the genotype × year interaction was considered as the genotype × environment interaction. The averaged values of these malt traits for each of the seven cultivars and their F_2s in two years are shown in Table 1.

Statistical methods

A genetic model for malting quality traits (Yan et al., 1998) was modified to include genotype × environment (i.e. year) interaction. The genetic model can be written as a mixed linear model. The phenotypic mean of genetic entry from parent i × parent j ($i = j$ for inbred line and $i \neq j$ for F_2) in the *k-th* replicate within the *h-th* environment is expressed as:

For inbred line P_i,

$$Y_{hiik} = \mu + E_h + 2Ao_i + Do_{ii} + 3Ae_i + 3De_{ii} + 2AoE_{hi} + DoE_{hii} + 3AeE_{hi} + 3DeE_{hii} + \varepsilon_{hiik}$$

For F_{2ij} obtained from F_{1ij}'s self-pollinating,

$$\begin{aligned} Y_{hijk} = {} & \mu + E_h + Ao_i + Ao_j + 0.25Do_{ii} \\ & + 0.25Do_{jj} + 0.5Do_{ij} + 1.5Ae_i + 1.5Ae_j \\ & + De_{ii} + De_{jj} + De_{ij} + AoE_{hi} + AoE_{hj} \\ & + 0.25DoE_{hii} + 0.25DoE_{hjj} + 0.5DoE_{hij} \\ & + 1.5AeE_{hi} + 1.5AeE_{hj} + DeE_{hii} \\ & + DeE_{hjj} + DeE_{hij} + \varepsilon_{hijk} \end{aligned}$$

Where μ is the constant population mean; E_h is the environmental effect, i.e. year effect; ε_{hiik} or ε_{hijk} is the residual error. 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) $\sim (0, \sigma^2_{Ao})$ is the cumulative additive effect of embryo genes from line i (or line j); Do_{ii} (or Do_{jj} or Do_{ij}) $\sim (0, \sigma^2_{Do})$ is the cumulative dominance effect of embryo genes from line i × line j ($i \leq j$); Ae_i (or Ae_j) $\sim (0, \sigma^2_{Ae})$ is the cumulative additive effect of endosperm genes; De_{ii} (or De_{jj} or De_{ij}) $\sim (0, \sigma^2_{De})$ is the cumulative dominance effect of endosperm genes from i × line j ($i \leq j$); AoE_{hi} (or AeE_{hj}) $\sim (0, \sigma^2_{AoE})$ is the Ao_i (or Ao_j) × E_h interaction effect; DoE_{hii} (or DoE_{hjj} or DoE_{hij}) $\sim (0, \sigma^2_{DoE})$ is the Do_{ii} (or Do_{jj} or Do_{ij}) × E_h interaction effect; AeE_{hi} (or AeE_{hj}) $\sim (0, \sigma^2_{AeE})$ is the Ae_i (or Ae_j) × E_h interaction effect; and DeE_{hii} (or DeE_{hjj} or DeE_{hij}) $\sim (0, \sigma^2_{DeE})$ is the De_{ii} (or De_{jj} or De_{jj}) × E_h interaction effect.

Minimum norm quadratic unbiased estimation (MINQUE(1)) method (Rao, 1971; Zhu & Weir, 1996) was used for estimating variance components and covariance components between traits. Phenotypic variance (V_P) is composed of several genetic components,

$$\begin{aligned} V_P &= V_G + V_{GE} + V_\varepsilon \\ &= V_{Ao} + V_{Do} + V_{Ae} + V_{De} + V_{AoE} \\ &\quad + V_{DoE} + V_{AeE} + V_{DeE} + V_\varepsilon \end{aligned}$$

where V_G = genetic main variance, V_{GE} = GE interaction variance, V_{Ao} = embryo additive variance, V_{Do} = embryo dominance variance, V_{Ae} = endosperm additive variance, V_{De} = endosperm dominance variance, V_{AoE} = embryo additive interaction variance, V_{DoE} = embryo dominance interaction variance, V_{AeE} = endosperm additive interaction variance, V_{DeE} = endosperm dominance interaction variance, and V_ε = residual variance. Phenotypic covariance can be partitioned in the same way as variance.

According to the theory of genetic model construction, the heritability can be partitioned into several components (Zhu, 1997):

$$\begin{aligned} h^2 &= h^2_G + h^2_{GE} \\ &= (h^2_{Go} + h^2_{Ge}) + (h^2_{GoE} + h^2_{GeE}) \end{aligned}$$

The total narrow-sense heritability (h^2) consists of general heritability ($h^2_G = V_G/V_P$) and interaction heritability ($h^2_{GE} = V_{GE}/V_P$). The general heritability has components of embryo general heritability ($h^2_{Go} = V_{Go}/V_P$) and endosperm general heritability ($h^2_{Ge} = V_{Ge}/V_P$). The interaction heritability (h^2_{GE}) has components of embryo interaction heritability ($h^2_{GoE} = V_{GoE}/V_P$) and endosperm interaction heritability ($h^2_{GeE} = V_{GeE}/V_P$).

A Jackknife procedure is used for estimating the sampling variances of estimated variances, heritabilities and covariances (Miller, 1974; Zhu & Weir, 1994a, b). Thus, a t-test with 55 degree of freedom following the Jackknifing was employed to detect the significance of estimated parameters when genetic entries served as re-sampling units (Zhu, 1992).

Results

Phenotypic means of the parent varieties

The phenotypic values of all the malt traits differed considerably among the seven cultivars over years (Table 1). Range in 1995 was smaller than that in 1995. For example, the range for DP was from 108 WK to 367 WK in 1995 and from 166 WK to 324 WK in 1992, for βAA from 71 WK to 337 WK in 1995 and from 91 WK to 266 WK in 1992. Performance of a cultivar in two years was different for the malt traits and the order of cultivars varied greatly in phenotypic values. For instance, 'Supi 1' among the seven varieties ranked first for the DP value in 1995, but fifth in 1992. Across the cultivars, DP was 232 WK in 1992, but 281 WK in 1995. This revealed that the variation of the four malting traits might be influenced by genotypic and environmental effects as well as genotype × environment interaction.

Performance of most F_2s generations showed that for DP, αAA and βAA, mean of all F_2 generations involving a common parent was higher than that of their parent. For example, 'Ganmu 2' was 224 WK for DP in 1992, while mean of all its F_2s was 285 WK. However, for malt N content, means of F_2s was lower than that of their common parent in most cases. This

Table 1. Phenotypic means of malting traits of 7 cultivars and F_2 generations in two years

Entry	DP (WK)		αAA (WK)		βAA (WK)		Malt N content (%)	
	1992	1995	1992	1995	1992	1995	1992	1995
Parent								
Ganmu 2 (P_1)	224	345	72	61	152	284	1.50	1.87
Supi 1 (P_2)	209	367	69	30	146	337	1.75	1.92
Qianzhe 1 (P_3)	249	267	58	41	190	227	1.69	2.09
Zhenong 3 (P_4)	258	348	59	61	199	286	1.58	1.96
Zhipi (P_5)	324	339	57	48	266	291	1.88	2.25
S-096 (P_6)	198	196	66	50	133	146	1.75	1.90
RisΦ 1508 (P_7)	166	108	80	81	91	27	1.57	1.65
Parent Mean	232	281	66	53	168	228	1.67	1.95
F_2 generation [a]								
F_2 ($P_{1.}$)	285	275	83	66	201	208	1.53	1.84
F_2 ($P_{2.}$)	253	285	82	68	171	215	1.52	1.79
F_2 ($P_{3.}$)	264	289	66	58	199	229	1.52	1.81
F_2 ($P_{4.}$)	235	299	62	64	175	241	1.47	1.78
F_2 ($P_{5.}$)	286	287	61	50	224	237	1.65	1.82
F_2 ($P_{6.}$)	252	258	66	67	184	196	1.45	1.64
F_2 ($P_{7.}$)	208	230	74	69	135	161	1.45	1.63
F_2 mean	255	275	70	63	184	212	1.51	1.76

[a] F_2 ($P_{i.}$) represents the mean of all the F_2 generations derived from the combination involving parent i.

suggested that there would be a certain heterosis in F_2s seeds for the four malting quality traits.

Variance components

The estimation of genetic variance components showed that the contribution of endosperm and embryo genetic effects to the variation of four malting quality traits varied greatly (Table 2). The endosperm dominance variance (V_{De}), embryo genetic × environment interaction variance (V_{AoE} and V_{DoE}) and endosperm additive × environment interaction variance (V_{AeE}) were significantly greater than zero for DP and βAA. The contribution of the V_{De} and V_{DoE} to the phenotypic variation was quite larger than that of others. Although no embryo genetic variance components (V_{Ao} and V_{Do}) were detected, embryo × environment interaction effects on the DP and βAA would not be negligible because of the presence of the significance of V_{AoE}. That is, embryo genetic effects would express differently across environments or years.

Genetic variation of αAA and malt N content was due to both embryo and endosperm genetic effects. Variance of embryo dominance effects and endosperm additive effects (V_{Do} + V_{Ae}) made up 92.32% and 92.28% of the total genetic variances (V_{Ao} + V_{Do} + V_{Ae} + V_{De}) for αAA and malt N, respectively. It was shown that inheritance of αAA and malt N was mainly determined by embryo dominance and endosperm additive effects. Variances of the embryo *Do* × *E* in-

Table 2. Estimation of variance components of four malting quality traits

Parameter	DP	αAA	βAA	Malt N (× 10^{-3})
V_{Ao}	0.0	132.7**	0.0	12.6**
V_{Do}	0.0	914.2**	0.0	87.8**
V_{Ae}	0.0	672.2**	0.0	63.7**
V_{De}	17424.3**	0.0	16358.5**	0.0
V_{AoE}	1902.5**	109.0**	1461.4**	8.9**
V_{DoE}	14433.8**	690.3**	11616.4**	56.2**
V_{AeE}	9645.1**	550.7	7408.1**	45.1**
V_{DeE}	0.0	0.0	0.0	0.0
V_ε	25.8**	13.2**	87.0*	0.2**
V_P	43431.5**	3082.3**	36932.5**	274.6**

* $p \leq 0.05$; ** $p \leq 0.01$.
V_{Ao} = embryo additive variance, V_{Do} = embryo dominance variance, V_{Ae} = endosperm additive variance, V_{De} = endosperm dominance variance, V_{AoE} = embryo additive interaction variance, V_{DoE} = embryo dominance interaction variance, V_{AeE} = endosperm additive interaction variance, V_{DeE} = endosperm dominance interaction variance, V_ε = residual variance, and V_P = phenotype variance.

Table 3. Heritabilities of four malting quality traits

Parameter	DP	αAA	βAA	Malt N ($\times 10^{-3}$)
h^2_{Go}	0.000	0.043**	0.000	0.046**
h^2_{Ge}	0.000	0.218**	0.000	0.232**
h^2_{GoE}	0.044**	0.035**	0.040**	0.033**
h^2_{GeE}	0.222**	0.179**	0.201**	0.164**

* $p \leq 0.05$; ** $p \leq 0.01$.
h^2_{Go} = embryo general heritability; h^2_{Ge} = endosperm general heritability; h^2_{GoE} = embryo interaction heritability; and h^2_{GeE} = endosperm interaction heritability.

teraction and endosperm $Ae \times E$ interaction (V_{AoE} and V_{DoE}) also were significant, but no variance of endosperm dominance × environment interaction (V_{DeE}) was observed. It was implied that effects of environmental factors on the two traits acted through the complex interaction with embryo dominance effects and endosperm additive effects. However, it seems that the environments would not affect the expression of endosperm dominance effects.

Although the error variance (V_ε) was significantly greater than zero for all the traits studied, the ratio of V_ε to the phenotypic variance was very small (<2%). It was suggested that the genetic model used in this study was effective for analyzing the malting quality traits because the items of genetic effects and environmental interaction effects included in the model could account for more than 98% of the phenotypic variation.

Heritability

The estimation of heritability components for the four traits indicated that the general heritabilities ($h^2_G = h^2_{Go} + h^2_{Ge}$) of αAA and malt N content were about 26.1% and 27.8% respectively (Table 3), while the interaction heritabilities ($h^2_{GE} = h^2_{GoE} + h^2_{GeE}$) of DP and βAA were around 26.6% and 24.1%, respectively. For the αAA and malt N content, the general heritability (h^2_G), which is applicable to multiply environments, was higher than the interaction heritability (h^2_{GE}), which is only applicable to specific environments. The interaction heritability would bring a (positive or negative) bias to the general heritability in a special environment. Therefore, selection for αAA and malt N in different environments (or years) was effective to some extent, but this effectiveness would be different in different environments. On the other hand, the endosperm general heritability (h^2_{Ge}) and endosperm interaction heritability (h^2_{GeE}) were much larger than the embryo general heritability (h^2_{Go}) and embryo interaction heritability (h^2_{GoE}) for αAA and malt N content. This suggested that contribution of the endosperm to effectiveness of selection for αAA and malt N content was more important than that of the embryo. Since the dominance effects were predominant over the inheritance for DP and βAA, the two traits tended to be very low general heritabilities. Thus, the improvement in DP and βAA for the entries in this study would not be effective in all environments, but it would be effective in special environments because the existence of the endosperm interaction heritability (h^2_{GeE}).

Covariance components

The estimation of phenotype covariance (C_P) indicated that malt N content was positively correlated with DP and βAA but negatively with αAA (Table 4). βAA also exhibited a significant positive relationship with DP but negative with αAA. A significant covariance failed to be detected between DP and αAA.

Although the phenotype covariances between malt N content and other traits and between αAA and βAA were significant, none of the genetic covariance components was significantly observed (Table 4). It was revealed that for those paired traits, the association of each kind of the genetic effect was not very strong, but the accumulation of all the genetic effects could make strong association between traits. As a result, it would lead to a significant phenotypic covariance. The phenotypic covariance or the genetic covariance components was not significant between DP and αAA. However, a significant poistive covariance of the embryo dominance × environment interaction was found between DP and βAA. It was implied that the action of environments on embryo dominance effects of one trait was the same direction as on that of the other. That is, if embryo dominance × environmental interaction effects for DP were significantly positive for most of cross combinations in one environment, such effects for βAA were significantly positive in the same environment. The reverse was also true.

Discussion

With the increasing need for high quality beer, barley breeders need to develop cultivars with superior malting quality and have a better understanding of the inheritance of the malting traits. However, genetic control of malt traits is complex. In malting,

Table 4. Covariance components among malting quality traits in barley

Parameter	αAA	βAA	Malt N ($\times 10^{-2}$)
DP			
C_P	−134.9	2844.1**	502.8**
C_{Ao}	−123.8	−454.3	121.8
C_{Do}	−505.6	−4716.2	229.1
C_{Ae}	−625.1	−2289.1	616.3
C_{De}	1105.3	9418.7	−690.5
C_{AoE}	217.8	720.5	−92.5
C_{DoE}	1325.8	7663.9*	−609.1
C_{AeE}	1116.8	3732.5	−470.3
C_{DeE}	−2647.3	−11238.5	1397.2
αAA			
C_P		−318.7**	−117.6**
C_{Ao}		−211.3	19.7
C_{Do}		−1141.4	145.7
C_{Ae}		−1067.2	99.5
C_{De}		2139.1	−348.2
C_{AoE}		186.0	7.7
C_{DoE}		1110.7	89.2
C_{AeE}		956.5	38.5
C_{DeE}		−2292.9	−169.6
βAA			
C_P			601.9**
C_{Ao}			85.4
C_{Do}			−17.0
C_{Ae}			432.4
C_{De}			−129.9
C_{AoE}			−93.4
C_{DoE}			−656.3
C_{AeE}			−474.4
C_{DeE}			1456.0

* $p \leq 0.05$; ** $p \leq 0.01$.
C_{Ao} = embryo additive covariance; C_{Do} = embryo dominance covariance; C_{Ae} = endosperm additive covariance; C_{De} = endosperm dominance covariance; C_{AoE} = embryo additive × environment covariance; C_{DoE} = embryo dominance × environment covariance; C_{AeE} = endosperm additive × environment covariance; C_{DeE} = endosperm dominance × environment covariance; and C_P = phenotype covariance.

barley grains are germinated for a limited period of time and then dried. The germinated kernel is called malt. During germination, the diploid germinating-embryo secretes gibberellin (GA_3) into triploid cells of the aleurone layers. GA_3 induces the synthesis of hydrolytic enzymes that catalyze breakdown of the cell walls and reserves of endosperm tissues and make them available for the developing embryo, or soluble for malt extracts (Cook, 1962; MacGregor et al., 1972). Therefore, the performance of malt traits may be controlled not only by endosperm genes but also by embryo genes. Thus the standard diploid model (Zhu & Weir, 1994a) or triploid endosperm model (Zhu & Weir, 1994b) can not be applied to study the special genetic control of malt traits. The genetic effects of embryo as well as endosperm should be considered in one model. It was shown in this study that the malt traits were controlled by both the embryo and endosperm genes and also affected by the environment interactions.

Diastatic power, alpha-amylase, beta-amylase activities and malt N content are four important quality attributes in malting barley. Malting barley cultivars with acceptable quality are requested to have an adequate level of DP, αAA and βAA, and a moderate level of malt N content (Cook, 1962; Guan, 1985; Zhu et al., 1991). Of the cultivars investigated here, 'Ganmu 2', 'Zhipi', 'Zhenong 3' and 'Supi 1' could be used as preferable parents for improving malting quality in barley breeding because of their high diastatic power.

Variation of DP and βAA was mainly determined by endosperm genetic effects, while variation of αAA and malt N content was controlled by both embryo and endosperm genetic effects. This discrepancy in genetic control may be explained by the different stages of development at which the enzymes are produced and by the interrelationships among the three traits. On the one hand, the DP is mainly composed of αAA and βAA. Beta-amylase, the most abundant barley enzyme (Enari & Linko, 1969), is produced in the endosperm during grain filling as an inactive bound form. Beta-amylase is not synthesized during germination, but there is a release of a free beta-amylase from a bound form during germination (Lagerge & Meredith, 1971). Thus, the beta-amylase may not be largely impacted by embryo genes. Unlike beta-amylase, alpha-amylase is produced in triploid cells of the aleurone in response to GA_3 secreted by the embryo (MacGregor, et al., 1972). αAA shows a linear relation with the concentration of the gibberellins within a certain extent (Zhu et al., 1991). Therefore, αAA may be considerably controlled by embryo genetic effects.

In this study, the genetic effects for the four malt traits was significantly affected by environments, being consistent with earlier studies (Kneen & Hads, 1945; Kaeppler & Rasmusson, 1991; Rutger et al., 1966). A significant embryo genotype × environment interaction for the malt quality traits (see Table 2) may be due to the susceptibility of the germinating-embryo to environmental factors. For DP and βAA, it is re-

ported that genotype was the main source of variation (Arends et al., 1995; Hayter & Riggs, 1973; Kneen & Hads, 1945). Our study confirmed previous reports that variation of DP and βAA was larger among cultivars than between years. Moreover, Xu et al. (1991) and Kaeppler et al. (1991) observed a high heterosis over the high-parent for DP, αAA and βAA. They attributed the heterosis to dominance effects. Like their fundings, our study also found that DP and βAA were mainly controlled by endosperm dominance effects, while αAA and malt N content were determined by embryo dominance effects and endosperm additive effects.

Diastatic power is a measure for the potential of amylolytic enzymes in malt to decompose the starch in the endosperm and cereal adjuncts during mashing (Cook, 1962; Hayter & Riggs, 1973; Enari & Linko, 1969). A number of previous studies reported that beta-amylase was the main contributor to total diastatic power (Arends et al., 1995; Hayter & Allison, 1975; Hayter & Riggs, 1973; Kneen & Meredith, 1971; Lee et al., 1987). Our study also obtained a significant positive correlation between βAA and DP. Although αAA is a contributor to DP, both were lack of an apparent correlation between them. This agreed with the finding obtained by Rutger et al. (1967).

Rutger et al. (1967) reported that alpha- and beta-amylase activities were not correlated and seem to be independently inherited. Our results also showed that the correlation between αAA and βAA was relatively weak in comparison with that between βAA and DP. It is suggested that development of barley cultivars with high levels of diastase activity may need a separate selection for the αAA and βAA.

Previous studies (Arends et al., 1995; Den Hartog & Lambert, 1953; Enari & Linko, 1969; Hayter & Allison, 1975; Rasmusson & Glass, 1965; Rutger et al., 1966) and our studies all found that DP and βAA were closely correlated with malt N content. The positive correlation between DP and malt N could be largely explained by the close relationship of both characters with βAA. The association between βAA and malt N content and between high DP and βAA are important for selection of quality characteristics in barley. Improvement of DP in barley can be obtained by indirect selection for the grain N content, because the malt N content is determined easier than DP and has a close correlation with grain N content with a high heritability.

For the heritability of the malt traits, there are different results obtained by various researchers. Rutger et al. (1966) and Foster et al. (1967) reported that heritabilities for DP, αAA, βAA and Malt N were over 0.75. In many other studies, heritabilities were not very high. For example, the range of heritability estimated by regression of offspring on parents was from 37% to 65% in F_3 seeds, and 39% to 74% in F_4 seeds for αAA (Kaeppler & Rasmusson, 1991). The range, when estimated by analysis of variance, was from 29% to 48% of the narrow sense heritability for DP (Zhu et al., 1991) and from 31% to 34% of the broad sense heritability (Day et al., 1955). The heritabilities were not very high for four malting quality traits concerned in our study. The unlikeness may be due to different materials and statistical methods used in the different studies.

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References

Arends, A.M., G.P. Fox, R.J. Henry, R.J. Marschle & M.H. Symons, 1995. Genetic and environmental variation in the diastatic power of Australian barley. J Cereal Sci 21: 63–70.

Baker, R.J., V.M. Bendelow & K.W. Buchccnnom, 1968. Early generation inheritance of malting quality characters in a barley cross. Crop Sci 8: 446–448.

Bogyo, T.P., R.C.M. Lance, P. Chevalier & R.A. Nilan, 1988. Genetic models for quantitatively inherited endosperm characteris. Heredity 60: 61–67.

Cook, A.H., 1962. Barley and Malt Biology, Biochemistry, and Technology. Academic Press, New York, pp. 303–427.

Day, A.D., E.E. Down & K.J. Prey, 1955. Association between diastatic power and certain visible characteristics and heritability of diastatic power in barley. Agron J 47: 163–165.

Den Hartog, G.T. & J.W. Lambert, 1953. The relationship between certain agronomic and malting characteristics of barley. Agron J 45: 208–212.

Enari, T.M. & M. Linko, 1969. Significance of barley and malt amylases. Ann Agric Fenn 8: 149–156.

Foolad, M.R. & R.A. Jones, 1992. Models to estimate maternally controlled genetic variation in quantitative seed characters. Theor Appl Genet 83: 360–366.

Foster, A.E., G.A. Peterson & O.J. Banasik, 1967. Heritability of factors affecting malting quality of barley. Crop Sci 7: 611–613.

Greenberg, D.C., 1977. A diallel cross analysis of gum content in barley (*Hordeum vulgare*). Theor Appl Genet 50: 41-46.

Guan, D.Y., 1985. Manual of Beer Industry. Light Industrial Press, Beijing, pp. 120–198 (in Chinese).

Hayter, A.M. & M.J. Allison, 1975. Breeding for high diastatic power. In: Proc 3rd Int Barley Genet Symp. pp. 612–619.

Hayter, A.M. & T.J. Riggs, 1973. Environmental and varietal differences in diastatic power and four associated characteristics of spring barley. J Agric Sci (Camb) 80: 297–302.

Hayter, A.M. & T.J. Riggs, 1978. The inheritance of diastatic power and alpha-amylase contents in spring barley. Theor Appl Genet 50: 41–46.

His, C.H. & J.W. Lambert, 1954. Inter- and intra-annual relationships of some agronomic and malting quality characters of barley. Agron J 46: 470–474.

Kaeppler, H.F. & D.C. Rasmusson, 1991. Heritability, heterosis and maternal effects of alpha-amylase activity in barley. Crop Sci 31: 1452–1455.

Kneen, E. & K.L. Hads, 1945. Effects of variety and environment on the amylase of germinated wheat and barley. Cereal Chemist 22: 407–418.

Laberge, D.E. & W.O. Meredith, 1971. The α-amylase enzymes of barley and malt. I. Purification of the malt enzymes. J Inst Brew 77: 435–442.

Lee, D.M., N. Albertsen & D.C. Rasmusson, 1987. Cytoplasmic effects on agronomic and malting quality traits in barley. Crop Sci 27: 669–673.

Lin, Y.K. & Z.L. Yu, 1991. Hybrid vigor of β-amylase and correlated studies in barley. J Hangzhou Univ (Natural Science) 18(2): 203–210 (in Chinese).

MacGregor, A.W., A.G. Gordon, W.O.S. Meredith & L. Lacroix, 1972. Site of alpha-amylase in developing barley kernels. J Inst Brew 78: 174–179.

Mo, H.D., 1988. Genetic expression of endosperm traits. In: B.S. Weir et al. (Eds), Proc 2nd Int Conf Quant Genet, pp. 478–487. Sinauer Assoc, Boston Mass.

Rasmusson, D.C. & R.L. Glass, 1967. Estimates of genetic and environmental variability in barley. Crop Sci 7: 185–188.

Rasmusson, D.C. & R.L. Glass, 1965. Effectiveness of early generation selection for four quality characters in barley. Crop Sci 5: 389–391.

Rao, C.R., 1971. Estimation of variance and covariance components: MINQUE theory. J Multivariate Analysis 1: 257–275.

Rutger, J.N., C.W. Schaller & A.D. Dickson, 1967. Variation and covariation in agronomic and malting quality characteristics in barley. II. Interrelationships of characters. Crop Sci 7: 325–326.

Rutger, J.N., C.W. Schaller, A.D. Dickson & J.C. Williams, 1966. Variation and covariation in agronomic and malting quality characters in barley. I. Heritability estimates. Crop Sci 6: 231–234.

Xu, A.B., M.Y. Zhu, M.B. Yuan, C.N. Huang & J.J. Yu, 1991. The analysis of heterosis and correlation for four malt qualities in barley (*Hordeum vaulgar*, L.). J. Hangzhou Univ (Natural Science) 18(3): 336–341 (in Chinese).

Xu, S.Y., X.F. Yan, Z.R. Xu & J. Zhu, 1996. Genetic analysis of nonessential amino acid contents in two-rowed barley. J Zhejiang Agric Univ 22(6): 567–573 (in Chinese).

Yan, X.F., S.Y. Xu, J. Zhu & X.Y. Xu, 1998. A genetic model and analytic methods for malt quality traits (in Chinese), Chinese J Biomath 13(4): 531–536 (in Chinese).

Yan, X.F., S.Y. Xu, W.F. Li & J. Zhu, 1997. Analysis of seed and maternal genetic effects for contents of seven essential amino acids in two-rowed barley. Scientia Agriculturae Sinica 30(2): 34–41 (in Chinese).

Zhu, J., 1992. Mixed model approaches for estimating variances and covariances. Chin J Biomath 7(1): 1–11.

Zhu, J., 1997. Analysis Methods for Genetic Models. China Agriculture Press, Beijing (in Chinese).

Zhu, J. & B.S. Weir, 1994a. Analysis of cytoplasmic and maternal effects. I. A genetic model for diploid plant seeds and animals. Theor Appl Genet 89: 153–159.

Zhu, J. & B.S. Weir, 1994b. Analysis of cytoplasmic and maternal effects. II. Genetic models for triploid endosperm. Theor Appl Genet 89: 160–166.

Zhu, J. & B.S. Weir, 1996. Diallel analysis for sex-linked and maternal effects. Theor Appl Genet 92: 1–9.

Zhu, J. & F.H. Xu, 1994. A genetic model and analysis method for endosperm traits. Acta Agronomica Sinia 20(2): 246–270 (in Chinese).

Zhu, M.Y., M.B. Yuan, A.B. Xu, C.N. Huang, Z.L. Xy, X.M. Hu & G.J. Yu, 1991. Genetic analysis of high diastatic power in barley (*Hordeum vaulgar*, L.). J Hangzhou Univ (Natural Science) 18(1): 67–71 (in Chinese).