J. Appl. Genet. 43(1), 2002, pp. 33-42

Interaction of gene effects with environments for malting quality of barley doubled haploids

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Abstract. Barley doubled haploids covering a wide range of malting quality, along with their parental cultivars and F_2, F_3 hybrids, were investigated in six environments (three locations, two years) to study the genotype-environment (G × E) interaction structure and the influence of environments on additive, dominance and epistatic gene effects. Grain and malt characters, such as 1000-grain weight, percentage of plump kernels, malt extract yield, protein content, Kolbach index and malt fine-coarse difference (FCD), were measured. Main effects for genetic parameters were estimated and regression analysis was used to explain the interaction of gene effects with environments. The results show that additive effects had the greatest interaction with environments for all the analysed traits, but only for malt characters this interaction was linear. Interaction of dominance effects was much lower and only in the case of 1000-grain weight, protein content and Kolbach index it proved to be significant. The results suggest that effects of heterozygous loci are more stable in contrasting environments than effects of homozygous loci.

Key words: barley, doubled haploids, genetic parameters, GE interaction, malting quality.

Introduction

Malt and grain characters are inherited quantitatively and their phenotypic performance is dependend on both genetic factors and environmental conditions (EAGLES et al. 1995, MOLINA-CANO et al. 1997, KACZMAREK et al. 1999). Besides year and location effects, genotype-environment (G × E) interaction for malt characters in barley cultivars and lines was also observed (EAGLES et al. 1995, KACZMAREK et al. 1999).

Received: May 25, 2001. Accepted: October 30, 2001.
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Information on genetic determination of quantitative traits may be obtained by estimation of genetic parameters determining additive [d], dominance [h] and epistatic (additive × additive [i], additive × dominance [j] and dominance × dominance [l]) gene effects. These genetic parameters have been defined as a sum of individual effects of all segregating loci, with the assumption of equal effect in each locus (MATHER, JINKS 1982). Estimators of the parameters are some functions of mean values of the proper generation set, i.e., parents and hybrids (P_1, P_2, F_1, F_2, F_3, B_1, B_2) and/or homozygous lines derived from a cross between two homozygous parents (MATHER, JINKS 1982, SURMA et al. 1984, 1997). As phenotypic values of traits are conditioned by both genetic and environmental factors, mean values of hybrids and lines may change depending on conditions in which the experiments have been performed. The presence of genotype-environment interaction may greatly influence the differences between the studied generations, thus influencing values of estimates of genetic parameters. Therefore, to obtain credible information on inheritance of quantitative traits, the G × E interaction should be taken into account in the genetic analysis. Such an analysis was described by KACZMAREK (1986) for GCA (general combining ability) and SCA (specific combining ability) parameters, and by ADAMSKI (1993) and ADAMSKI et al. (1996) for genetic parameters [d], [h], [i] and [l].

The aim of the present paper was to study the structure of interaction of additive, dominance and epistatic gene effects with environments for grain and malt characters of barley doubled haploid (DH) lines.

Material and methods

The materials for the study were 30 barley DH lines derived from F_1 hybrids Grit × Havila, the parental cultivars, and F_2 and F_3 hybrids. These generations were studied in a series of field experiments carried out in six environments (three locations: Cerekwica, Kruszwica, Łagiewniki in two years: 1995, 1996) denoted here as CER95, KRU95, LAG95, CER96, KRU96, LAG96. The locations differed mainly in soil type: Cerekwica – poor, sandy-clay soil, Kruszwica and Łagiewniki – rich, loamy soil. In each environment the experiment was conducted in a randomized block design with three replications. The following grain and malt characters were analysed: 1000-grain weight, percentage of plump kernels, malt protein content, ratio of soluble protein to crude protein (Kolbach index), malt extract yield, and malt fine-coarse difference. A detailed description of the experiments and the methods applied for determining grain and malt characters was presented by KACZMAREK et al. (1999).

Statistical analyses

Additive, dominance and nonallelic interaction effects were estimated on the basis of mean values of extreme lines (DH_{max}, DH_{min}), the mean value of all the lines (DH_m) and the means of F_2 and F_3 hybrids (SURMA et al. 1997). The extreme lines

were chosen on the basis of mean performance of studied lines across environments.

The study of interaction of gene effects with environments followed the procedure described by KACZMAREK (1986) and KACZMAREK et al. (2000). This method allows estimation and testing of the mean effects of genetic parameters, analysis of the interactions of individual parameters with environments, and explanation of this interaction by means of linear regression of interaction effects on environmental effects.

Results

Mean values of studied traits over environments for all DH lines, lines with minimum and maximum values of these traits, as well as for parents and F_2 and F_3 hybrids, are presented in Table 1. The largest differences between extreme lines in environments, reaching up to 35% of the value, were observed for fine-coarse difference, percentage of plump kernels and 1000-grain weight. The smallest differences were recorded for malt extract yield and protein content (data not shown).

Table 2 shows estimates of [d], [h], [i] and [l] parameters in each of the six environments. Marked differences in values and sign of these parameters estimated in particular environments can be observed. An analysis of variance performed for series of six experiments indicated a significant influence of environments and G × E interaction on estimation of gene effects for all grain and malt characters. Mean estimates of gene effects over environments and results of testing of their significance are presented in Table 3.

1000-grain weight

For 1000-grain weight additive gene effects and additive × additive epistasis proved to be significant (F-statistic values are higher than $F_{0.01}$ for [d] and higher than $F_{0.05}$ for [i]) (Table 3). These effects show also interaction with the environments. Interaction of additive effects with environments could not be explained by regression because of the small value of determination coefficients (22.57%), while in the case of additive × additive effects this relationship was linear, which is evidenced by the significant value of regression coefficient ($F = 33.80$) and a high coefficient of determination (89.42%). Mean estimates of the [h] and [l] parameters, determining dominance and dominance × dominance effects, respectively, were not significant. Differences between environments in values and sign of these parameters were observed (Table 2), but only for [h] parameter F-statistic value for interaction was higher than the critical F-value at the level of 0.05 (Table 3). Interaction of dominance effects [h] with environments may be explained to some extent by linear regression (regression coefficient significant at the level of 0.10, coefficient of determination 44.78%). The insignificant

Table 1. Mean values (over environments) for grain and malt characters of barley DH lines, parental cultivars and F_2, F_3 hybrids

Genotype	1000-grain weight (g)	Plump kernels (%)	Protein content (%)	Kolbach index (%)	Fine extract (%)	Fine-coarse difference (%)
DH_{max}	50.94	88.86	13.30	40.97	81.40	6.87
DH_{min}	35.61	58.02	12.21	34.49	79.06	3.78
DH_{mean}	44.11	78.87	12.81	37.64	80.22	5.17
Grit (G)	43.50	84.86	12.37	42.02	81.32	3.66
Havila (H)	45.09	84.17	12.86	35.12	79.07	5.94
F_2 (G × H)	46.31	87.12	12.51	39.44	80.33	4.56
F_3 (G × H)	45.34	85.62	12.67	44.72	80.48	4.47

F-statistic value for interaction of parameter [l] shows that the variation in estimates of this parameter in environments was random, independent of changes in environmental conditions.

Plump kernels

Mean estimates of all genetic parameters for percentage of plump kernels were significantly different from zero, which indicates that phenotypic values of this trait are influenced by additive, dominance and epistatic effects. A significant ($P < 0.01$) interaction with environments was found only for additive and additive × additive effects ([d] and [i] parameters), but its nature was indefinite because deviations from regression were significant (Table 3). Estimates of dominance and dominance × dominance effects in individual environments were similar and had the same (negative) sign (Table 2).

Protein content

Protein content in the studied population of DH lines was markedly influenced by additive gene effects (a significant value of parameter [d]). Estimates of these effects were dependent on environmental conditions, but only about 50% of the observed interaction of these effects with environments could be explained by means of linear regression (coefficient of regression was significant at the level of 0.10, deviations from regression were significant at the level of 0.01). Mean estimates of parameters [h] and [l] were close to zero (Table 3). Table 2 shows that in various environments values of these parameters differed in sign. F-statistic values for interaction and deviations from regression were higher than $F_{0.01}$ for both [h] and [l], which indicates that interaction of dominance and dominance × dominance effects with environments was not linear (Table 3).

Table 2. Estimates of genetic parameters for grain and malt characters in particular environments

Parameter	Environment					
	KRU95	LAG95	CER95	CER96	LAG96	KRU96
			1000-grain weight			
[d]	6.55	8.17	7.60	9.96	7.90	5.83
[h]	16.03	3.22	–24.18	19.99	1.68	16.27
[i]	–0.83	–1.60	–1.26	0.75	–1.16	–0.90
[l]	–13.96	–0.29	37.57	–13.88	–6.11	–28.80
			Plump kernels			
[d]	16.33	9.35	21.00	15.00	17.67	13.17
[h]	53.73	13.03	17.60	31.53	32.87	76.14
[i]	–5.60	1.92	–12.25	–5.72	–7.36	–3.59
[l]	–43.19	–16.84	–21.50	–36.36	–35.82	–97.97
			Protein content			
[d]	0.86	0.08	0.84	0.73	0.15	0.91
[h]	7.66	–4.29	–3.99	2.41	–1.12	–4.03
[i]	–0.49	–0.07	0.24	–0.19	–0.30	0.46
[l]	–15.65	4.81	3.24	–4.34	1.58	9.91
			Kolbach index			
[d]	1.73	4.29	4.43	4.00	0.90	4..10
[h]	–6.10	22.33	21.24	–1.43	47.07	–15.12
[i]	–0.77	1.76	0.88	0.85	–2.38	0.19
[l]	15.25	–30.18	–20.34	1.20	–96.18	30.48
			Fine extract			
[d]	1.26	1.10	1.85	0.93	0.65	1.25
[h]	–4.25	2.53	8.61	–0.61	3.05	1.94
[i]	–0.41	–0.17	–0.08	0.60	0.46	–0.29
[l]	6.57	–2.94	–11.48	0.99	–6.10	–6.86
			Fine-coarse difference			
[d]	1.77	1.89	2.54	1.78	1.08	0.22
[h]	–1.83	–9.14	–2.09	–1.05	–3.98	–7.93
[i]	0.06	–0.35	1.05	–0.10	–0.32	0.64
[l]	1.71	12.43	2.60	2.70	3.53	14.48

Table 3. Mean estimates of genetic parameters and results of testing the hypotheses concerning their interaction with environments

Parameter	Estimate of parameter	*F*-statistic value for		Coefficient of		*F*-statistic value for	
		parameter	interaction	regression	determination	regression	deviations
				1000-grain weight			
[d]	7.67	173.50	4.34	0.56	22.57	1.17	4.20
[h]	5.50	0.68	2.74	9.04	44.78	5.24	1.89
[i]	–0.83	6.70	2.48	0.64	89.42	33.80	0.06
[l]	–2.21	0.06	1.47	–10.63	31.37	1.83	1.26
				Plump kernels			
[d]	15.42	90.15	12.97	0.24	6.61	0.28	15.14
[h]	37.48	15.01	2.21	3.57	42.63	2.97	1.59
[i]	–5.43	8.22	5.89	–0.32	8.74	0.38	6.71
[l]	–41.95	12.40	0.91	-4.03	35.89	2.24	0.73
				Protein content			
[d]	0.55	8.52	6.49	0.28	49.94	4.99	4.06
[h]	–0.56	0.08	3.41	1.17	7.97	0.35	3.92
[i]	–0.06	0.16	1.28	0.08	6.55	0.28	1.50
[l]	–0.08	0.00	3.22	–1.19	2.39	0.10	3.93
				Kolbach index			
[d]	3.24	27.23	19.13	0.01	0.01	0.00	23.91
[h]	11.33	1.45	21.14	6.47	19.80	0.99	21.20
[i]	0.09	0.02	5.95	–0.07	0.56	0.02	7.40
[l]	–16.63	0.82	21.67	–14.25	25.43	1.36	20.20
				Fine extract			
[d]	1.17	50.86	2.73	–0.16	54.56	4.80	1.55
[h]	1.88	1.17	1.47	–0.11	0.24	0.01	1.83
[i]	0.02	0.01	0.97	0.16	53.62	4.62	0.56
[l]	–3.30	1.61	0.89	0.14	0.18	0.01	1.11
				Fine-coarse difference			
[d]	1.55	22.48	15.23	–0.78	53.84	4.67	8.79
[h]	–4.33	9.67	1.34	–2.99	43.69	3.10	0.94
[i]	0.16	0.50	2.53	0.00	0.00	0.00	3.17
[l]	6.24	7.31	0.99	4.56	37.08	2.36	0.78
$F_{0.10}$		4.06	1.86			4.54	1.96
$F_{0.05}$		6.61	2.24			7.71	2.39
$F_{0.01}$		16.26	3.06			21.20	3.37

Kolbach index

For Kolbach index, like in the case of protein content, only mean estimates of additive effects proved to be significant. Estimates of the other parameters in individual environments differed in value and sign (Table 2) and mean estimates (over environments) did not differ significantly from zero. A highly significant ($P < 0.01$) interaction of all gene effects with environments was observed, although for no gene effects this interaction could be explained by means of regression (Table 3).

Fine extract

For fine extract only mean estimates of parameter [d] proved to be significant, indicating, however, an interaction with environments. This interaction may be explained to some extent by linear regression, since coefficient of determination was 54.56%, regression coefficient was significant at the level of 0.10, and the value of the statistic for deviation from regression was not significant. Mean estimates of the other parameters were not significant, and no interaction with environments was detected (Table 3).

Fine-coarse difference

Analysis of malt fine-coarse difference indicated that additive, dominance and dominance × dominance effects estimated over environments were significant (Table 3). Interaction of additive effects with environments was very high (F-statistic for interaction amounted to 15.23, compared to $F_{0.01} = 3.06$). Analysis of regression showed a partial ($P = 0.10$) linear relationship between [d] values and environmental effects (determination coefficient 53.84%). Mean estimate of parameter [i] was insignificant and in individual environments marked differences in the values and sign of this parameter can be observed (Table 2). Interaction of additive × additive effects with environments appeared to be significant (at $P = 0.05$), but this interaction could not be explained by regression. Dominance and dominance × dominance effects proved to be highly stable, which is evidenced by small and insignificant F-statistic values for interaction of [h] and [l] parameters (Table 3).

Discussion

Results of the presented study show that the analysed traits were controlled mainly by genes with additive effects. This applies both to grain characteristics (1000-grain weight, percentage of plump kernels) and to malt characteristics (protein content, Kolbach index, extract yield, fine-coarse difference). In genetics of quantitative traits, including the analysed malt and grain characteristics, additive effects are associated with homozygous loci (MATHER, JINKS 1982), so they

may be fixed as a result of selection. It is known that the level of homozygosity increases in successive generations. Thus, the impact of additive effects in the observed genetic variation of the population grows. In the case of DH lines, which are a completely homozygous material, the observed genetic variation results from additive and additive × additive gene effects (CHOO 1981, SNAPE 1997). In the presented experiments, hybrids of early generations (F_2, F_3) were included, whose expected means depend on effects of heterozygous loci (MATHER, JINKS 1982). Such experiments enabled broadening the scope of obtained genetic data by estimation of dominance and dominance × dominance effects. Estimates of those effects in individual environments showed marked differences in their values and sign for all the analysed traits except percentage of plump kernels and fine-coarse difference. This shows that selection for these traits in early generations may prove to be ineffective, because in the successive generations values of selected breeding lines will be changing as a result of their increasing homozygosity.

The applied statistical methods enabled determining to what extent the estimates of gene effects are dependent on the environment. The results showed that additive effects had a great interaction with the environment for all the analysed traits, but only for protein content, fine extract and fine-coarse difference this interaction could be explained by linear regression. Interaction of dominance effects was much lower and only in the case of 1000-grain weight, protein content and Kolbach index it proved to be significant. It should be noted that with the exception of Kolbach index, F-statistic values for interaction of additive effects with environments were higher than those for dominance effects.

As it was mentioned earlier, in classical quantitative genetics the values of genetic parameters [d], [h], [i] and [l] are defined as the sums of corresponding gene effects over all segregating loci. In the past decade a marked progress in molecular genetics resulted in developing more precise methods for studying the inheritance of metrical traits. These methods allow to locate quantitative trait loci (QTL), to estimate the effect of individual QTL and to study QTL × environment interaction (QTL × E). TINKER et al. (1996) examined effects of QTL and QTL × E interaction for several agronomic traits in barley. They found the occurrence of primary and secondary QTL × E interactions for – among others – yield and kernel weight. Those interactions were caused mainly by changes in magnitude (not in sign) of allelic effect. HAYES et al. (1993) found QTL × E interaction effects for yield and grain protein in barley DH lines. Effects of QTL for malt extract appeared to be constant across environments. In that study only additive effects were taken into account. In our studies we could examine, besides additive, also dominance and epistatic effects, but only as a sum of the effects over all loci conditioning grain and malt traits. Interaction with environments of dominance and dominance × dominance effects, that was significant only in the case of protein content and Kolbach index, resulted from changes both in magnitude and sign

of gene effects across environments, but interaction of additive effects was caused only by changes in their magnitude.

The obtained results suggest that effects of heterozygous loci are more stable in contrasting environments than effects of homozygous loci. This may result in a lower adaptability of homozygous than heterozygous populations to varied environmental conditions, which has been reported by some authors (e.g., SOLIMAN, ALLARD 1991, SURMA 1996). Probably for this reason the studied doubled haploid lines, as fully homozygous genotypes, appeared to be unstable (KACZMAREK et al. 1999).

Acknowledgements. The study was supported by the Polish Committee for Scientific Research, Project No. 5PO6A03508.

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