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Geographic distribution of alleles at the *Ga2* locus for segregation distortion in barley

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Summary. A distorted segregation of esterase alleles at the complex loci, *Est1*, *Est2* and *Est4*, was found in an F_2 population. This distortion is typical for cross combinations between the *Ga2Ga2* and *ga2ga2* genotypes responsible for segregation distortion, since the *Ga2* locus is linked with the complex loci encoding the esterase isozymes. The segregation of esterase isozyme patterns in F_2 populations between 473 varieties of barley and a tester of *ga2ga2* genotype was examined, and the genotypes inducing segregation distortion were detected. Varieties with a *ga2ga2* genotype are widely distributed throughout the world, whereas *Ga2Ga2* varieties are found only in eastern and southern regions of Asia, from Japan to North India, with a low frequency. In varieties collected from these regions, some associations were detected between alleles at the *Ga2* locus and esterase isozyme patterns. Additionally, most of the *Ga2* barley varieties are naked and possess a *BtBtbt2bt2* genotype for a non-brittle rachis.

Key words: *Hordeum vulgare* – Segregation distortion – Esterase isozymes – Geographic distribution

Introduction

Segregation distortion is a widespread phenomenon in higher plants, but has scarcely been reported in barley. Recently, Konishi et al. (1990) found that segregation of esterase isozyme patterns, controlled by allelic combinations at the complex loci *Est1*, *Est2* and *Est4*, was distorted in hybrid populations derived from a cross between Ko A (a Japanese two-rowed variety) and Mokusekko 3 (a Chinese six-rowed landrace). In the F_2 population, the segregation frequency of the esterase isozyme pattern of Ko A was significantly higher than the normal or theoretical one (25%), while that of Mokusekko 3 was lower. This segregation distortion is not caused by pollen tube competition for fertilization as in the case of maize, but is induced by a gametic selection of pollen controlled by alleles at the *Ga2* locus which is linked with the complex loci encoding the esterase isozymes. From these results, it was concluded that one of the parents, Ko A, has a *Ga2Ga2* genotype, while the other parent, Mokusseko 3, is *ga2ga2* in genotype. Subsequently, transmission of the *Ga2* allele in Ko A was investigated together with an examination of the pedigree of Japanese two-rowed varieties, and it was established that only five of the 46 varieties tested possessed a *Ga2Ga2* genotype, while the others had a *ga2ga2* genotype (Konishi et al. 1992).

In the present study, we have examined the genotypes of barley varieties collected from different regions of the world, responsible for the segregation distortion, and discuss the geographic distribution of the *Ga2Ga2* and *ga2ga2* genotypes.

Materials and methods

A total of 473 barley varieties collected from different regions ranging from Japan to Ethiopia were crossed with a either *ga2*, *ga2* tester, Mokusekko 3 (Okayama University Accession Number, OUC 627) or Obeh (OUI 140). F_1 plants were grown in the field and harvested individually. The F_2 seedlings were grown in a growth chamber at a temperature of 18 °C with 12 h illumination per day. Crude extracts from the first leaf of 100 individually

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per F_2 population were used for starch-gel electrophoresis as previously described (Konishi et al. 1989).

When the segregation frequency of esterase patterns fit the theoretical ratio of 1:2:1 (25% P_1 pattern: 50% F_1 or heterozygous pattern: 25% P_2 pattern, i.e., that of the *ga2* tester), the variety tested was classified as having a *ga2ga2* genotype, or simply defined as belonging to the *ga2* type. If the frequency was significantly distorted, the variety was defined as belonging to the *Ga2* type: In such F_2 populations, the frequency of the P_1 patterns was significantly higher than 25%, whereas that of P_2 was lower. The frequency of heterozygous patterns (F_1) did not deviate from 50% in every population. If the F_1 pattern was not distinguishable from that of either P_1 or P_2, the distorted segregation was examined by the χ^2 test for $3(P_1+F_1):1(P_2)$ or $1(P_1):3(F_1+P_2)$, respectively.

Rachis brittleness of barley is governed by two complementary and tightly linked genes, *Bt* and *Bt2*, and varieties of barley can be classified into two groups for non-brittle rachis: *BtBtbt2bt2* and *btbtBt2Bt2* (Takahashi and Hayashi 1964). The genotype for non-brittle rachis of all the varieties used in this study was determined, based on the brittleness of the rachis of the F_1 plants from crosses with either of the *ga2* testers. This is possible because the genotypes of Mokusekko 3 and Obeh were respectively *BtBtbt2bt2* (E type) and *btbtBt2Bt2* (W type). If F_1 plants from a Mokusekko 3 cross had a brittle rachis, the genotype of the variety tested was *btbtBt2Bt2*. The F_1 plants with a non-brittle rachis indicated that the genotype of the variety was *BtBtbt2bt2*. Similarly, because the genotype of the tester Obeh was *btbtBt2Bt2*, the genotypes of the varieties tested were inferred accordingly.

Results

Figure 1 illustrates an example of the segregation frequencies of P_1 and P_2 patterns of esterase isozymes in F_2 populations derived from crosses between 30 Japanese varieties (P_1) and the *ga2* tester Obeh (P_2). The F_2 populations were easily classified into two groups: 24 F_2 populations (open circles) were normal, showing frequencies of P_1 and P_2 patterns nearly equal to 25%. This indicates that these varieties (P_1) have the same *ga2ga2* genotype as the *ga2* tester. The six other F_2 populations (solid circles), grouped at the lower right side of Fig. 1, had P_1 frequencies which were significantly higher than those of P_2, indicating that this group of varieties had a *Ga2Ga2* genotype.

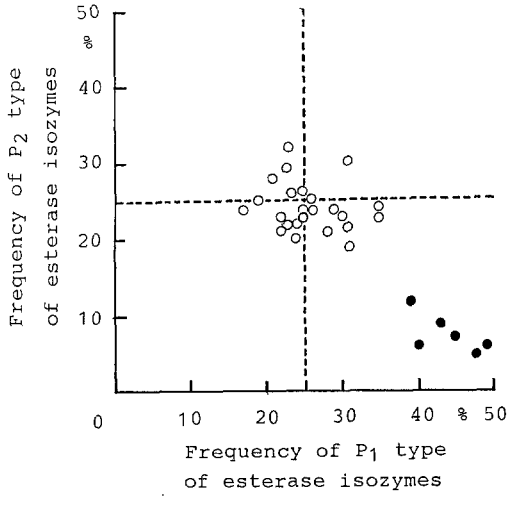

Fig. 1. Segregation frequencies of P_1 and P_2 types of esterase isozymes in F_2 populations derived from crosses between 30 Japanese varieties (P_1) and the *ga2* tester Obeh (P_2)

Table 1. Geographic distribution of barley varieties with respect of the allelic state at the *Ga2* locus

Region of origin of variety	No. of varieties with the genotype			% of *Ga2*
	Ga2Ga2	*ga2ga2*	Total	
Japan	11	76	87	12.6
Korea	7	33	40	17.5
China	10	45	55	18.2
Nepal	9	49	58	15.5
India and Pakistan	2	41	43	4.7
S. W. Asia	0	58	58	0.0
Turkey	0	57	57	0.0
Europe	0	49	49	0.0
Ethiopia	0	26	26	0.0
Total	39	434	473	8.2

The geographic distribution of barley genotypes with respect to their allelic state at the *Ga2* locus is shown in Table 1. The majority of the varieties (434 out of 473) were of the *ga2* type. Varieties of the *Ga2* type were distributed only in eastern and southern regions of Asia including Japan, Korea, China, Nepal, India and Pakistan, with a low frequency.

Table 2 shows esterase isozyme patterns present in the *Ga2* or *ga2* varieties. Ten major isozyme patterns were detected, the nomenclature in the table following that of Konishi (1988). Seven patterns (A–G) were evident in the *Ga2* varieties. They were also observed in the *ga2* varieties of the same regions, but together with I and other patterns. In comparing the *Ga2* and *ga2* varieties of East and South Asia, the I patterns of Japanese and Korean varieties were not considered, because these varieties have most likely been introduced from western regions where the *ga2* varieties with a similar esterase pattern predominate (Konishi 1988). In East and South Asia, a significant difference between the *Ga2* and *ga2* varieties was recognized in the frequencies of patterns A to G ($\chi^2=19.377$, $P=0.01$–0.001): Patterns A, C and D prevailed among the *Ga2* varieties, while patterns A, C and F were only abundant in the *ga2* genotypes. This difference suggests an association between one allelic state at the *Ga2* locus and some esterase isozymes.

When the 283 varieties collected from East and South Asia were considered, similar differences in the distribution of *Ga2* genotypes were found between

Table 2. Number of esterase isozyme patterns present in *Ga2* or *ga2* varieties of barley

Region of origin of variety	Pattern of esterase isozymes										
	A	B	C	D	E	F	G	H	I	J	Other
Est1	*Af*	*Ca*	*Ca*	*Ca*	*Pr*	*Al*	*Pr*	*Ca*	*Ca*	*Ca*	
Est2	*ne*	*ne*	*Un*	*Un*	*Fr*	*Fr*	*Fr*	*Fr*	*Fr*	*Dr*	
Est4	*Su*	*Nz*	*Su*	*Nz*	*At*	*At*	*Su*	*At*	*Su*	*Nz*	
(*Ga2*)											
Japan	7	–	4	–	–	–	–	–	–	–	–
Korea	2	–	4	1	–	–	–	–	–	–	–
China	4	1	2	3	–	–	–	–	–	–	–
Nepal	–	–	–	4	2	2	1	–	–	–	–
India and Pakistan	–	–	–	1	–	1	–	–	–	–	–
Total	13	1	10	9	2	3	1	–	–	–	–
(*ga2*)											
Japan	28	10	25	5	–	–	–	–	8	–	–
Korea	12	1	16	1	–	–	1	–	2	–	–
China	7	16	9	4	4	1	1	–	–	–	3
Nepal	–	–	–	–	9	38	1	–	–	–	1
India and Pakistan	–	–	–	6	12	18	4	–	–	–	1
Total	47	27	50	16	25	57	7	–	10	–	5
(*ga2*)											
S. W. Asia	5	1	4	–	6	17	13	2	7	–	2
Turky	–	–	–	1	–	16	24	–	14	2	–
Europe	–	–	–	1	–	2	23	3	12	3	5
Ethiopia	–	–	–	–	–	8	14	–	–	–	3

Table 3. Characterization of *Ga2* and *ga2* varieties collected in East and South Asia with respect to kernel character and the genotype for non-brittleness of the rachis

Type of variety	Kernel		Non-brittleness		Total
	Covered	Naked	Type E[a]	Type W[b]	
Ga2	11	28	36	3	39
ga2	142	102	188	56	244
Total	153	130	224	59	283

[a] Type E: *BtBtbt2bt2* genotype
[b] Type W: *btbtBt2Bt2* genotype

groups of varieties classified on kernel character or based the genotype for non-brittleness of the rachis. As shown in Table 3, the majority of *Ga2* varieties had a naked kernel and the genotype *BtBtbt2bt2* (type E), while more than 50% of the *ga2* varieties were covered barley with the genotype *btbtBt2Bt2* (type W). These differences between the *Ga2* and *ga2* varieties were significant for kernel character ($\chi^2 = 12.179$, $P < 0.001$) and for non-brittle rachis ($\chi^2 = 4.745$, $P = 0.05$–0.01), suggesting an association between alleles at the segregation distortion locus (*Ga2*) and alleles for kernel character (*n*) and non-brittle rachis (*bt* and *bt2*). The loci are, nevertheless, genetically non-linked: *Ga2* is located on the long arm of chromosome 3 (3L), *n* on 1L, while *bt* and *bt2* are closely linked on 3S.

Discussion

The genotype of a variety at the *Ga2* locus is detectable only by examining the segregation of esterase isozyme patterns in an F_2 population derived from a cross between the variety and either of the *Ga2* and *ga2* testers. The *ga2* varieties are widely distributed all over the world, while those of *Ga2* are found only with a low frequency in eastern and southern regions of Asia. This suggests that early cultivated barleys were of the *ga2* type and that a mutation produced the *Ga2* type. It is generally accepted that cultivated barley originated in the Fertile Crescent of Southwest Asia and migrated to eastern and western regions of the world. During this migration, the *Ga2* mutation may have occurred in North India, the most western margin of Asia where *Ga2* varieties have been detected. Two *Ga2* varieties in North India have covered kernels of the *BtBtbt2bt2* genotype for non-brittle rachis, but their esterase patterns are D and F, respectively. The *Ga2* varieties in Nepal are much different from those of North India

being naked barleys with a *BtBtbt2bt2* genotype for a non-brittle rachis, and with D, E, F and G esterase patterns. Moreover, the *Ga2* varieties of East Asia are also now mainly found as naked barleys of *BtBtbt2bt2* genotype but with esterase patterns ranging from A to D, and hence different from those of both North India and Nepal. These regional differences in the distribution of esterase patterns support the interpretation that some *Ga2* varieties migrated from North India to Nepal, while other *Ga2* varieties moved to East Asia.

The wide range of esterase patterns in the *Ga2* varieties may have resulted from differentiation-hybridization cycles of barley as discussed in Harlan (1966). It is noteworthy that most of the *Ga2* varieties in East and South Asia are of the naked type controlled by the *n* gene on chromosome 1, independent of the *Ga2* gene on chromosome 3. Such a gene association may have resulted from random drift or from a founder effect during migration, after a cross between *Ga2* covered and *ga2* naked barleys because no pleiotropic effects of the *n* gene on any agronomic characters have been found (Takahashi et al. 1961; Witcombe and Murphy 1986).

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