Identification of Quantitative Trait Loci (QTLs) Controlling Heading Time in the Population Generated from a Cross between Oriental and Occidental Barley Cultivars (*Hordeum vulgare* L.)

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The present study was carried out to identify QTLs controlling heading time of barley. A total of 89 recombinant inbred lines (RILs) generated from a cross between the Oriental-type winter cultivar 'Azumamugi' and the Occidental-type spring cultivar 'Kanto Nakate Gold' were examined. Two field experiments consisting of one spring sowing and one autumn sowing and a greenhouse experiment under 24 h illumination were conducted. Two genes for the spring habit and five QTLs controlling heading time were identified. The two genes for the spring habit, *sgh1* and *Sgh2* were located on chromosomes 4HL and 5HL, respectively; four QTLs were mapped close to the heading time genes identified in the previous studies on chromosomes 1HL, 2HS, 2HL and 7HS; and one was a new QTL detected on chromosome 7H.

Key Words: *Hordeum vulgare*, recombinant inbred lines, spring habit gene, earliness, composite interval mapping.

Introduction

Heading time is an important trait for the adaptation of crops to variable environments. The mode of inheritance of this trait in barley (*Hordeum vulgare* L.) is complex and assumed to involve numerous genetic factors that interact with environmental conditions (Kjaer *et al.* 1995). Heading time of barley is controlled by three kinds of genetic factors; spring growth habit (no vernalization requirement), photoperiodic response, and earliness in a narrow sense (Takahashi and Yasuda 1970). Three epistatic genes, *sgh1*, *Sgh2* and *Sgh3*, located on chromosomes 4H, 5H and 1H control the spring growth habit of barley (Takahashi and Yasuda 1956, 1970). Laurie *et al.* (1995) identified five major loci and eight quantitative trait loci (QTLs) affecting heading time under controlled environmental conditions. Several QTLs have been identified for heading time under field conditions (Hayes *et al.* 1993, Laurie *et al.* 1995, Tinker *et al.*

1996, Tohno-oka *et al.* 2000, Marquez-Cedillo *et al.* 2001). However, Oriental cultivars had not been examined in these studies. Since Oriental and Occidental cultivars are genetically divergent (Takahashi 1955), they are likely to harbor specific heading time genes. We developed a linkage map using recombinant inbred lines (RILs) from a cross between the winter cultivar 'Azumamugi' and spring cultivar 'Kanto Nakate Gold' (Mano *et al.* 2001). Since Azumamugi is a typical Japanese six-rowed cultivar, bred from a cross between Japanese barley landraces, this cultivar belongs to the Oriental type. Kanto Nakate Gold is a Japanese two-rowed cultivar, but its genetic background belongs to the Occidental type. Therefore, the RILs developed from the two parental lines should be suitable for the detection of the genes controlling heading time. Since RILs can be multiplied, a large number of analyses can be carried out under different environmental conditions. The objective of the present study was to identify QTLs for heading time in a population of RILs from a cross between Oriental and Occidental type cultivars.

Materials and Methods

Azumamugi is a winter type (*Sgh1/sgh2/sgh3*) six-rowed cultivar and Kanto Nakate Gold is a spring type (*sgh1/Sgh2/sgh3*) two-rowed cultivar (Takahashi *et al.* 1983, Komatsuda *et al.* 1993). RILs (F₁₂) generated from the cross between Azumamugi and Kanto Nakate Gold have been developed by the single seed descent method. For the determination of the genotype of RILs for *Sgh2* - *sgh2*, a single plant of each 89 RILs was pollinated by Hayakiso 2 (*Sgh1/sgh2/sgh3*) to obtain 89 F₁ families.

Greenhouse experiments were designed to identify QTLs for earliness in a narrow sense. RILs and parental cultivars were grown in a randomized complete block design of two plants for each plot in two separate greenhouses (block) under continuous illumination at a temperature maintained between 15°C and 22°C. Heading time was recorded for each plant as the number of days to awn emergence. F₁ families of RIL × Hayakiso 2 were grown in greenhouses with the same experimental design to test the *Sgh2-sgh2* alleles of the RILs. A spring sowing field experiment was conducted to test the spring growth habit. In the spring sowing experiment, RILs were grown from April 9 to July 19. During that time, day-length ranged from 12 h 54 min to 14 h 18 min and mean temperature was in the range of 8.5–30.1°C (18.8°C

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on the average). For the autumn sowing experiment, RILs were sown in separate fields in October 2002. Days to heading of RILs were scored for both spring-sown and autumn-sown materials. Photoperiodic response was not tested in this study.

For the QTL analysis we used the base map with 100 markers (Mano and Komatsuda 2002) to obtain a density of 5 to 10 cM intervals without clustering markers. Map distances were estimated by using Kosambi's map function (Kosambi 1944). Composite interval mapping (CIM) was performed using the computer program QTL Cartographer version 1.14 (Basten *et al.* 2000). A LOD score threshold of 3.0 was used to identify the genomic regions containing putative loci associated with heading time.

Results

Mapping of the *Sgh2* locus

Figure 1 shows the frequency distribution of days to heading in different populations or under different growth conditions. Figure 1A shows the data of the F₁ families of RILs×Hayakiso 2 averaged over two replications (rooms) in a greenhouse under 24 h illumination. The histogram revealed the presence of two distinct modes, suggesting the contribution of a single major gene to heading time. As for the controls, parental cultivars Azumamugi, Hayakiso 2 and

Kanto Nakate Gold, heading occurred at 139, 124 and 47 days after sowing respectively.

We classified 45 F₁ families of the earlier mode (50 to 90 days) in to the spring type with *Sgh2sgh2*, and 44 F₁ families of the later mode (100 to 180 days) into the winter type with *sgh2sgh2* (Table 1). The segregation (45 : 44) fitted to the expected ratio of 1 : 1 ($\chi^2=0.011$, $P=0.92$). The *Sgh2* locus was mapped on the linkage group of chromosome 5H and was located between the *e07m25.3* and *e12m19.9* markers (Fig. 2).

Mapping of the *sgh1* locus

The *sgh1* locus was mapped by combining the data listed in Figure 1A and Figure 1C. Figure 1C shows the frequency distribution of days to heading of 89 RILs in the spring sowing field experiment. The data clearly enabled to classify the RILs into two groups, heading between 45 and 65 days for 69 lines (spring type), while in the remaining 20 lines vegetative growth continued until 102 days without heading (winter type). In Kanto Nakate Gold, awn emergence occurred at 57 days, while in Azumamugi and Hayakiso 2, awn emergence failed in the spring sowing experiment. The segregation ratio of 69 for the spring type: 20 for the winter type fitted to the 3 : 1 ratio expected by 2-factor segregation by *sgh1* and *Sgh2* in the RILs ($\chi^2=0.303$, $P=0.58$). When the RILs belonged to the *sgh2* type, alleles at the *sgh1* locus

Fig. 1. Frequency distribution of days to heading of A) F₁ families of RILs×Hayakiso 2 under 24 h illumination, B) RILs in a green house under 24 h illumination, C) RILs in the field spring sowing. Ear emergence failed in 20 lines shown at 100–105 interval, and D) RILs in the field autumn sowing.

could be determined for the RILs (Table 1). Thus 44 RILs segregated into 24 for the spring type (*sgh1*): 20 for the winter type (*Sgh1*), and the segregation fitted to the 1 : 1 ratio ($\chi^2=0.364$, $P=0.55$). The *sgh1* locus was mapped between the *e04m32.8* and *e12m19.8* markers on chromosome 4H (Fig. 2).

QTLs detected under 24 h illumination

Figure 1B shows the frequency distribution of the days to heading of the RILs averaged over two rooms in a greenhouse under 24 h illumination. The RILs continuously reached heading by 180 days except for the RILs #28 and #67 which remained at the vegetative stage until 140 days when they died. Therefore, we could not determine the heading time of these two lines and we analyzed the data of the remaining 87 RILs. We detected two QTLs on chromosomes 1H and 4H (Table 2). One QTL (LOD score=8.9) on chro-

mosome 1H explained 22% of the total phenotypic variance and in the lines with the Azumamugi allele, heading occurred later (15.7 days). The other QTL (LOD score=9.9) was flanked by the *e04m32.8* and *e12m19.8* markers on chromosome 4H. The QTL accounted for 25% of the total phenotypic variance and in the lines with the Azumamugi allele, heading occurred later (17.0 days).

To attenuate the effects associated with the growth habit genes, the RILs were separated into winter and spring sub-populations, based on the criteria obtained in the separate experiments (Fig. 1C) and 69 lines were used for further CIM. Three QTLs were detected on chromosomes 1H, 4H and 5H in the spring sub-population (Table 2). Among the three QTLs, two were located at the same position on chromosomes 1H and 4H as that of the QTLs detected in the full population; the other QTL was mapped at the same interval including the *Sgh2* locus on chromosome 5H. However,

Table 1. Segregation for growth habit in F_1 families of RILs $\times$ Hayakiso 2 (*Sgh1/sgh2*) and RILs of Azumamugi (*Sgh1/sgh2*) $\times$ Kanto Nakate Gold (*sgh1/Sgh2*)

Populations	Genotype of RILs (gametes)			
	<i>sgh1/Sgh2</i>	<i>Sgh1/Sgh2</i>	<i>sgh1/sgh2</i>	<i>Sgh1/sgh2</i>
RILs $\times$ Hayakiso 2 (F_1) ¹⁾	spring	spring	winter	winter
RILs (spring sown) ^{2,3)}	spring	spring	spring	winter
	45		24	20

¹⁾ χ^2 (1 spring : 1 winter) = 0.011, $P=0.92$.

²⁾ χ^2 (3 spring : 1 winter) = 0.303, $P=0.58$.

³⁾ χ^2 (1 *sgh1/sgh2* : 1 *Sgh1/sgh2*) = 0.364, $P=0.55$.

Table 2. QTLs for heading time detected by composite interval mapping in RILs derived from a cross between Azumamugi and Kanto Nakate Gold

Environment	Chromosome	Flanking markers	Position of peak (cM)	LOD score	AE ¹⁾	R ²
Greenhouse ²⁾						
-Full population						
	1HL	<i>ABC261-ABG055</i>	145.0	8.9	15.7	0.22
	4HL	<i>e04m32.8-e12m19.8</i>	85.4	9.9	17.0	0.25
-Spring sub-population ³⁾						
	1HL	<i>ABC261-ABG055</i>	145.0	26.3	14.4	0.58
	4HL	<i>e04m32.8-e12m19.8</i>	85.4	4.2	4.7	0.04
	5HL	<i>e07m25.3-e12m19.9</i>	112.1	6.5	-5.4	0.08
Field spring sowing						
-Spring sub-population ³⁾						
	2HS	<i>ABG602-e13m23.6</i>	43.3	4.6	-1.7	0.13
	2HL	<i>MWG882-e15m31.1</i>	103.2	4.2	-1.6	0.14
	5HL	<i>e07m25.3-e12m19.9</i>	110.1	6.7	-2.1	0.23
	7HS	<i>ABG616-e15m31.6</i>	34.0	3.5	-1.5	0.11
	7H	<i>e11m17.10-e12m19.10</i>	91.5	4.8	1.8	0.16
Field autumn sowing						
	1HL	<i>ABC261-ABG055</i>	145.0	4.9	2.5	0.16
	2HS	<i>ABG602-e13m23.6</i>	47.3	4.2	-2.4	0.14
	2HL	<i>e15m31.1-e11m19.3</i>	105.7	3.2	-1.8	0.08
	5HL	<i>e07m25.3-e12m19.9</i>	108.1	11.1	-4.1	0.43

¹⁾ Additive effect of Azumamugi allele.

²⁾ Under 24 h illumination at a temperature maintained between 15°C and 22°C.

³⁾ Consisted of 69 lines with spring growth habit in the field spring sowing.

since in the lines with the Azumamugi allele heading occurred earlier, gene action was opposite to that of the *Sgh2* locus.

QTLs detected in the spring sowing

The spring sub-population consisting of 69 RILs (Fig. 1C) was subjected to composite interval mapping. Two QTLs were detected on chromosome 2H, one on chromosome 5H and two on chromosome 7H (Table 2). The two QTLs on chromosome 7H were detected only under the spring sowing conditions. The QTL on chromosome 5H was mapped at the same interval including the *Sgh2* locus, but in the lines with the Azumamugi allele heading again occurred earlier.

QTLs detected in the autumn sowing

Figure 1D shows the frequency distribution of the days to heading of the RILs in the autumn sowing. The RILs continuously reached heading by 196 days. We detected four QTLs on chromosomes 1H, 2H and 5H (Table 2). The QTL detected on chromosome 5H (LOD score=11.1) was flanked by the *e07m25.3* and *e12m19.9* markers. The QTL accounted for 43% of the total phenotypic variance and in the lines with the Azumamugi allele heading occurred earlier (4.1 days). One QTL (LOD score=4.9) on chromosome 1H ex-

plained 16% of the total phenotypic variance and in the lines with the Azumamugi allele, heading occurred later (2.5 days). The position of this QTL was the same as that of the QTL detected in the spring sub-population under 24 h illumination. The other two QTLs were detected on chromosome 2H (LOD scores=4.2 and 3.2) and the position of these two QTLs was the same as that of the QTLs detected under the spring sowing conditions.

Discussion

Chromosome 1H

Ppd-H2 is a photoperiod-sensitive gene for heading time, which had been mapped on chromosome 1HL, the position being 20.6 cM proximal to that of the *cMWG733* marker (Laurie *et al.* 1995). The *cMWG733* marker was located approximately at a position 10 cM proximal to that of the *ABC261* marker on the barley consensus map in GrainGenes (<http://www.graingenes.org>) and the *ABC261* marker was located at a position 12.2 cM proximal to that of the QTL detected in this study. Because the 90% confidence interval (LOD score decrease of 1.0 on either side of the maximum value (Lander and Botstein 1989)) of our QTL did not include the *ABC261* or *cMWG733* markers, the QTL was

Fig. 2. QTLs for heading time identified in the present study. Recombinant inbred lines were obtained from the cross between Azumamugi and Kanto Nakate Gold. Distances between markers are given in cM. Position of each QTL is denoted by an open arrowhead (Azumamugi allele induces later heading) or a closed arrowhead (Azumamugi allele induces earlier heading). Ninety percent confidence intervals of QTLs are denoted by boxes: Open boxes, greenhouse under 24 h illumination; hatched boxes, field spring sowing; closed boxes, field autumn sowing. Two genes for spring growth habit (*sgl1* and *Sgh2*) were mapped on this linkage map. Five heading time genes reported before this study were superimposed on the genetic map (*Ppd-H2*, *eam8*, *eps2S*, *eps7S* and unnamed QTL).

considered to be different from the *Ppd-H2* locus. Our QTL was detected in the 24 h photoperiod experiments, whereas *Ppd-H2* was detected under a short day (less than 10 h). This fact also indicates the difference between *Ppd-H2* and the QTL detected in this study. The QTL detected in our study may be identical with that identified by Tohno-oka *et al.* (2000). They identified a QTL for heading date under the autumn sowing conditions on chromosome 1HL between the *ABC322B* and *ABC261* markers using Steptoe $\times$ Morex doubled haploid lines. The *ABC261* marker was common for the two QTLs, which are closely linked on the barley consensus map. Also Marquez-Cedillo *et al.* (2001) identified a QTL for heading date in the spring sowing on chromosome 1HL using Harrington $\times$ Morex doubled haploid lines. The *ABC159c* and *MWG912* markers flanked the QTL. The QTL detected in our study could be identical with this QTL, because the *MWG912* and *ABC261* markers were closely linked on the barley consensus map by a distance of 5 cM. This QTL could be identical with the *eam8* locus (early maturity 8) identified by Takahashi and Yasuda (1970) (T. Tohno-oka, personal communication), and the position of the *eam8* locus was approximately 14 cM distal to that of the *ABC261* marker on chromosome 1HL (Franckowiak *et al.* 1997). Since the *eam8* locus is present in Japanese two-rowed barley (ex. Kinai 5 and Kagoshima Gold), it is possible that Kanto Nakate Gold (two-rowed) harbors an allele, which confers earliness under a 24h photoperiod (earliness in a narrow sense). Ishii *et al.* (2002) detected another QTL flanked by the *ABC307A* and *cMWG706A* markers on chromosome 1H. The QTL was detected under a 12 and 12.5 h photoperiod but not under longer photoperiod conditions, and the QTL was mapped at a position 35 cM proximal to that of the *eam8* locus. Therefore this QTL could be identical with the *Ppd-H2* locus.

Chromosome 2H

We detected a QTL on chromosome 2H, that was closely linked to the *ABG602* marker. The QTL was detected in both spring and autumn sowing experiments in the RILs grown in the field (Table 2), indicating that the QTL is photoperiod-insensitive. The 90% confidence interval of this QTL spanned about 15 cM including the *ABG602* marker. Laurie *et al.* (1995) detected the *eps2S* (earliness *per se*) gene at the 21.2 cM interval between the *Xpsb24* and *Xpsr571* markers on chromosome 2HS. Because the positions of the *Xpsr571* and *ABG602* markers were 31.4 cM and 37 cM, respectively, proximal to that of the *MWG865* marker (0.6 cM distal to the *vrsl* locus, Mano *et al.* 2001), the confidence interval of our QTL included the *eps2S* locus. Therefore, it remains to be determined whether the two loci are identical or closely linked.

Another QTL on the long arm of chromosome 2H was mapped at a location 9.9 cM distal to that of the *MWG882* marker, where the 90% confidence interval of the QTL did not include the *MWG882* marker. Since the position of the *MWG882* marker is distal to that of the *MWG865* marker,

the 90% confidence interval of the *eps2S* locus was proximal to the *MWG865* marker without including the *MWG865* marker (Laurie *et al.* 1995). Therefore the *eps2S* locus and the second QTL detected on chromosome 2HL were considered to be different. The QTL was detected in the spring and autumn sowing field experiments. The QTL was detected in the vicinity of the QTLs detected by Hayes *et al.* (1993) and Tinker *et al.* (1996) in the spring sowing experiments.

Chromosome 4H

A recessive spring growth habit gene, *sgh1*, was identified by Takahashi and Yasuda (1956) and mapped on chromosome 4H (Takahashi *et al.* 1957, Laurie *et al.* 1995). The spring habit gene detected in this study on chromosome 4HL may correspond to *sgh1*. A major QTL controlling heading time was mapped close to the *sgh1* locus, and the 90% confidence intervals of the QTL included the *sgh1* locus. It remains to be determined whether the two loci are identical or closely linked. We consider that the QTL is identical with the *sgh1* locus, because the position of the two loci was very close as they were mapped in the same population, and the recessive *sgh1* allele induces earlier heading in general.

Chromosome 5H

Sgh2 is a dominant spring growth habit gene located on chromosome 5HL (Takahashi and Yasuda 1956) and Kanto Nakate Gold harbors the *Sgh2* gene, which induces earlier heading under non-vernalized conditions (Komatsuda *et al.* 1993). In the present study, one major QTL was mapped in the *Sgh2* region under all three conditions, and in the lines with the Kanto Nakate Gold allele (*Sgh2*) heading occurred consistently later under the three cultivation conditions (Table 2). This result was in agreement with the findings of Yasuda and Okinaga (1977) who showed that the *Sgh2* genes induced an earlier or later heading time, depending on the genetic background, although each effect was constant, regardless of the winter and spring sowing conditions. The detected QTLs were close to each other (108.1 to 112.1 cM) and very close to the *Sgh2* locus located at 107.7 cM (Fig. 2). In particular, the QTLs in the winter and spring sowing experiments displayed a narrow confidence interval that included the *Sgh2* locus. Based on the map position and function, the QTL detected on chromosome 5H is presumably identical with the *Sgh2* locus.

Chromosome 7H

Laurie *et al.* (1995) mapped the *eps7S* gene on chromosome 7HS. The 90% confidence interval of the *eps7S* locus covered 50 cM including the interval between the *XBCD129* and *XMWG89/Xpsr604* markers. We also detected a QTL on chromosome 7HS, and the 90% confidence intervals of the *eps7S* locus and the QTL we detected overlapped (Fig. 2 and barley consensus map). In addition, our QTL and the *eps7S* locus, which were detected in the spring sowing, were not detected in the autumn sowing where RILs with the Azumamugi allele were consistently associated with earlier

heading. These results suggested that the QTL might be identical with the *eps7S* locus. However, since the confidence interval of the *eps7S* locus was as large as 50 cM (Laurie *et al.* 1995), the *eps7S* locus and the QTL may not be identical.

We detected another QTL in the proximal region of chromosome 7H. The position of the QTL was 43 cM proximal to that of the *ABG608* marker and the 90% confidence interval did not include the *ABG608* marker. The *ABG608* marker was located close to the *MWG539* marker on the barley consensus map (5 cM). Laurie *et al.* (1995) indicated that the location of the *eps7L* locus was more than 50 cM distal to that of the *MWG539* marker and the 90% confidence interval of the *eps7L* locus did not include the *MWG539* marker. Therefore, it is considered that the QTL detected in this study is a new locus and is not identical with the *eps7L* locus.

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Literature Cited

- Basten, C.J., B.S. Weir and Z.B. Zeng (2000) QTL cartographer version 1.14. Department of statistics, North Carolina State University, Raleigh, North Carolina, USA.
- Franckowiak, J.D., U. Lundqvist, T. Konishi and L.W. Gallagher (1997) Revised linkage maps for morphological markers in barley, *Hordeum vulgare*. *Barley Genet. Newsl.* 26: 213-215.
- Hayes, P.M., B.H. Liu, S.J. Knapp, F. Chen, B. Jones, T. Blake, J. Franckowiak, D. Rasmusson, M. Sorrells, S.E. Ullrich, D. Wesenberg and A. Kleinhofs (1993) Quantitative trait locus effects and environmental interaction in a sample of North American barley germplasm. *Theor. Appl. Genet.* 87: 392-401.
- Ishii, M., T. Tohno-oka and K. Takeda (2002) QTL analysis of earliness in barley under various photoperiodic conditions. *Breed. Res.* 4 (Suppl.1): 219 (in Japanese).
- Kjaer, B., J. Jensen and H. Giese (1995) Quantitative trait loci for heading date and straw characters in barley. *Genome* 38: 1098-1104.
- Komatsuda, T., T. Annaka and S. Oka (1993) Genetic mapping of a quantitative trait locus (QTL) that enhances the shoot differentiation rate in *Hordeum vulgare* L. *Theor. Appl. Genet.* 86: 713-720.
- Kosambi, D.D. (1944) The estimation of map distances from recombination values. *Ann. Eugen.* 12: 172-175.
- Lander, E.S. and D. Botstein (1989) Mapping Mendelian factors underlying quantitative traits using RFLP linkage maps. *Genetics* 121: 185-199.
- Laurie, D.A., N. Pratchett, J.H. Bezzant and J.W. Snape (1995) RFLP mapping of five major genes and eight quantitative trait loci controlling flowering time in a winter $\times$ spring barley (*Hordeum vulgare* L.) cross. *Genome* 38: 575-585.
- Mano, Y., S. Kawasaki, F. Takaiwa and T. Komatsuda (2001) Construction of a genetic map of barley (*Hordeum vulgare* L.) cross 'Azumamugi' $\times$ 'Kanto Nakate Gold' using a simple and efficient amplified fragment-length polymorphism system. *Genome* 44: 284-292.
- Mano, Y. and T. Komatsuda (2002) Identification of QTLs controlling tissue-culture traits in barley (*Hordeum vulgare* L.). *Theor. Appl. Genet.* 105: 708-715.
- Marquez-Cedillo, L.A., P.M. Hayes, A. Kleinhofs, W.G. Legge, B.G. Rossnagel, K. Sato, S.E. Ullrich, D.M. Wesenberg and the North American Barley Genome Mapping Project (2001) QTL analysis of agronomic traits in barley based on the doubled haploid progeny of two elite North American varieties representing different germplasm groups. *Theor. Appl. Genet.* 103: 625-637.
- Takahashi, R. (1955) The origin and evolution of cultivated barley. *Advances in Genetics* 7: 227-266. Academic Press, New York.
- Takahashi, R. and S. Yasuda (1956) Genetic studies of spring and winter habit of growth in barley. *Ber. Ohara Inst. landwirtsch. Biol. Okayama Univ.* 10: 245-308.
- Takahashi, R., J. Hayashi and S. Yasuda (1958) Four genes in linkage which are inherited independently of the markers in the known seven linkage groups in barley. *Nogaku Kenkyu* 45: 49-58 (in Japanese).
- Takahashi, R. and S. Yasuda (1970) Genetics of earliness and growth habit in barley. *Barley Genetics* II: 388-408.
- Takahashi, R., S. Yasuda, J. Hayashi, T. Fukuyama, I. Moriya and T. Konishi (1983) Catalogue of barley germplasm preserved in Okayama University. Okayama University, Kurashiki, Japan.
- Tinker, N.A., D.E. Mather, B.G. Rossnagel, K.J. Kasha, A. Kleinhofs *et al.* (1996) Regions of the genome that affect agronomic performance in two-row barley. *Crop Sci.* 36: 1053-1062.
- Tohno-oka, T., M. Ishii, R. Kanatani, H. Takahashi and K. Takeda (2000) Genetic analysis of photoperiodic response of barley in different day-length conditions. *Barley Genetics* 8, Proceeding of the 8th International Barley Genetics Symposium, Adelaide, 239-241.
- Yasuda, S. and Y. Okinaga (1977) Physiology and genetics of ear emergence in barley and wheat. X. Effects of four genes for spring habit on yield and yield components in barley. *Nogaku Kenkyu* 56: 143-154 (in Japanese).