Genetic Analysis of Semidwarfism of the *japonica* Rice Cultivar Kinuhikari

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The origin of the semidwarfing gene(s) in the *japonica* rice cultivar Kinuhikari and its location on chromosome was studied. A quantitative trait locus (QTL) analysis using restriction fragment length polymorphism (RFLP) markers was conducted in the F₂ from the cross Kinuhikari / Koshihikari and B₁F₁ from the cross Koshihikari / Kinuhikari // Koshihikari. Seven RFLP loci showed a polymorphism between Kinuhikari and Koshihikari. A strong QTL reducing culm length when the genotype was of the Kinuhikari-type (homozygous) was detected close to the RFLP loci C86 and C385 on chromosome 1. This QTL explained 74% of the total variation of culm length in the F₂ population. The analysis of polymorphism for the C86 and C385 loci among Kinuhikari and all the cultivars used to breed it showed that the region containing the semidwarfing QTL on chromosome 1 in Kinuhikari was derived from the *indica* rice cultivar IR8, which is known to harbour a semidwarfing gene *sd1* between these two RFLP loci. These results indicate that the semidwarfing gene in this chromosome region in Kinuhikari is *sd1*. An allelism test using QTL analysis showed that the *sd1* in Kinuhikari was different from a semidwarfing gene *d49* in Reimei, which had been assumed to be identical with *sd1*. Another QTL was found near the RFLP locus G1073 on chromosome 8. This QTL led to a longer culm when the allelic constitution corresponded to the Kinuhikari-type, and explained about 18% of the total variation of culm length. In the F₂ population from the crosses Kinuhikari / Koshihikari and Kinuhikari / Reimei, the homozygous plants for the *sd1* locus showed a transgressive segregation for short culm. The combined effect of the two QTLs could not completely explain the distinct transgressive segregation. It was suggested that other genes modify the effect of *sd1* (a recessive allele at the QTL on chromosome 1) in Kinuhikari.

Key Words: *Oryza sativa*, QTL analysis, RFLP marker, Kinuhikari, semidwarfing gene, *sd1*.

Introduction

Lodging resistance is one of the most important objec-

tives for the breeding and cultivation of rice (*Oryza sativa* L.). Many semidwarf cultivars with a strong lodging resistance have been developed throughout the world since the 1960s (Okada *et al.* 1967, Hargrove *et al.* 1980, Sato 1982, Kikuchi and Ikehashi 1983). Several semidwarf cultivars, Dee-geo-woo-gen, Taichung native 1, I-geo-tze, Calrose76, Jikkoku and Reimei, have been intensively used as genetic resources of semidwarfism. However, conventional genetic analyses revealed that in all the cultivars semidwarfism was controlled by an allele at the *sd1* locus (Foster and Rutger 1978, MacKill and Rutger 1979, Kikuchi and Ikehashi 1983). Linkage analysis using morphological markers showed that *sd1* was located on chromosome 1 (Suh and Heu 1978).

Genetic analysis of culm length is difficult in that it is a quantitative trait which is influenced by other traits such as heading date (Aquino and Jennings 1966). Development of genetic analysis methods using molecular markers such as restriction fragment length polymorphism (RFLP) and randomly amplified polymorphic DNA (RAPD) (McCouch *et al.* 1988, Saito *et al.* 1991, Kurata *et al.* 1994, Harushima *et al.* 1998), has enhanced the efficiency of analyzing the phenotypes controlled by quantitative trait locus (QTL) (reviewed in Yano and Sasaki 1997). Also for the genetic analysis of culm length, these methods are useful and detailed maps of the *sd1* locus were constructed (Ogi *et al.* 1993, Yu *et al.* 1992, Cho *et al.* 1994, Maeda *et al.* 1997).

The *japonica* rice cultivar Kinuhikari was developed at the Hokuriku National Agricultural Experiment Station, Japan (Koga *et al.* 1989). This cultivar exhibits a strong lodging resistance because the culm is more than 10 cm shorter than that of its ancestral *japonica* cultivar Koshihikari, which is cultivated most widely in Japan due to its superior eating quality (Koga *et al.* 1989). Kinuhikari also shows a high eating quality equivalent to that of Koshihikari. Because of these favorable traits in addition to its high adaptability to environmental conditions, the cultivation of Kinuhikari has been widely disseminated across Japan (Uehara *et al.* 1999). Moreover, this cultivar has been extensively used as a cross parent in practical rice breeding to introduce its favorable traits (Uehara *et al.* 1995, Uehara *et al.* 1998). Despite the importance of its characterization and identification, genetic analysis of the semidwarfism of Kinuhikari has not yet been conducted.

Kinuhikari was derived from a cross between the plants obtained by the crossing of Shu2800 / Hokuriku100 and the *japonica* rice cultivar Nagoyutaka (Koga *et al.*

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1989). Shu2800 is a semidwarf strain bred after two back-crossings of Koshihikari to F_1 plants of IR8 / Fujiminori (Koga *et al.* 1989). IR8 is a semidwarf *indica* cultivar which has played an important role in "the Green Revolution", and inherited a semidwarfing gene *sd1* from the *indica* rice cultivar Dee-geo-woo-gen (Hargrove *et al.* 1980). Hokuriku 100, a γ -ray-induced semidwarf mutant strain of Koshihikari (Samoto and Kanai 1975), harbours a semidwarfing gene *d60* on chromosome 7 (Tomita *et al.* 1989, Tanisaka *et al.* 1990), but Tomita *et al.* (1997) reported that Kinuhikari did not carry *d60*. Thus, the semidwarfing gene in Kinuhikari is probably derived from IR8.

In the present study, we first performed a genetic analysis with RFLP markers to identify the locus of the semidwarfing gene(s) in Kinuhikari in the F_2 population from the cross Kinuhikari / Koshihikari and the B_1F_1 population from the cross Koshihikari / Kinuhikari // Koshihikari. Subsequently, we attempted to identify the donor cultivar of the semidwarfing gene to Kinuhikari. An allelism test was also conducted between Kinuhikari and Reimei that carries *d49* which is assumed to be an allele at the *sd1* locus (Kikuchi and Ikehashi 1983).

Materials and Methods

Plant materials

One hundred and one F_2 plants from the cross Kinuhikari / Koshihikari and their cross parents (10 plants in each parent) were grown in a paddy field at the Hokuriku National Agricultural Experiment Station, Japan. Forty-nine B_1F_1 plants from the cross Koshihikari / Kinuhikari // Koshihikari, and their cross parents (20 plants in each parent) were grown at the Niigata Prefecture Agricultural Research Institute, Japan. These F_2 and B_1F_1 plants were subjected to a conventional genetic analysis and a linkage analysis for culm length using RFLP loci. In addition to Kinuhikari and Koshihikari, three cultivars, IR8, Fujiminori, and Nagoyutaka, and a strain Hokuriku100, all of which were used as cross parents to breed Kinuhikari (Koga *et al.* 1989), were grown to study the origin of the semidwarfing gene(s) in Kinuhikari through RFLP analysis. To determine whether the semidwarfing gene in Kinuhikari was identical with that of Reimei, 46 F_2 plants from the cross Kinuhikari / Reimei were grown together with their cross parents (10 plants in each parent) at the Hokuriku National Agricultural Experiment Station. The culm length of the tallest tiller in each plant was measured after maturity.

DNA analysis

For the two cross combinations, Kinuhikari / Koshihikari and Kinuhikari / Reimei, the leaves of the F_3 seedlings were bulked and were used to extract DNA, whereas for Koshihikari / Kinuhikari // Koshihikari, growing leaves of B_1F_1 plants were used.

Total genomic DNAs were extracted by the CTAB method (Murray and Thompson 1980), and were digested

with seven restriction enzymes, *Bam*HI, *Dra*I, *Eco*RI, *Eco*RV, *Hind*III and *Pvu*II. After electrophoresis with 0.8% agarose gel, the DNAs were blotted onto a positively charged nylon membrane (Roche), and were subjected to Southern hybridization using RFLP probes labeled with ECL non-R1 labeling system (Amersham Pharmacia Biotech).

The Rice Genome Research Program (RGP), a joint project of the National Institute of Agrobiological Resources and the Institute of the Society for Techno-innovation of Agriculture, Forestry and Fisheries, Japan, reported on its website (<http://www.staff.or.jp/>) that 35 RFLP loci showed a polymorphism between Kinuhikari and Koshihikari. Based on the information from this site and other sources (see Results), we selected seven RFLP loci, namely *C86*, *C385* and *R1928* on chromosome 1, *C513* on chromosome 4, *G1073* on chromosome 8, *G1454* on chromosome 9 and *G1465* on chromosome 11, as linkage markers of the genes affecting culm length.

QTL analysis

A QTL analysis of culm length was conducted by comparing the culm length between the two genotypes for an RFLP locus, Kinuhikari-type and Koshihikari-type homozygote, in the F_2 population from the cross Kinuhikari / Koshihikari, and heterozygote and Koshihikari-type homozygote in the B_1F_1 population from the cross Koshihikari / Kinuhikari // Koshihikari. If a QTL controlling culm length was to be present near the RFLP locus, there should be a significant difference in the *t*-test between the two genotypes. The contribution rate (R^2) of the RFLP locus to the total variation of culm length was also calculated. The linkage relationships between the RFLP loci were estimated using the computer program MAPMAKER / EXE ver. 3.0 (Lincoln *et al.* 1992). The interaction between the RFLP loci linked to the QTLs controlling culm length was investigated by calculating the correlation coefficient using the computer program SAS (SAS Institute).

Results

Conventional genetic analysis

The F_2 population from the cross Kinuhikari / Koshihikari showed a bimodal distribution with many distinct short-culm transgressive segregants (Fig.1a). The ratio of short culm : long culm fitted to the 1 : 3 segregation expected for one gene locus ($\chi^2=0.0033$, $P>0.95$). Since the mean culm length of Kinuhikari and Koshihikari was 79.6 and 89.1 cm, respectively, these results suggest that Kinuhikari carries a semidwarfing gene that markedly reduces the culm length. However, the appearance of distinct short-culm transgressive segregants suggested that Koshihikari carries some genetic factor(s) enhancing the effect of the semidwarfing gene in Kinuhikari. In the B_1F_1 from the cross Koshihikari / Kinuhikari // Koshihikari, transgressive segregants did not appear, and the ratio of heterozygous plants:

Koshihikari-type plants fitted to the 1:1 ratio (Fig.1f and g). In addition, all the heterozygous plants exhibited a longer culm length than the mean culm length of Kinuhikari (Fig.1e and f). These results indicate that Kinuhikari carries an incomplete recessive semidwarfing gene.

QTL analysis of culm length

For QTL analysis, we checked 10 of the 35 RFLP markers displayed on the RGP website and confirmed that six showed a polymorphism between Kinuhikari and Koshihikari. At the Niigata Prefecture Agricultural Research Institute, we also observed polymorphism at the RFLP locus C385 on chromosome 1 (Table 1, Fig.2), which was not listed on the website. These seven markers were used to analyze the semidwarfing gene(s) in Kinuhikari (see Materials and Methods, and Table 1).

The QTL analysis of culm length was conducted in the

F₂ population from the cross Kinuhikari / Koshihikari using the above seven markers (Table 1). Highly significant differences in the culm length were observed between two homozygous groups, Kinuhikari-type and Koshihikari-type, for the C86 and C385 loci on chromosome 1 ($P=2.4 \times 10^{-15}$, $P=1.1 \times 10^{-16}$, respectively). Since these two loci were closely linked with a distance of 5.4 cM, it is suggested that a locus controlling culm length was located near these two RFLP loci. This QTL reduced the culm length when the genotype corresponded to the Kinuhikari-type (homozygous). The difference in the culm length between Kinuhikari-type and Koshihikari-type groups for the C86 and C385 loci was 14.9 cm and 14.7 cm, respectively. Thus, this QTL explained more than 74% of the total variation of culm length in the F₂ population. Fig.1b, c and d show the distribution of the culm length in three F₂ genotypic groups for the C385 locus, Kinuhikari-type, heterozygote, and Koshi-

Fig. 1. Segregation of culm length.

Frequency distribution of culm length in F₂ from the cross Kinuhikari / Koshihikari (a-d), in B₁F₁ from the cross Koshihikari / Kinuhikari // Koshihikari (e-g), and in F₂ from the cross Kinuhikari / Reimei (h-k).

a: Whole F₂ population, n=101

b: Kinuhikari-type (homozygote) for the C385 locus, n=26

c: Heterozygote for the C385 locus, n=50

d: Koshihikari-type (homozygote) for the C385 locus, n=25

e: Whole B₁F₁ population, n=49

f: Heterozygote for the C385 locus, n=23

g: Koshihikari-type (homozygote) for the C385 locus, n=23

h: Whole F₂ population, n=46

i: Kinuhikari-type (homozygote) for the C86 locus, n=9

j: Heterozygote for the C86 locus, n=22

k: Reimei-type (homozygote) for the C86 locus, n=15

Bars show the distribution ranges of parents and closed triangles show the mean culm length of segregating populations and their parents.

Table 1. Effect of the DNA regions near the seven RFLP loci on culm length in F₂ from the cross Kinuhikari/Koshihikari and B₁F₁ from the cross Koshihikari/Kinuhikari//Koshihikari

Population	RFLP locus	Chromosome No.	Mean culm length (No. of plants)				<i>t</i> ¹⁾	R ² (%) ²⁾
			AA	AB	BB	total		
F ₂	<i>C86</i>	1	74.6 (24)	83.5 (52)	89.5 (25)	82.9 (101)	11.6 ⁴⁾	74.0
F ₂	<i>C385</i>	1	74.3 (26)	84.2 (50)	89.0 (25)	82.9 (101)	12.4 ⁴⁾	76.0
F ₂	<i>R1928</i>	1	81.7 (21)	82.8 (46)	83.5 (34)	82.9 (101)	1.0	1.9
F ₂	<i>C513</i>	4	83.6 (20)	82.3 (56)	83.6 (25)	82.9 (101)	0.0	0.0
F ₂	<i>G1073</i>	8	84.6 (29)	83.5 (50)	79.1 (22)	82.9 (101)	3.2 ⁵⁾	18.0
F ₂	<i>C1454</i>	9	81.9 (26)	83.5 (39)	83.7 (16)	83.0 (81)	0.9	2.0
F ₂	<i>G1465</i>	11	82.5 (25)	81.8 (52)	85.8 (22)	82.9 (99)	2.0	7.7
B ₁ F ₁	<i>C385, C86</i> ³⁾	1		90.6 (26)	97.5 (23)	93.8 (49)	6.2 ⁴⁾	45.1

AA: Kinuhikari-type (homozygote).

AB: Heterozygote.

BB: Koshihikari-type (homozygote).

¹⁾ *t* values were calculated between AA and BB in the F₂ and between AB and BB in the B₁F₁.²⁾ The contribution rate (R²) of the RFLP locus to total variation of culm length was calculated between AA and BB in the F₂ and between AB and BB in the B₁F₁.³⁾ Two RFLP loci *C86* and *C385* did not segregate in the B₁F₁.⁴⁾ Significant at 0.1% level.⁵⁾ Significant at 1% level.

hikari-type, respectively. The Kinuhikari-type group showed a mean culm length of 74.3 cm which was significantly shorter than that of Kinuhikari ($P=5.1 \times 10^{-4}$): in more than three-quarters of the plants in this group the culm was shorter than that of Kinuhikari. On the contrary, the Koshihikari-type group involved few transgressive segregants: the mean culm length of this group was 89.0 cm, almost the same value as that of the taller parent Koshihikari (Fig. 1d). Similar results were obtained for the *C86* locus (data not shown). These results suggest that Kinuhikari carries a gene(s) reducing the effect of the semidwarfing gene closely located near the *C86* and *C385* loci. The heterozygous group showed an intermediate mean culm length (84.2 cm) significantly different from that of the Kinuhikari-type ($P=1.3 \times 10^{-13}$) and Koshihikari-type ($P=2.5 \times 10^{-5}$) (Fig. 1c, b and d, Table 1), indicating that the semidwarfing gene at this QTL is an incomplete recessive gene.

In the B₁F₁ population from the cross Koshihikari / Kinuhikari // Koshihikari, no Kinuhikari-type plants appeared (Table 1, Fig. 1f and g). Therefore, we calculated the difference in the variation in the culm length between the heterozygous group and Koshihikari-type group. Consequently, about 45% of the total variation of this population was explained by the loci *C86* and *C385*, both of which did not segregate probably because of the small population size. Short-culm transgressive segregants did not appear in this population, presumably due to the lack of Kinuhikari-type plants. Heterozygous plants showed a culm length value almost equal to the midparent value between Koshihikari and Kinuhikari (Fig. 1f compare to e), suggesting that the gene at the QTL located near the *C86* and *C385* loci is an incomplete recessive gene.

Another QTL controlling culm length was found to be closely located near the *G1073* locus on chromosome 8, be-

cause the Koshihikari-type plants for this RFLP locus showed a significantly shorter culm than the Kinuhikari-type plants. The difference in mean culm length between the Koshihikari-type and Kinuhikari-type was 5.5 cm (Table 1). This QTL explained 18.0% of the total variation of culm length. However, the 5.5 cm value for the difference seemed to be overestimated, as described below. Table 2 shows the combined genotypic effects of the *G1073* locus and *C385* locus on the culm length in the F₂ population from the cross Kinuhikari / Koshihikari. In this table, the effect of *G1073* is shown within the Kinuhikari-type (AA), heterozygote (AB) and Koshihikari-type (BB) groups for the *C385* locus. The difference in the culm length between the Kinuhikari-type (CC) and Koshihikari-type (DD) for the *G1073* locus in the *C385* groups was 0.6 cm, 2.2 cm and 2.4 cm for AA, AB and BB, respectively. Although the values varied widely because of the small population size, they indicated that the effect of the QTL near *G1073* was less than 2.5 cm, and not 5.5 cm. The overestimation (5.5 cm) was due to the unexpected high appearance frequency of AA DD plants (10 plants), which exhibited the shortest culm length (Table 2). The interaction between the QTL on chromosome 8 and that on chromosome 1 was not significant ($P=0.44$), indicating that the QTL on chromosome 8 had a neutral effect on the culm length elongation controlled by the QTL on chromosome 1.

We then considered the possibility that the QTL located near *G1073* on chromosome 8 was responsible for the short-culm transgressive segregants that appeared in the F₂ population from the cross Kinuhikari / Koshihikari. However, the reducing effect of this locus (about 2.5 cm) was not sufficient to explain the 5.3 cm difference between the Kinuhikari-type plants for the *C385* locus and Kinuhikari. The mean culm length of the Kinuhikari-type plants for the

Table 2. Combined effects of the DNA regions near the two RFLP loci, *C385* and *G1073*, on culm length in F_2 from the cross Kinuhikari/Koshihikari

	Mean culm length (No. of plants)		
	AA	AB	BB
CC	73.5 (4)	85.0 (18)	89.8 (7)
CD	75.7 (12)	84.2 (24)	89.1 (14)
DD	72.9 (10)	82.8 (8)	87.4 (4)

AA: Kinuhikari-type (homozygote) for the *C385* locus.AB: Heterozygote for the *C385* locus.BB: Koshihikari-type (homozygote) for the *C385* locus.CC: Kinuhikari-type (homozygote) for the *G1073* locus.CD: Heterozygote for the *G1073* locus.DD: Koshihikari-type (homozygote) for the *G1073* locus.

G1073 locus in *C385* was much shorter than that of Kinuhikari (Table 2). In the F_2 population from the cross Kinuhikari / Koshihikari, long-culm transgressive segregants did not appear, although Koshihikari was found to carry a gene reducing the culm length near the *G1073* locus. However, the slight shift of the distribution peak of the Koshihikari-type plants for the *G1073* locus to the longer region from that of Koshihikari (Fig.1d) might be caused by the appearance of long-culm transgressive segregants.

Origin of semidwarfing QTL in Kinuhikari

To identify the origin of the semidwarfing gene in Kinuhikari, which was found to be located near the *C86* and *C385* loci on chromosome 1, polymorphisms of these two loci between Kinuhikari and its parental or ancestral cultivars, IR8, Fujiminori, Koshihikari, and Nagoyutaka, and a strain Hokuriku100 (Koga *et al.* 1989), were analyzed. Kinuhikari and IR8 showed the same banding pattern for the *C385* locus, which was different from that of the other cultivars / strain (Fig.2). The same results were obtained when using *C86* as a probe (data not shown). These results suggest that the region containing the semidwarfing gene on chromosome 1 in Kinuhikari originated from IR8. The banding pattern for the *G1073* locus was different between Kinuhikari and IR8 (data not shown), indicating that the QTL controlling the culm length on chromosome 8 in Kinuhikari was not derived from IR8.

Fig. 2. Polymorphism analysis of parental strains.

Polymorphism of the RFLP loci *C385* on chromosome 1 between Kinuhikari and its parental and ancestral cultivars/strain when using *Dra* I as a restriction enzyme.

Allelism test between Kinuhikari and Reimei

Kikuchi and Ikehashi (1983) reported that a semidwarfing gene *d49* of Reimei might be an allele at the *sd1* locus. We determined whether the semidwarfing gene in Kinuhikari is identical with *d49*, using the RFLP marker *C86*. The F_2 population from the cross Kinuhikari / Reimei showed a continuous distribution for culm length with many distinct short-culm transgressive segregants (Fig.1h), most of which (short-culm) belonged to the Kinuhikari-type group for the *C86* locus (Fig.1i). The mean culm length of this group was 5.5 cm shorter than that of the Reimei-type group (significant at 5% level) (Table 3). The culm length of the heterozygous plants was similar to that of the Reimei-type. These results indicate that the semidwarfing gene is different from *d49*, although the allelic relationship between them still remains unknown.

Discussion

The first objective of our study was to determine whether the dwarfing gene in Kinuhikari is really identical

Table 3. Effect of the DNA region near the *C86* locus on culm length in F_2 from the cross Kinuhikari/Reimei

Population	RFLP locus	Chromosome No.	Mean culm length (No. of plants)				$t^1)$
			AA	AB	BB	total	
F_2	<i>C86</i>	1	67.8 (9)	73.9 (22)	73.3 (15)	72.5 (46)	2.8 ²⁾

AA: Kinuhikari-type (homozygote).

AB: Heterozygote.

BB: Reimei-type (homozygote).

¹⁾ t value was calculated between AA and BB.²⁾ Significant at 5% level.

with *sd1* originating in IR8. Our results showed that a strong QTL controlling semidwarfism on Kinuhikari was located near the RFLP loci *C86* and *C385* on chromosome 1. According to Maeda *et al.* (1997), the *sd1* originating in IR8 was located on chromosome 1 at a distance of 1.8 cM from the *C385* locus. Fukuta (1995) reported that the *sd1* in a grain shattering habit mutant line SR-1 induced from the *indica* cultivar Nan-jing11 was located at a distance of 2.2 cM from the *C86* locus. Based on these reports, the QTL on chromosome 1 found in the present study can be considered to correspond to the *sd1* locus. By comparing the banding patterns of *C385* and *C86* between Kinuhikari and its ancestral cultivars / strain, it was found that Kinuhikari carried a semidwarfing gene at the QTL (*sd1* locus) on chromosome 1, which originated from IR8. In the present study, the heterozygous plants for the *sd1* locus showed a culm length value equivalent to the midparent value. Such an incomplete recessiveness of the *sd1* gene had been reported by many researchers (Kikuchi and Ikehashi 1983, Tanisaka *et al.* 1994, Murai *et al.* 1995).

Kikuchi and Ikehashi (1983) reported that the semidwarfing gene *d49* in Reimei was located at the *sd1* locus. However, our results clearly showed that *sd1* in Kinuhikari was different from the semidwarfing gene in Reimei. But it still remains to be determined whether these two genes are allelic or non-allelic, and further analysis should be carried out.

Another QTL reducing culm length for the allelic constitution of Koshihikari-type was detected close to the *G1073* locus on chromosome 8, suggesting that Koshihikari carries a semidwarfing gene that is not harboured by Kinuhikari. However, the effect of this gene was not so pronounced as that of *sd1*, and the culm length was reduced by less than 2.5 cm. This QTL had no interaction with *sd1*, implying that it is genetically independent of the *sd1* locus. We, therefore, analyzed the effect of this QTL for each genotypic group of the *C385* locus close to the *sd1* locus (Table 2). The analysis showed that the QTL close to *G1073* is responsible for the culm length in all the groups, although the effect of this QTL for the *C385* locus was less appreciable in the Kinuhikari-type group, the shortest genotypic group, than in any other groups. Long-culm transgressive segregation which should be observed in the F_2 population from Kinuhikari / Koshihikari was absent, presumably due to the fact that the effect of the QTL on chromosome 8 was negligible, although further analysis should be carried out to validate this assumption.

Interestingly, in both F_2 populations of Kinuhikari / Koshihikari and Kinuhikari / Reimei, transgressive segregation was observed only in the short culm direction, and the Kinuhikari-type homozygous plants for the *sd1* locus showed a much shorter culm than the parent Kinuhikari in both combinations. The role of the QTL near *G1073* in this transgressive segregation was examined. However, it was considered that this QTL could not sufficiently explain it, for the following three reasons: (1) the effect was not con-

spicuous, (2) the distribution range of long-culm segregants for the *G1073* locus with the allelic constitution of Kinuhikari-type for the *C385* locus considerably deviated from that of the short parent Kinuhikari, and (3) the effect was independent of the effect of the *sd1* locus, which could not explain the biased transgressive segregation toward short culm. Therefore, it was assumed that some other genetic factor(s) that could suppress the effect of *sd1* must be involved in Kinuhikari. This was also suggested from the fact that both the F_2 populations from the crosses Kinuhikari / Koshihikari and Kinuhikari / Reimei showed a similar transgressive segregation pattern.

Heading date is an important factor that influences culm length (Aquino and Jennings 1966). However, we did not record the heading date and it is possible that the QTL near the *G1073* locus may be a heading time gene locus. The suppressor gene, the presence of which was suggested in the present study may also be related to heading time. Further studies should be carried out to confirm this assumption.

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