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New dm-type Dwarf Mutants Varying in Internode Elongation Patterns are Controlled by Different Mutant Genes at the Same Locus in Rice (*Oryza sativa* L.)

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Summary

Four new dm-type dwarf mutants DMT-7, DMT-8, DMT-10-1 and DMT-11 were induced from the rice cultivar Taichung 65 (T65) by treatment with N-methyl-N-nitrosourea. These mutants were characterized by a remarkable reduction of the 2nd internode length. Experimental results on the morphological characterization showed that these mutants could be classified into two different groups, type 1 (DMT-7 and DMT-8) and type 2 (DMT-10-1 and DMT-11). Type 1 mutants developed not only dm-type but also dn-type culms in a plant whereas type 2 mutants showed mostly pseudo-d6-type and rarely dm-type culms in a plant. Gene analysis using F_2 populations from the crosses of these mutants with T65 demonstrated that the four mutants were controlled by single recessive genes. Allelism tests indicated that all the mutant genes were located at the same locus. Thus, different phenotypes between the two groups were controlled by different alleles at one locus. Moreover, the alleles of type 1 were dominant over those of type 2. However, no remarkable phenotypic differences were observed between the mutants within each group. Hence, gene symbols for DMT-7 (type 1) and DMT-11 (type 2) were designated as *d61-1* and *d61-2*, respectively. The results of linkage analysis using three morphological markers revealed that *d61* was linked to *shr1* (shrunken endosperm 1) on chromosome 1 with a recombination value of 21.7%.

Key Words : rice, dwarf mutant, internode elongation, multiple alleles, gene analysis, linkage analysis.

Introduction

Dwarfing genes generally reduce the internode length and/or the number of elongated internodes and eventually culm length in rice. However, the effect on the elongation of each internode varies considerably among the dwarfing genes and leads to diverse internode elongation patterns.

According to earlier reports, rice cultivars and dwarf mutants were classified into six groups on the basis of the internode elongation pattern; N-, dn-, dm-, d6-, nl- and sh-type (Takahashi and Takeda 1969, Takeda and Takahashi 1969, Takeda 1974, 1977). Among them, the dm-type is characterized by reduced elongation specifically in the 2nd internode counted from the top. Several recessive dwarfing genes, such as *d1*, *d2*, *d11* (Takahashi and Takeda 1969, 1970) and a dominant gene *Ssi1* (Yamaguchi 1976, Wu *et al.* 1997) are known to confer such a characteristic. Since the 2nd internode is elongated at the reproductive stage before flowering, the dm-type mutants could be used as materials for studying the regulatory mechanism of rice internode elongation especially in relation to genetic programs of reproductive development.

Although many dwarf mutants have been subjected to a gene analysis and more than 60 dwarfing genes have been identified (Kamijima *et al.* 1996), there are only a few reports describing internode elongation patterns of dwarf mutants. In this report, we investigated the internode elongation patterns of four newly induced dm-type dwarf mutants and analyzed their mutant genes. Linkage analysis for the mutant genes was also performed using several morphological marker genes.

Materials and Methods

Plant Materials

A series of dm-type dwarf mutants were induced from a rice cultivar Taichung 65 (T65) by treatments with a 1.0 mM solution of N-methyl-N-nitrosourea, as described by Satoh and Omura (1986). These mutants were designated as DMT lines, from which DMT-7, DMT-8, DMT-10 and DMT-11 were selected for the present study (Fig. 1). Among them, DMT-10 was found to harbor two different dwarfing mutations based on an F_2 segregation analysis for the cross DMT-10 × T65. Then, the plant showing only the pseudo-d6-type was selected from the F_2 population of the cross DMT-10 × T65 (Fig. 1-E). This plant was named DMT-10-1 and used for the mutant characterization and allelism test. The original mutant DMT-10 was used for the linkage analysis to identify the location of its two mutant genes.

Characterization of the mutants

The dm-type is not always expressed in all the culms of a plant: some culms show the dm-type and others the normal type (dn-type). Therefore, the "expressivity" of the dm-type (EDM) was represented by the percentage

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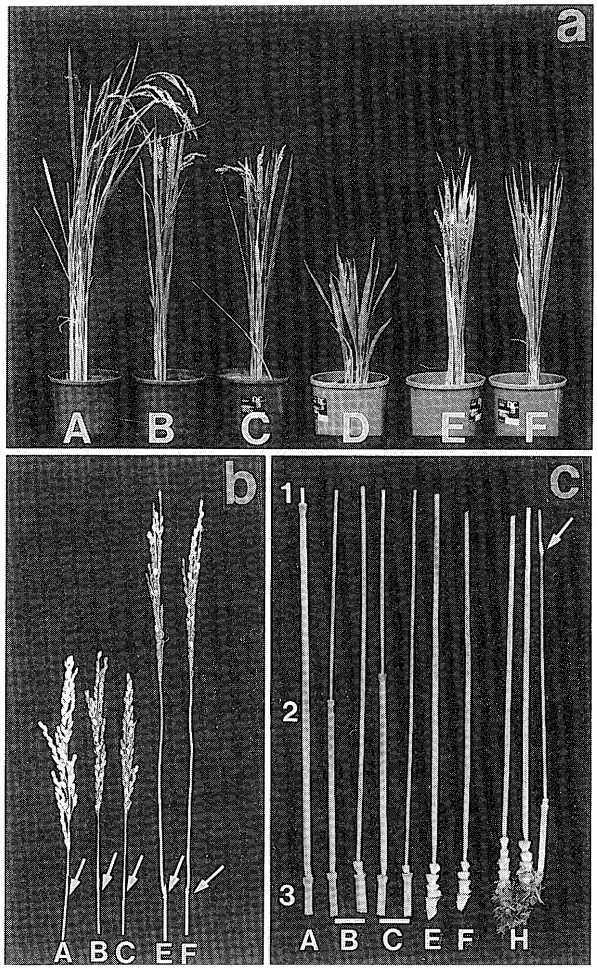

Fig. 1. Plant type (a), panicle (b) and naked culm internodes (c) in the four dwarf mutants and Taichung 65 (T65). Numbers in (c) show the 1st, 2nd and 3rd internodes. Arrows indicate the neck of spike.
A: Original cultivar, T65. B: DMT-7. C: DMT-8.
D: DMT-10. E: DMT-10-1. F: DMT-11.
H: A sample of dm-type culm with elongated lower internodes (DMT-11).

of dm-type culms to the total number of culms per plant. Average value of EDM was calculated from the data transformed into arcsin $\sqrt{}$ % value. Duncan's Multiple Range test (Duncan 1955) was used for the statistical analysis of culm length and flag leaf angle (the angle between the flag leaf and culm).

Gene analysis of the mutants

To examine the mode of inheritance of the mutant characters, all the mutants were crossed with T65 (Table 2). For allelism tests, five cross combinations were used (Table 3). For linkage analysis, each mutant was crossed with two linkage testers, EM-20 and K-293 (Table 4). EM-20 carries the gene *shr1* (shrunken endosperm 1) on chromosome 1 (Yano *et al.* 1984, Matsuo *et al.* 1986) while K-293 carries two marker genes *d18* (dwarf 18) and *fs2* (fine stripe 2) on chromosome 1 (Nagao and Takahashi 1963, Iwata and Omura 1971, 1984, Shinbashi *et al.* 1976). The recombination value was calculated using the maximum likelihood method (Immer 1934, Allard 1956).

Results

Characterization of the mutants

Culm length, EDM and flag leaf angles of the mutants and T65 are shown in Table 1. Panicle and elongated internode lengths are also schematically displayed in Fig. 2. Relative internode elongation patterns of the mutants and T65 are shown in Fig. 3 along with a diagram of the internode elongation pattern described by Takeda (1977).

Compared with T65, all the mutants exhibited a significantly reduced culm length. DMT-7 and DMT-8 showed different internode elongation patterns, dm-type and dn-type in a plant at the rates of 36% and 60% EDM, respectively. In contrast, DMT-10-1 and DMT-11 displayed a remarkable reduction of length in the 2nd to lower internodes and elongated only the 1st internode in almost all the culms, showing a pseudo-d6-type (Fig. 2 and Fig. 3). However, in rare cases, these mutants partly elongated the 3rd to lower internodes but their 2nd internodes were completely reduced (Fig. 1-H). Although the pseudo-d6-type culm is morphologically different from the dm-type (Fig. 3), the EDM of both mutants was computed as 100% because they had

Table 1. Comparison of morphological characters and EDM (Expressivity of dm-type) among four dm-type mutants and their original cultivar Taichung 65 (T65)

Line	Culm length			EDM (%)	Flag leaf angle (°) (mean ± S.E.)
	Wild or dn (cm) (mean ± S.E.)	dm (cm) (mean ± S.E.)	Pseudo d6 (cm) (mean ± S.E.)		
T65	84.7 ± 1.87a[1)]	NC[2)]	NC	0	42.0 ± 1.23a
DMT-7	59.2 ± 1.52b	45.6 ± 3.30c	NC	36	11.0 ± 2.45b
DMT-8	55.8 ± 1.10b	46.6 ± 0.83c	NC	60	10.0 ± 0.00b
DMT-10-1	NC	NC	25.5 ± 1.23d	100	8.5 ± 1.07b
DMT-11	NC	NC	26.9 ± 1.00d	100	9.0 ± 0.67b

[1)] Means followed by the same letters are not significantly different according to Duncan's Multiple Range test ($p = 0.05$).
[2)] No culm.

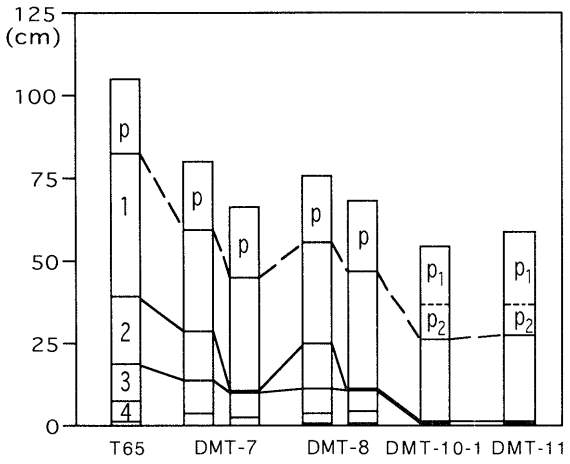

Fig. 2. Panicle and internode lengths in the four dwarf mutants and Taichung 65 (T65). P: panicle, P_1: panicle from the top to the node of the primary branch closest to the neck of spike, P_2: abnormal part of extremely elongated panicle.

the ability to express the dm-type and actually did not elongate the 2nd internode. The dm-type culms of DMT-7 and DMT-8 were significantly shorter than their respective dn-type culms because of the reduction of the 2nd internode length. Culm length of these mutants was significantly longer than that of DMT-10-1 and DMT-11. However, there was no appreciable difference in the culm length between DMT-7 and DMT-8 and between DMT-10-1 and DMT-11. DMT-7 and DMT-8 displayed similar internode elongation patterns in terms of dm-type and dn-type culms. Likewise, DMT-10-1 and DMT-11 showed similar patterns (Fig. 3-b) with an abnormally elongated panicle, a characteristic scarcely found in DMT-7 and DMT-8 (Fig. 1-b and Fig. 2). On the other hand, comparison of the leaf character showed that the flag leaf in all the mutants was more erect than that of T65. However, no significant difference in this character was observed among the mutants (Table 1).

Results of these characterizations revealed that the four dwarf mutants could be classified into two groups, type 1 (DMT-7 and DMT-8) and type 2 (DMT-10-1 and DMT-11).

Mode of inheritance and allelism test

F_1 phenotype and F_2 segregation ratios for culm length in the crosses between the mutants and T65 are shown in Table 2. F_1 plants of all the crosses showed the wild type. F_2 segregation in the crosses of DMT-7, DMT-8 and DMT-11 with T65 all fitted to the 3:1 ratio expected for one-locus segregation. In contrast, F_2 population in the cross of DMT-10 × T65 was classified into four different phenotypes, i.e. wild type, dwarf type-1 (pseudo-d6-type), dwarf type-2 (dn-type) and double recessive type (DMT-10 type). The segregation fitted to the 9:3:3:1 ratio expected for two-locus segregation, suggesting that two different mutations causing the pseudo-d6-type and the other dn-type dwarf simultaneously occurred in DMT-10.

Phenotype of F_1 plant and F_2 segregation in the crosses between the mutants are shown in Table 3. In all the crosses, no F_1 plants expressed the wild type. F_1 plants from the crosses DMT-7 × DMT-11 and DMT-10-1 × DMT-7 showed the DMT-7 type dwarf while those from DMT-10-1 × DMT-8 showed the DMT-8 type dwarf. On the other hand, F_1 plants from the crosses DMT-8 × DMT-7 and DMT-10-1 × DMT-11 displayed their respective parental types.

In none of the F_2 populations, did wild or double recessive dwarf types appear. In the F_2 population of DMT-8 × DMT-7 and DMT-10-1 × DMT-11, all the plants showed the same phenotype as that of their respective parents and no segregation was observed. In other crosses, DMT-7 × DMT-11, DMT-10-1 × DMT-7 and DMT-10-1 × DMT-8, the F_2 population was divided into two phenotypes corresponding to their parental types. The segregation of these crosses all fitted to the 3:1 (or 1:3) ratio. These results indicated that each dwarf mutant carries one recessive gene and all the

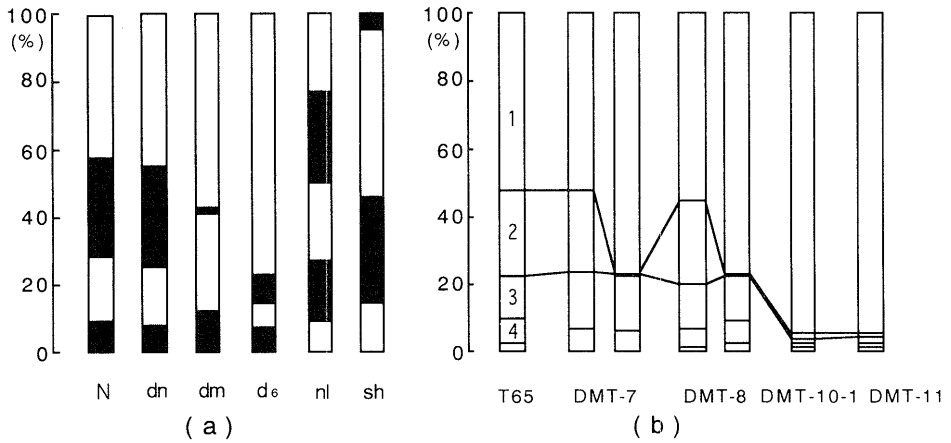

Fig. 3. Internode elongation patterns in (a) dwarf and wild plants, N-, dn-, dm-, d6-, nl-, sh-type denoted by Takeda (1977), and in (b) four dwarf mutants and Taichung 65 (T65). DMT-7 and DMT-8 exhibited the dm-type and dn-type culms in a plant, respectively. DMT-10-1 and DMT-11 exhibited pseudo-d6-type culms.

Table 2. F_1 phenotype and F_2 segregation in crosses between four mutants and Taichung 65 (T65)

Cross combination \ Phenotype	F_1	F_2						
	Wild	Wild	Dwarf type-1[1]	Dwarf type-2[2]	Maternal type	Total	χ^2	P.
DMT-7 × T65	All	190			61	251	0.065 (3:1)	> 0.90
DMT-8 × T65	All	191			64	255	0.001 (3:1)	> 0.90
DMT-11 × T65	All	186			51	237	1.532 (3:1)	0.10~0.25
DMT-10 × T65	All	124	44	36	8	212	3.076 (9:3:3:1)	0.25~0.50

[1] Pseudo d6-type dwarf.
[2] dn-type dwarf.

Table 3. F_1 phenotype and F_2 segregation in crosses between mutants

Cross combination \ Phenotype	F_1	F_2				
	Dwarf	Maternal type	Paternal type	Total	χ^2	P.
DMT-7 × DMT-11	DMT-7	274	107	381	1.93 (3:1)	0.10~0.25
DMT-10-1 × DMT-7	DMT-7	46	106	152	2.246 (1:3)	0.10~0.25
DMT-10-1 × DMT-8	DMT-8	32	71	103	2.023 (1:3)	0.10~0.25
DMT-8 × DMT-7	Parents[1]	No segregation		242		
DMT-10-1 × DMT-11	Parents[1]	〃	〃	187		

[1] Showing similar phenotype to that of the parents.

mutant genes are located at the same locus. Based on the results of characterization and allelism test of the mutants, the dwarfing genes of DMT-7 in type 1 and DMT-11 in type 2 were designated as *d61-1* and *d61-2*, respectively.

Linkage analysis

The results of linkage analyses are shown in Table 4. In the cross combinations of DMT-8, DMT-10-1 and DMT-11 with a marker line EM-20, all the F_1 plants showed the wild type and their F_2 populations segregated into four phenotypes, i.e. wild, dm-type dwarf, shrunken endosperm and double recessive types. The segregation of these four phenotypes was significantly different from the expected 9:3:3:1 ratio. Recombination values in the three crosses were 20.5 ± 4.0, 22.8 ± 6.0 and 22.4 ± 3.9% and their weighted mean value was 21.7 ± 2.6% (Table 4-a).

Phenotype of F_1 plants and F_2 segregation patterns in the crosses of DMT-7, DMT-8, DMT-10 and DMT-11 with a marker line K-293 carrying two marker genes *d18* and *fs2* are shown in Table 4-b. All the F_1 plants showed the wild type except for the cross DMT-10 × K-293 where the dwarf type similar to K-293 but different from DMT-10 was obtained. F_2 populations of the crosses DMT-7 × K-293, DMT-8 × K-293 and DMT-11 × K-293 segregated into four phenotypes, i.e. wild, *d61*, *d18* and double recessive types and fitted to the 9:3:3:1 ratio. However, the F_2 population in the cross of DMT-10 × K-293 segregated only into two different phenotypes, K-293 and DMT-10 type dwarfs, and fitted to the 3:1 ratio. These results indicated that one of the mutations in DMT-10 occurred at the *d18* locus (Table 4-b-1). The segregation between *d61* and *fs2* fitted to the 9:3:3:1 ratio in all the cross combinations (Table 4-b-2). On the other hand, the segregation between *fs2* and *d18* was significantly different from the 9:3:3:1 ratio. Recombination values in the three crosses were 14.1 ± 1.7, 16.3 ± 1.9 and 15.2 ± 1.5% and their weighted mean value was 15.1 ± 1.0% (Table 4-b-3).

Discussion

The present study revealed that four new dm-type mutants were controlled by single recessive mutant genes at the same locus (*d61*) on chromosome 1. The

Table 4. Linkage analysis a) between *d61* and *shr1*, b) among *d61*, *d18* and *fs2*

a) Combination	F_1 Phenotype	F_2 Wild	*d61*	*shr1*	Double	Total	χ^2	R.V.%[1)]
DMT-8 × EM-20	Wild	291 (291.4)	128 (136.8)	146 (136.8)	6 (6.0)	571	45.789 (9:3:3:1)	20.5 ± 4.0
DMT-10-1 × EM-20	Wild	130 (127.2)	57 (58.8)	58 (58.8)	3 (3.2)	248	15.943 (9:3:3:1)	22.8 ± 6.0
DMT-11 × EM-20	Wild	283 (294.2)	131 (136.3)	152 (136.3)	8 (7.2)	574	49.957 (9:3:3:1)	22.4 ± 3.9
Weighted mean								21.7 ± 2.6
b) b-1)		Wild	*d61*	*d18*	Double	Total	χ^2	P.
DMT-7 × K-293	Wild	290 (282.4)	89 (94.1)	95 (94.1)	28 (31.4)	502	3.912 (9:3:3:1)	0.25~0.50
DMT-8 × K-293	Wild	251 (263.3)	103 (87.8)	82 (87.8)	32 (29.3)	468	3.856 (9:3:3:1)	0.25~0.50
DMT-10 × K-293	Dwarf	0	0	225 (218.2)	66 (72.8)	291	0.835 (3:1)	0.25~0.50
DMT-11 × K-293	Wild	392 (380)	128 (127)	126 (127)	29 (42.2)	675	4.540 (9:3:3:1)	0.10~0.25
b-2)		Wild	*d61*	*fs2*	Double	Total	χ^2	P.
DMT-7 × K-293	Wild	295 (282.4)	94 (94.1)	90 (94.1)	23 (31.4)	502	2.981 (9:3:3:1)	0.25~0.50
DMT-8 × K-293	Wild	255 (263.2)	95 (87.8)	78 (87.8)	40 (29.2)	468	5.679 (9:3:3:1)	0.10~0.25
DMT-10 × K-293	Dwarf	166 (163.6)	49 (54.6)	59 (54.6)	17 (18.2)	291	1.038 (9:3:3:1)	0.75~0.90
DMT-11 × K-293	Wild	380 (379.7)	127 (126.6)	138 (126.6)	30 (42.1)	675	4.556 (9:3:3:1)	0.10~0.25
b-3)		Wild	*fs2*	*d18*	Double	Total	χ^2	R.V.%
DMT-7 × K-293	Wild	352 (343.6)	27 (32.9)	37 (32.9)	86 (92.6)	502	194.811 (9:3:3:1)	14.1 ± 1.7
DMT-8 × K-293	Wild	317 (316.0)	37 (35.0)	33 (35.0)	81 (82.0)	468	166.044 (9:3:3:1)	16.3 ± 1.9
DMT-10 × K-293	Dwarf	0	0	215 (218.2)	76 (72.8)	291	0.194 (3:1)	
DMT-11 × K-293	Wild	467 (458.8)	53 (47.4)	40 (47.4)	115 (121.4)	675	247.709 (9:3:3:1)	15.2 ± 1.5
Weighted mean								15.1 ± 1.0

Values enclosed in ( ) are the expected number based on the recombination values or the segregation ratios (9:3:3:1 or 3:1).
[1)] Recombination value %.

characterization of the mutants enabled to classify them into two different groups, type 1 (DMT-7 and DMT-8) and type 2 (DMT-10-1 and DMT-11). Type 1 and Type 2 were distinguished by their peculiar internode elongation patterns, i.e. dm-type and pseudo-d6-type. However, no significant difference was observed within each group. It remains to be determined whether the mutant genes in each group are different or not and future studies will be carried out to clarify this aspect.

The mutants of type 1 showed not only dm-type but also dn-type culms in a plant, suggesting that the mutant genes conferred an incomplete inhibition of the 2nd internode elongation. Different values of EDM were obtained between DMT-7 (36%) and DMT-8 (60%), but EDM is known to fluctuate under different environmental conditions (Takahashi and Hosoi 1974, Hosoi 1976). Our previous results on the mutants also revealed a large variation in EDM (Wu *et al.* 1995). Hence, the difference in EDM between the mutants was caused most likely by environmental factors. Type 2 mutants

showed mostly pseudo-d6-type culms wherein only the 1st internodes are elongated. However, in rare cases, these mutants could elongate the 3rd to lower internodes while the 2nd internodes remained completely unelongated (Fig. 1-H). Such characteristics suggested that the mutant genes had the potential of expressing the dm-type.

Takeda (1977) reported that three dwarfing genes *d1*, *d2* and *d11* expressed the dm-type while *d6* gene expressed the d6-type internode elongation pattern. However, these dwarfing genes were non-allelic to the newly identified multiple alleles locus *d61* on chromosome 1 because they were located on other chromosomes (Nagao and Takahashi 1963, Kinoshita 1984, Yu. *et al.* 1992, Ideta *et al.* 1994). Although *d2* is located on chromosome 1, allelism test with *d61* showed that these two genes are non-allelic to each other (data not shown).

The *d61* gene was found to be linked to *shr1* on chromosome 1 with a recombination value of 21.7%. In addition, a linkage relationship was also detected between *d18* and *fs2* with a recombination value of 15%, which approximately coincides with the value of 18% reported in a recently developed genetic map (Kinoshita 1995). According to this map, the genetic distance between *shr1* and *d18* is 46% but our linkage analysis revealed that *d61* was independent of *d18* and *fs2* (Table 4-b). These results indicated that *d61* could not be located either between *d18* and *fs2* or between *d18* and *shr1*. Consequently, these gene loci could be arranged in the order of *fs2-d18-shr1-d61*.

In rice, it is known that many characters such as waxy protein (Nagao and Takahashi 1963, Sano 1984, Satoh and Omura 1986) and anthocyanin production (Nagao and Takahashi 1963) are controlled by multiple alleles. However, multiple alleles that control culm-related traits are limited to only a few loci. Multiple alleles at the *sd1* locus conferring semidwarfism have contributed to the production of a large number of semidwarf and high-yielding cultivars (Hu 1973, Kikuchi *et al.* 1985, Ogi *et al.* 1993, Tanisaka *et al.* 1994). The multiple alleles at this locus bring about similar effects on the culm-related traits, eventually resulting in similar internode elongation patterns (Ogi *et al.* 1993). Shinbashi *et al.* (1976) reported that $d18^k$ and $d18^h$ confer the dn-type dwarfism (Kotake-tamanishiki) and extraordinary dwarfism (Hosetsu dwarf), respectively. Although these two alleles remarkably differ in the effect on culm length, they express similar internode elongation patterns. The *d61* locus is quite unique in that multiple alleles express different internode elongation patterns.

It is well known that lodging resistance is one of the most important agronomic characters for developing high-yielding rice cultivars. This resistance is closely associated with a lower internode length (Watanabe 1984). Our mutants may thus be useful materials for studying the regulation of lower internode growth to improve the lodging resistance of rice cultivars. In addition, the mutants could provide a suitable model for studying the complex regulatory mechanisms of internode elongation patterns in rice.

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