A Dwarfing Gene sd1-d (Dee-geo-woo-gen dwarf) on Lodging Resistance and Related Traits in Rice

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ABSTRACT

A dwarfing allele at the sd1 locus on chromosome 1 in rice, sd1-d, has been playing important role for developing lodging-resistant and high-yielding indica varieties IR8 and IR36. The dominant allele SD1 for long culm at the locus is differentiated into SD1-in and SD1-ja that are harbored in indica and japonica subspecies, respectively. The sd1-d of IR36 was substituted with SD1-in or SD1-ja by 17 backcrosses with IR36, and two isogenic tall lines were developed by using an indica variety IR5867 and a japonica one ‘Koshihikari’ as donors, which were denoted by “5867-36” and “Koshi-36”, respectively. The present study was conducted to examine the effect of dwarfing gene sd1-d on lodging resistance and related traits, compared with SD1-in and SD1-ja. Two isogenic lines and IR36 were cultivated in the field of the Faculty of Agriculture and Marine Science, Kochi University, Japan during 2017. Regarding index of lodging strength (g cm/g × 100), genotypes were in the order: 5867-36 (97.4) > Koshi-36 (74.1) > IR36 (46.0) on the 21st-day after 80%-heading, and they were in the same order on 10th-day after 80%-heading. The 4th-paneicle length (cm) was in the order: 5867-36 (118.7) > Koshi-36 (97.6) > IR36 (78.6). Similarly, the 4th-top weight (g) was in the order: 5867-36 (12.2) > Koshi-36 (10.2) > IR36 (9.6). The highest breaking strength (g) was recorded in IR36 (1649) followed by 5867-36 (1493) whereas the lowest breaking strength (g) was recorded in Koshi-36 (1360). Consequently, it is inferred that sd1-d enhances lodging resistance due to the decreases in the length and weight above the 4th-internode as well as the increase of breaking strength. The effect of SD1-in on lodging resistance is lower than that of SD1-ja.

Keywords: Dwarfing allele, Lodging, Rice, sd1-d, SD1-in, SD1-ja

शास्त्रीय

धानको बोटलाई हो चौर मान्ने sd1-d एतल्लो क्रोमोज़ोम स्लबमा १ हो र जुन यो sd1-d एतल्लो गुण भएका आइ आर ८ र आइ आर ३६ जात्त्वेको धात स्वाद डाल्ने जातीय विशेषता भएका जात्त्वेको महत्त्वपूण्य भूमिका खोलिङ्गेर छ। यो डोमिनान्ट एतल्लो (दुस्रो) SD1 अपलो धानको बोट हुने गुण भएको क्रममा दुई बटा घटुटा घटर्ने आइसोजेनिक लाईन SD1-in (इन्डिया) र SD1-ja (जापानिका) बाट तयार परियोजना र यो सानो sd1-d एतल्लो गुण भएको आइ आर ३६ धातको जात्त्विक आई आर ४५५६ लाई क्रममा १७ पटक क्रसिंग गरी बनाईएको आइसोजेनिक लाईन SD1-in (इन्डिया) र आई आर ३६ सितो कोसिहिकाली जापानिका जात्त्विक क्रममा १७ पटक क्रसिंग गरी बनाईएको आइसोजेनिक लाईन SD1-ja जापानिका को विकास गरियो र जसको नामकरण क्रममा “४५५६-३६” (इन्डिया)
The short-culm and lodging-resistant indica rice (*Oryza sativa* L., 2n=2x=24) varieties such as IR8, IR36 and IR72, which harbor *sd1-d* gene on chromosome 1 originating from the Taiwanese variety ‘Dee-geo-woo-gen’, are widely cultivated in Southeast Asia (De Datta et al 1968, Pang et al 1999). According to Murai et al (1995, 2002a, 2002b), *sd1-d* reduced culm length by 25.7 to 32.2 cm (27 to 37%) on the genetic background of the *japonica* variety Taichung 65, under various seven environmental conditions involving different fertilizer levels and years, and distant experimental sites in Japan. The wild type allele *SD1* encodes a gibberellin biosynthetic enzyme GA20 oxidase (GA20ox-2) that catalyzes late steps of gibberellin biosynthesis, while *sd1-d* includes the deletion of 383bp between the two sites of the exon 1 and 2, resulting in the loss of the enzymatic function (Ashikari et al 2002, Monna et al 2002, Spielmeyer et al 2002). The dominant allele *SD1* at the locus is differentiated into *SD1-in* and *SD1-ja* which is harbored in *indica* and *japonica* subspecies, respectively (Murai et al 2011). The effect of elongating culm was higher in the former allele than in the latter one, which could be one of the causes of inter-sub-specific difference in height (Murai et al 2011). Non-synonymous single-nucleotide polymorphism between *SD1-in* and *SD1-ja* was detected at the two sites in the exon 1 and 3 of the *sd1* locus (Murai et al 2011, Asano et al 2011). According to Murai et al (2011), the *sd1-d* of IR36 was substituted with *SD1-in* or *SD1-ja* by backcrossing with IR36 recurrently, and two tall isogenic lines regarding the respective dominant alleles were developed.

The lodging in the rice cultivation by transplanting can be classified into the breaking and bending types (Hitaka 1969, Yagi 1983). The former type of lodging often causes yield loss and deterioration of grain quality, resulting from reduction of photosynthesis by disturbing canopy structure, prevention of translocating water and nutrient elements from roots to leaves, and viviparity (Hitaka et al 1969). Seko (1962) devised the index of lodging, viz. the ratio of the moment (weight × length) above a basal internode to the breaking strength at the internode, and demonstrated its utility to evaluate the lodging resistance of a maturing rice plant. This index has been applied in several studies (Matsuzaki et al 1970 and 1972, Ichii and Hada 1983, Yagi 1983, Okawa and Ishihara 1992, Amano et al 1993). Lodging resistance in paddy field is lowest at about 20-25 days after heading in general, because most of the starch stored in culms and leaf sheaths is utilized for grain filling until this time; thereafter, the breaking strength becomes higher due to re-accumulation of starch and other substances into the basal internodes (Sato 1957, Seko 1962, Matsuda et al 1983, Ichii and Hada 1983, Yagi 1983).

Murai et al (2004) investigate the effect of *sd1-d* on lodging resistance on the genetic background of Taichung 65, and obtained the results that *sd1-d* enhances lodging resistance, reducing the value of the index of lodging, due to the two main factors, viz. 1) to reduce the length from the 4th internode to
panicle top, and 2) to increase the braking strength at the internode. However, such investigation regarding the effect of sd1-d has not been performed on the genetic background of an indica variety.

In the present study, the two tall isogenic lines and IR36 were grown in an experimental paddy field. The index of lodging, its three components, viz. the length from the 4th internode to panicle top, the total weight of panicle, leaves and internodes above the internode, and the braking strength at the internode, the number of leaving leaf sheaths on the internode were measured for the three lines/variety. The measurements were performed on 10 and 21 days after 80%-heading. On the basis of the results obtained, the effects of sd1-d on lodging resistance and related traits, compared with the SD1-in and SD1-ja, were examined on the common genetic background of IR36. Furthermore, the effects of SD1-in and SD1-ja were compared mutually.

MATERIALS AND METHODS

Two tall isogenic lines

The tall isogenic lines possessing SD1-in was developed by the following way (Murai et al 2011). An indica variety IR5867 carrying SD1-in was crossed with IR36. An F1 plant (SD1-in/sd1-d) was backcrossed with IR36. Among B1F1 plants (SD1-in/sd1-d and sd1-d/sd1-d), a tall (SD1-in/sd1-d) plant was backcrossed with IR36. Similarly, backcrossing and selecting tall plant were repeated to B1F1 generation. Among B1F2 plants, a tall (SD1-in/SD1-in) plant was selected. From B1F3 to B1F4 generations, non-segregation regarding plant height and other traits was ascertained, and the SD1-in isogenic line denoted by “5867-36” was completed. The SD1-ja isogenic line denoted by “Koshi-36” was completed by the same procedure as that in 5867-36 using a japonica variety ‘Koshihikari’ as the donor of SD1-ja.

Cultivation in Experimental Field

Seeds were sterilized with hot water of 62 to 55°C for 15 minutes for sterilization, to control blast, bakanae disease, grain rot, rice leaf tip nematode, etc. On 21st April 2017, sterilized seeds were sown on plastic trays filled with granulated soil containing N, P2O5 and K2O and being adjusted at pH 4.5. Seedlings were grown at 25°C for 5 days, and then at 21°C for 7 days in a natural-light type growth chamber. Twelve-day old seedling were transplanted at a spacing of 30cm × 15cm (22.2 hills/m²) with two seedlings per hill to an experimental field of the Faculty of Agriculture and Marine Science, Kochi University, Nankoku, Japan (33°35’N), on 3rd May. The field trial for the two tall isogenic lines and IR36 was conducted by the randomized complete block design with three replications. Each plot comprised 29 hills × 6 rows (174 hills).

On 14th April 2017, just before plowing, an ordinary chemical fertilizer was applied as basal dressing at the rate of 2.67 g/m² for each of N, P2O5 and K2O. Top-dressing was performed 62 and 64 days before 80% heading for the two tall isogenic lines and IR36, respectively, at the rate of 5.33, 4.19 and 4.95 g/m² for N, P2O5 and K2O, respectively, with a slow release and coated fertilizer ECOLONG® 413-180 type (about 3% of each nutrient element is readily available), manufactured by JCAME AGRI Co., Ltd. Accordingly, the total amount of the chemical fertilizers applied was at a rate of 8.00, 6.86 and 7.62 g/m² for N, P2O5 and K2O, respectively (Table 1).

Table 1. Chemical fertilizers applied in the experimental field

| Way of apply | Chemical fertilizers applied         | N (g/m²) | P2O5 (g/m²) | K2O (g/m²) |
|--------------|-------------------------------------|----------|-------------|------------|
| Basal dressing | Ordinary chemical fertilizer         | 2.67     | 2.67        | 2.67       |
| Top-dressing | ECOLONG® 413-180 type               | 5.33     | 4.19        | 4.95       |
| Total        |                                     | 8.00     | 6.86        | 7.62       |

ECOLON® 413-180: 3% of each nutrient element is readily available.

Index of lodging and traits related with lodging

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Seko (1962) observed that the breaking occurred mainly at the 4th or 5th internode in lodged rice plants, when its length was higher than 6 cm. The length of 4th internode of three genotypes 5867-36, Koshi-36 and IR36 was recorded 12.9, 6.5 and 3.9 cm, respectively whereas that of the 5th internode was 7.0, 3.9 and 2.3 cm, respectively (Table 3). The 5th internode length of IR36 was too short to measure its breaking strength by the fulcrum distance of 3.0 cm. On the other hand, the 4th internode lengths of the lines-variety were above 3.0 cm, indicating that their breaking strengths at this internode were commonly measurable. Accordingly, the index of lodging was applied for the 4th internode. The 4th-panicle length (the length from the base of the 4th internode to panicle top) (a), the 4th-top weight (the total fresh weight of panicle, leaves and the 1st to 4th internodes) (b), and the breaking strength at the 4th internode (c) were measured for the longest culm in each hill. The Breaking Strength Meter for Cereal Culm TR-S (Fujiwara Seisakusho Co., Ltd., Tokyo, Japan) was used for the measurement (Figure 1). The breaking strength at the central site of the 4th internode with leaf sheaths was measured by placing it on the twined hook with its midrib downward to be drawn by the single hook, because the thickness from the midrib to the opposite side was greater (hard to break) than the thickness across it (easy to break). The index of lodging was calculated by the formula 100 × ab / c. We used the fulcrum distance of 3.0 cm instead of that of 5.0 cm (Table 3). Measurements were performed at the two times of ripening, viz. 10 days and 21 days after 80%-heading. At each time, the longest culm in each of 24 hills was sampled from each replication (72 hills in total) in the three lines/variety, and the traits were measured. The lengths of panicle and the 1st to 5th internodes were measured for each of the culms. The culm length from the ground level was measured for the highest culm in each hill for ten hills per plot (30 hills per line/variety) at maturity.

Figure 1. Breaking Strength Meter for Cereal Culm. The two fulcrums at the distance of 3.0 cm were set on the twined hook (a) which is connected to the spring balance (b). The center of the fourth internode was placed between the two fulcrums, and was drawn with the single hook rightward.

RESULTS
As shown in Table 2, the genotypes were headed in between 97-99 days, whereas maturity was ranged from 121 to 130 days, indicating little genetic difference among them in crop duration.

Table 2. Days to 80% heading and maturity of tested genotypes

| Traits            | Allele     | SD1in | SD1-ja | sdI-d |
|-------------------|------------|-------|--------|-------|
| Days to 80% heading | 5867-36   | 97    | 97     | 99    |
| Days to maturity  | Koshi-36   | 121   | 124    | 130   |


Table 3 shows the lengths of culm, the 1st to 5th internodes and panicle in 5867-36, Koshi-36 and IR36. In culm length, the genotypes were in the order of 5867-36 (101.9 cm) > Koshi-36 (80.1 cm) > IR36 (60.0 cm), where “>” indicates that the former is statistically higher than the latter at 5% level of significance. Accordingly, sd1-d reduced culm length by 41.9 and 20.1 cm, compared with SD1-in and SD1-ja, respectively. The effect of elongating culm was higher in the former allele than in the latter one.

Panicle length was in the order of 5867-36 (24 cm) > Koshi-36 (22.5 cm) ≥ IR36 (21.8 cm), where “≥” indicates that the former is higher than the latter but not statistically significant. The variation in this trait was smaller than that in culm length, since the panicles of 5867-36 and Koshi-36 were 110 and 103% longer than IR36 while the culm length was 170 and 133% longer than IR36, respectively.

Table 3. Lengths of culm, the 1st to 5th internodes and panicles in tested genotypes

| Trait                      | Allele       | LSD (0.05) |
|----------------------------|--------------|------------|
|                            | SD1-in       | SD1-ja     | sd1-d      |    |
| Culm length                | 101.9 a (170)| 80.1 b (133) | 60.0 c     | 3.6 |
| 1st internode length       | 38.2 a (122) | 35.6 b (114) | 31.3 c     | 0.6 |
| 2nd internode length       | 25.3 a (179) | 19.6 b (139)| 14.2 c     | 0.3 |
| 3rd internode length       | 17.9 a (241) | 13 b (178)  | 7.5 c      | 1.1 |
| 4th internode length       | 12.9 a (336) | 6.5 b (170) | 3.9 c      | 0.4 |
| 5th internode length       | 7.0 a (305)  | 3.9 b (170) | 2.3 c      | 0.8 |
| Panicle length             | 24.0 a (110) | 22.5 b (103) | 21.8 b     | 1.0 |

Values followed by the same letter within each trait are not significantly different at the 5% level, determined by LSDs in the table. (): Percentage of 5867-36 or Koshi-36 to IR36.

Table 4. Analysis of variance for lodging index, its three components and number of living leaf sheaths of 5867-36, Koshi-36 and IR36 on the 10th and 21st days after 80% heading, in which numerals show F-values

| Traits                      | Lines-variety (A) | Time after 80% heading (B) | Interaction A X B |
|-----------------------------|-------------------|-----------------------------|-------------------|
| Lodging index (g·cm/g)      | 154.61 **         | 102.70 **                   | 1.53              |
| 4th-panicle length (cm)     | 535.83 **         | 1.80                        | 1.20              |
| 4th-top weight (g)          | 210.96 **         | 29.56 **                    | 3.71              |
| Breaking strength (g)       | 8.68 **           | 66.32 **                    | 1.47              |
| No. of living leaf sheaths  | 3.24              | 54.74 **                    | 10.37 **          |

Degrees of freedom for lines-variety, times of measurement, the interaction and error are 2, 1, 2 and 10, respectively.

*, ** Significant at the 5% and 1% levels, respectively.
Table 5. Lodging index and its three components at the 4th internode in 5867-36, Koshi-36 and IR36 on the 10th and 21st day after 80% heading

| Traits                        | Time of measurement | 5867-36     | Koshi-36   | IR36      | LSD (5%) |
|-------------------------------|---------------------|-------------|------------|-----------|----------|
| Index of lodging (g./cm²/g)   | 10 day              | 73.1 b (253)| 48.0 c (166)| 28.9 d    | 8.6      |
|                               | 21 day              | 97.4 a (212)| 74.1 b (161)| 46.0 c    |          |
| 4th-panicle length (cm)       | 10 day              | 115.3 a (147)| 97.5 b (125)| 78.2 c    | 3.7      |
|                               | 21 day              | 118.7 a (151)| 97.6 b (124)| 78.6 c    |          |
| 4th-top weight (g)            | 10 day              | 11.9 a (140)| 9.7 c (115)| 8.5 d     | 0.5      |
|                               | 21 day              | 12.2 a (127)| 10.2 b (106)| 9.6 c     |          |
| Breaking strength (g)         | 10 day              | 1876 bc (82)| 1969 b (86)| 2290 a    | 258      |
|                               | 21 day              | 1493 de (91)| 1360 e (82)| 1649 cd   |          |
| No. of living leaf sheaths    | 10 day              | 1.08 b (68)| 1.51 a (96)| 1.58 a    | 0.27     |
|                               | 21 day              | 0.97 b (138)| 0.97 b (138)| 0.71 c    |          |

Values followed by the same letter within each trait are not significantly different at the 5% significant level as determined by the LSDs in the table. Figures in parenthesis are the percentage of lines to variety.

**Index of lodging and its related traits**

Table 4 shows analysis of variance for the index of lodging and the related traits of 5867-36, Koshi-36 and IR36 on 10th and 21st days after 80% heading. The effect of lines/variety was statistically significant in the four traits except number of living leaf sheath. The effect of the times of measurement was significant in the four traits except 4th-panicle length. The interaction between the lines/variety and the times of measurement was significant only in the number of living leaf sheaths.

Table 5 shows the lodging index, its three components and number of living leaf sheath in three genotypes 5867-36, Koshi-36 and IR36 on the 10th and 21st days after 80%-heading. Regarding lodging index, the genotypes were in the order of 5867-36 > Koshi-36 > IR36, which was identical between two times of measurement. In each line/variety, this trait was higher on the 21st days than on the 10th days after 80%-heading. Regarding 4th-panicle length, the lines/variety were in order of 5867-36 > Koshi-36 > IR36 in both the times of measurement. In each genotype, significant difference was not noticed in this trait for times of measurement. Regarding 4th-top weight, the genotypes were in the order of 5867-36 > Koshi-36 > IR36, which was identical for both the times of measurement. In each genotype, this trait was higher at the later time of measurement (21st day after 80% heading) than at the former one (10th day), although being not significant statistically in the case of 5867-36. Regarding breaking strength, the genotypes were in the order of IR36 > Koshi-36 ≥ 5867-36 at the former (10th day) time of measurement. Significant difference was not noticed between the two lines but IR36 was the highest. At the later (21st day) time of measurement, this trait was in the order of IR36 ≥ 5867-36 ≥ Koshi-36 (IR36 > Koshi-36). In each line/variety, this trait was higher at the former time of measurement than at the latter one. Regarding number of living leaf sheaths, the lines/variety was in the order of IR36 ≥ Koshi-36 > 5867-36 at the former time of measurement. At the later time of measurement, this trait was in the order of 5867-36 ≥ Koshi-36 > IR36. In each genotype, this trait was higher at the former time of measurement than at the later time of measurement, although the difference was not statistically significant in the case of 5867-36.

**DISCUSSION**

Breaking strength decreased from the 10th day to 21st day after 80% heading (Table 5), which is consistent with the previous studies (Sato 1957, Seko 1962, Matsuda et al 1983, Ichii and Hada 1983, Yagi 1983). During this period, 4th-top weight increased, resulting in the increase of lodging index.
decrease in number of living leaf sheaths seems to have accelerated it, because a lower internode is supported against breaking with living leaf sheaths covering the internode (Hitaka 1969, Matsuzaki et al 1972, Miyasaka and Takaya 1982, Takaya and Miyasaka 1983, Okawa and Ishihara 1992, Amano et al 1993). The significant effects of both the lines/variety and times of measurement, and the non-significant interactive effect regarding lodging index (Table 4) suggest that the lodging resistance of the genotypes were able to be evaluated consistently at the two times of measurement. It is inferred that sd1-d decreased lodging index by 112 and 61% compared with SD1-in and SD1-ja, respectively, at the later time of measurement (Table 5). Lodging index was positively correlated with 4th-panicle length and 4th-top weight among the six combinations of three genotypes and two times of measurement (r = 0.883 and 0.925, significant at the 5 and 1% levels, respectively). Accordingly, lodging index was principally associated with 4th-panicle length that is almost parallel to culm length. Secondly, 5867-36 and Koshi-36 were higher by 27 and 6%, respectively, in 4th-top weight than IR36 at the later time of measurement, indicating that this trait was related to the enhancement of lodging resistance by sd1-d. Correlation coefficient between index of lodging and breaking strength was negative but not significant at the 5% level (r = -0.750). The reason of this lower correlation is considered as follows: the genotypes were in the order of 5867-36 > Koshi-36 > IR36 in breaking strength in each time of measurement; in breaking strength, however, Koshi-36 was not significantly different from 5867-36 even though IR36 was the highest identically at the two times of measurement. Correlation coefficient between number of living leaf sheaths and breaking strength was positive but not significant at 5% level (r = 0.801). Accordingly, this trait seems to have contributed breaking strength but its effect was supportive and not decisive; for example, IR36 had the highest breaking strength but the fewest living leaf sheaths at the later time of measurement.

Genotype 5867-36 had the higher value of lodging index compared with IR36 on the 21st day after 80% heading, due to the higher 4th-panicle length, the higher 4th-top weight and the lower breaking strength, in which the extents of their effects on the lodging index were in this order 5867-36 > Koshi-36 > IR36 (Table 5). Therefore, it is inferred that sd1-d drastically enhances lodging resistance compared with SD1-in. Serious lodging was observed in 5867-36 at the late stage of maturity, while no lodging was observed in IR36. Consequently, it is indispensable to use sd1-d in breeding programs of indica rice. Koshi-36 had the intermediate value of lodging index between IR36 and 5867-36 on the 21st day after 80% heading, due to the intermediate values in both 4th-panicle length and 4th-top weight, and the lowest breaking strength. A similar result was obtained using the sd1-d isogenic line of Taichung 65 and japonica. Taichung 65 carrying SD1-ja, although the effect of sd1-d on enhancing lodging resistance compared with SD1-ja seems to be amplified on the genetic background of this variety (Murai et al 2004). The bending of culms was observed at maturity in Koshi-36, although being not serious. Hence, it is inferred that the effect of SD1-ja on lodging resistance is intermediate between those of sd1-d and SD1-in. This is consistent with the fact that only a few officially registered varieties carrying sd1-d are cultivated in Japan (Tabuchi et al 2000) while japonica varieties carrying SD1-ja such as Koshihikari predominate over there (Rice Stable Supply Support Organization, 2020).

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