

Research Paper

Effects of tall alleles *SD1-in* and *SD1-ja* to the dwarfing allele *sd1-d* originating from ‘Dee-geo-woo-gen’ on yield and related traits on the genetic background of *indica* IR36 in rice

Birendra Bahadur Rana¹⁾, Misa Kamimukai²⁾, Mukunda Bhattarai^{1,2)}, Lokendra Rana³⁾, Ayaka Matsumoto³⁾, Hironori Nagano⁴⁾, Hiroki Oue²⁾ and Masayuki Murai*⁵⁾

¹⁾ Nepal Agriculture Research Council (NARC), Khumaltar, Lalitpur, Kathmandu, Nepal

²⁾ The United Graduate School of Agricultural Sciences, Ehime University, 3-5-7 Tarumi, Matsuyama, Ehime 790-8566, Japan

³⁾ Faculty of Agriculture and Marine Science, Kochi University, 200 Otsu, Monobe, Nankoku, Kochi 783-8502, Japan

⁴⁾ Field Science Center for Northern Biosphere, Hokkaido University, Kita 11, Nishi 10, Kita-ku, Sapporo, Hokkaido 060-0810, Japan

⁵⁾ Emeritus Professor of Kochi University, Faculty of Agriculture and Marine Science, Kochi University, Nankoku, Kochi 783-8502, Japan

sd1-d originating from ‘Dee-geo-woo-gen’ has been utilized to develop short-culmed *indica* varieties adaptable to higher fertilizer-application. Its tall alleles *SD1-in* and *SD1-ja* are harbored in *indica* and *japonica* subspecies, respectively. The *sd1-d* of *indica* IR36 was substituted with *SD1-in* or *SD1-ja* by recurrent backcrossing with IR36, and two tall isogenic lines (“5867-36” and “Koshi-36”) were developed. IR36, 5867-36 and Koshi-36 were grown in a paddy field in three years, and yield and related traits were measured, the effects of *SD1-in* and *SD1-ja* on yielding ability and related characteristics were examined on the genetic background of IR 36. *SD1-in* decreased panicle number per m² but increased spikelet number per panicle, ripened-grain percentage and 1000-grain weight, compared with *sd1-d*, resulting in the increase of yield. The increase of 1000-grain weight by *SD1-in*, caused by the increases of length, width and thickness of grain, was due to the increases of the length and width of lemma. *SD1-ja* did not significantly affect yield, mainly because the decrease of panicle number per m² was compensated by the enlarged 1000-grain weight owing to the increase of lemma length. Serious lodging was observed in long-culmed 5867-36, suggesting that *sd1-d* is indispensable for *indica* breeding programs.

Key Words: *Oryza sativa*, dwarfing gene, *sd1*, yield, yield component, spikelet, grain.

Introduction

The *sd1-d* originating from an *indica* variety ‘Dee-geo-woo-gen’ is a dwarfing allele at the *sd1* locus on chromosome 1 in rice (*Oryza sativa* L.) (Aquino and Jennings 1966, Maeda *et al.* 1997, Murai and Yamamoto 2001, Murai *et al.* 2003, Suh and Heu 1978). This allele has been intensively used to develop high-yielding *indica* varieties adaptable to higher fertilizer-application, and is harbored by almost all elite varieties in Southeast Asia such as IR8, IR36 and IR72 (De Datta *et al.* 1968, Peng *et al.* 1999). Murai *et al.* (2004) reported that *sd1-d* involves the effect of enhancing lodging resistance due to the two main factors as follows: to reduce the length from the fourth internode to

panicle top, and to increase breaking strength at the fourth internode, on the genetic background of the *japonica* variety Taichung 65.

The wild type allele *SD1* encodes the gibberellin biosynthetic enzyme GA20 oxidase (*GA20ox-2*) that catalyzes late steps of gibberellin biosynthesis, while *sd1-d* includes the deletion of 383 bp between the two sites of the exon 1 and exon 2, resulting in the loss of the enzymic function (Ashikari *et al.* 2002, Monna *et al.* 2002, Spielmeier *et al.* 2002, Sasaki *et al.* 2002). The dominant allele *SD1* at the locus is differentiated into *SD1-in* and *SD1-ja* that are harbored in *indica* and *japonica* subspecies, respectively (Murai *et al.* 2011). The effect of elongating culm was higher in *SD1-in* than in *SD1-ja*, which could be one of the causes of inter-subspecific difference in height (Murai *et al.* 2011). Nonsynonymous single-nucleotide polymorphisms between *SD1-in* and *SD1-ja* were detected at the two sites in the exon 1 and exon 3 of the *sd1* locus (Asano *et al.* 2011, Murai *et al.* 2011).

Communicated by Ryuji Ishikawa

Received January 6, 2021. Accepted February 9, 2021.

First Published Online in J-STAGE on March 17, 2021.

*Corresponding author (e-mail: muraim@kochi-u.ac.jp)

The effects of *sd1-d* on yielding ability have been already investigated by using the *sd1-d* isogenic line of a tall *japonica* Taichung 65: *sd1-d* diminished yield by 5 to 13%, mainly due to the decrease of spikelet number per panicle (Murai *et al.* 2002a). However, such investigation using the *sd1-d* isogenic line of an *indica* variety has not been performed yet, as far as we know. The *sd1-d* of *indica* IR36 was substituted with *SD1-in* or *SD1-ja* by recurrent backcrossing with IR36, and two tall isogenic lines regarding the respective tall alleles were developed (Murai *et al.* 2011). The two tall isogenic lines and IR36 were grown in an experimental paddy field by an ordinary fertilizer level over three years in the present study. Besides yield, its components and sink size, length, width and thickness of brown-rice grain, length and width of lemma, and width of palea were measured.

On the basis of the results obtained, the effects of *SD1-in* and *SD1-ja* on yielding ability and related traits, particularly grain and spikelet characteristics, compared with *sd1-d*, were examined on the common genetic background of IR 36.

Materials and Methods

Tall isogenic lines

The tall isogenic line possessing *SD1-in* was developed by the following way (Murai *et al.* 2011). IR5867 carrying *SD1-in* was crossed with IR36. An F₁ plant (*sd1-d/SD1-in*) was backcrossed with IR36. Among B₁F₁ plants (*sd1-d/SD1-in* or *sd1-d/sd1-d*), a tall (*sd1-d/SD1-in*) plant was backcrossed with IR36. Similarly, backcrossing and selecting tall plants were repeated to the B₁₇F₁ generation. Among the B₁₇F₂ plants, a tall (*SD1-in/SD1-in*) plant was selected. From B₁₇F₃ to B₁₇F₄ generations, non-segregation regarding plant height and other traits was ascertained, and the long-culmed *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 for 5867-36 using ‘Koshihikari’ as the donor of *SD1-ja*. According to Murai *et al.* (2011), 5867-36 and Koshi-36 carry the respective chromosomal segments containing the *sd1* locus originating from IR5867 and Koshihikari, respectively.

Cultivation in experimental field

The two tall isogenic lines and IR36 were grown by the same way of cultivation in 2017, 2018 and 2019. Seeds of Koshi-36, 5867-36 and IR36 were sown on plastic trays filled with granulated soil containing N, P₂O₅ and K₂O and being adjusted at pH 4.5, on April 21. The plastic trays were placed in a natural light-type growth chamber. The day/night temperature was set at 25°C for the first 5 days, and then at 21°C for the next 7 days until the day of transplanting. Seedlings were transplanted at a spacing of 30 cm × 15 cm (22.2 hills/m²) with two seedlings per hill to a paddy field of Faculty of Agriculture and Marine Science,

Kochi University, Nankoku, Japan (33°35'N), on May 3. An ordinary chemical fertilizer containing N, P₂O₅ and K₂O was applied to the paddy field as basal dressing (Supplemental Table 1). Moreover, top-dressing was performed 60 to 64 days before 80%-heading (the date on which about 80% of all productive tillers initiate heading) for the three lines-variety with the slow-release coated fertilizer ECOLONG® 413-180 type manufactured by JCAM AGRICULTURE CO., LTD. The total amount of nitrogen element applied to the paddy field was at a rate of 8.00 g/m², together with phosphorous and potassium elements.

For the two tall isogenic lines and IR36, the randomized block design with three replications was employed. Each plot comprised 29 hills × 6 rows (174 hills).

Measurements of yield, yield components and related traits

The sampling of panicles for measuring yield was conducted when about 8% of all fertilized spikelets were still yellowish-green, viz. on the day about 5 days earlier than the ordinary time of harvest, in order to minimize loss by shattering with little influence on yield. All panicles of 25 hills were sampled from the 3rd to 27th hill of the 5th row of each plot; and were dried in a drying oven set at a temperature from 30 to 45°C (according to the wetness of the panicles) for a time from 20 to 30 hours until the moisture content of the rough rice decreased to 11% or less. The panicle weight of each hill was measured after cutting at 1.5 mm below panicle bases. Of nine hills randomly selected from 25 hills of each plot, five hills having intermediate panicle weights were selected. The panicles of the five hills were threshed, and all spikelets in each hill were counted. Each spikelet was hulled and examined for endosperm development, as described by Murai *et al.* (2002b): a spikelet containing any developed endosperm containing the layer and/or powder of starch was regarded as fertilized in the present study, and a stereo microscope was used to investigate either presence or absence of starch in an endosperm if necessary. The number of fertilized spikelets of each hill was counted. Grains after hulling (hereafter “grains”) were classified with the two sieves for selecting grains by the thicknesses of 1.5 and 1.7 mm. Grains in each class were separately counted and weighed in each of the five hills. The number of grains with the thickness less than 1.5 mm was estimated by subtracting the number of grains thicker than 1.5 mm from the number of all fertilized spikelets in each hill. The percentage of grain weight of each of the three classes to the panicle weight was calculated in the five selected hills of each plot; then, the grain weight of each class of 25 hills of each plot was estimated from these three percentages. The moisture content (%) of grains thicker 1.7 mm in each plot was measured, and the grain weight at 15% moisture was estimated. For *japonica* varieties in Japan, brown rice just after hulling is separated with a 1.7 mm-sieve or a wider one to select grains possessing sufficiently high quality for milling from

grains with lower quality. However, in the lines-variety, grains with the thickness between 1.5 and 1.7 mm were able to be regarded as possessing sufficiently high quality for milling, while almost all of grains with thickness less than 1.5 mm were already broken or readily broken in the process of milling (**Supplemental Fig. 1**). Accordingly, we included the grains with thickness between 1.5 and 1.7 mm into ripened grains. In each of the lines-variety, the percentages of grain number and grain weight in each of the three classes of thickness to the total number and total weight of all fertilized grains, respectively, were calculated, and the percentages from 2017 to 2019 in each class of thickness were averaged (**Supplemental Table 2**). In the average of the three experimental years, the number of grains with thickness greater than 1.7 mm accounted for 80.3 to 86.8% in the three lines-variety (**Supplemental Table 2**-(1)). In the lines-variety, the percentages with thickness higher than 1.7 mm inclusive were higher on the basis of grain weight (87.2 to 93.4%, **Supplemental Table 2**-(2)) than on the basis of grain number, mentioned above. In the class of 1.7 mm > thickness \geq 1.5 mm, the lines-variety were 6.0 to 11.9% and 4.5 to 10.2%, respectively, on the basis of grain number and grain weight. Accordingly, the grain weight with thickness between 1.5 and 1.7 mm contributed considerably to the grain yield (hereafter “yield”). In addition, the brown rice weight of all the fertilized spikelets was denoted by “total brown rice yield” (**Table 3**), although the percentages of the grain weight with thickness less than 1.5 mm were about 2 or 3% in the lines-variety.

Ripened-grain percentage is the percentage of the number of ripened grains to the total number of spikelets. Moreover, the percentage of ripened grains to the fertilized spikelets, without unfertilized spikelets, was calculated. This trait and fertilized-spikelet percentage (fertilized spikelets/all spikelets, %) enable us to examine whether failure of spikelet fertilization or insufficient grain-filling lowered ripened-grain percentage. The mean spikelet number per hill of the 25 hills in each plot was estimated from that of the five hills and the ratio of the mean panicle weight of the 25 hills to that of the five hills. “Sink size” was estimated by the formula of single grain weight \times spikelet number per m² (Murai *et al.* 2002a, 2002b).

Measurements of spikelet and grain traits

The length, width and thickness of a ripened grain were measured for 30 grains randomly-selected from each plot of the three replications in the three lines-variety, using a vernier caliper. The length of lemma without awn, and the widths of lemma and palea in a spikelet with yellowish color of maturity were measured for 16 spikelets randomly-selected from each plot of the three replications in the three lines-varieties, as follows: 1) the lemma and palea of a spikelet were separated from each other; 2) one of them was placed on a slide glass, and was fixed by covering with a piece of a cellophane adhesive tape squarely cut to about 2 \times 2 cm; 3) the lemma or the palea was fully flattened on

the slide glass by pushing with a scale through the tape; 4) the length and width of the lemma, and the width of the palea were measured using a stereo microscope; 5) when a difference was noticed in width between the two sides of a lemma (or a palea), the wider side was measured. These measurements provide the potential length of lemma, and the potential widths of lemma and palea, regardless of the extent of grain filling, which are related to the capacity of a spikelet for accumulating carbohydrates.

Analysis of variance

For each of the traits mentioned above, analysis of variance was performed according to the completely randomized design, assuming the three replications in each of the three lines-variety in each of the three experimental years as the source of the three randomized data, and the lines-variety and the years as the two factors based on the fixed effect model.

Results

Yield, spikelet number per panicle and panicle number per m²

In 80%-heading date, both 5867-36 and Koshi-36 were two days earlier than IR36 in 2017 and 2019, and the former two were three days earlier than the latter one in 2018, indicating little genetic difference among them in this trait (**Table 1**).

Table 2 shows the results of analysis of variance for all of the traits examined in 5867-36, Koshi-36 and IR36 from 2017 to 2019. For yield, total brown rice yield, spikelet number per panicle and panicle number per m², the effects of both the lines-variety and the years were statistically significant, but the interaction between them was not significantly effective. **Table 3** shows the performances of the lines-variety in the traits mentioned above in the three experimental years. Regarding yield, the lines-variety were in the order IR36 \geq 5867-36 \geq Koshi-36 in 2017, and were 5867-36 \geq Koshi-36 \geq IR36 (5867-36 > IR36) in each of 2018 and 2019, where “ \geq ” indicates that the former is higher than the latter but being not statistically significant at the 5% level of probability, and “>” indicates significant difference. Accordingly, Koshi-36 was not significantly different from IR36 in each of the three experimental years. 5867-36 was significantly higher than IR36 in 2018 and 2019, but such significance of difference was not noticed in 2017. The averages of the three years for this trait were in the order 5867-36 > Koshi-36 \geq IR36. This trait was highly

Table 1. 80%-heading dates of 5867-36, Koshi-36 and IR36 from 2017 to 2019

Years	5867-36	Koshi-36	IR36
2017	27th July	27th July	29th July
2018	27th July	27th July	30th July
2019	28th July	28th July	30th July

Table 2. Analysis of variance for all of the traits examined in 5867-36, Koshi-36 and IR36 from 2017 to 2019

Traits	Lines-variety (L)	Year (Y)	Interaction (L × Y)
Yield (g/m ²)	4.80*	7.44**	2.78
Total brown rice yield (g/m ²)	4.02*	5.75*	2.86
Spikelets/panicle	22.51**	79.37**	2.08
Panicles/m ²	24.65**	39.08**	<1
Ripened-grain percentage	7.10**	6.31**	2.34
Fertilized-spikelet percentage	23.80**	4.16*	<1
Percentage of ripened grains to fertilized spikelets	5.17*	21.02**	1.97
1000-grain weight (g)	121.49**	186.57**	6.49**
Grain length (mm)	2.72	3.46	1.38
Grain width (mm)	20.8**	24.22**	<1
Grain thickness (mm)	8.78**	15.79**	<1
Lemma length (mm)	10.46**	6.67*	3.93**
Lemma width (mm)	19.20**	7.10**	<1
Palea width (mm)	<1	4.99*	<1
Spikelets/m ²	2.42	12.66**	2.33
Sink size (g/m ²)	<1	3.58*	2.67
Culm length (cm)	1015.91**	1.20	<1
Panicle length (cm)	42.95**	72.75**	<1

*, ** Significant at the 5 and 1% levels of probability, respectively.

Degrees of freedom for the lines-variety, years and the interaction and the error are 2, 2, 4 and 18, respectively.

Table 3. Yield, spikelets/panicle, panicles/m², ripened-grain percentage and its two related traits in 5867-36, Koshi-36 and IR36 from 2017 to 2019

Traits	Year	5867-36	Koshi-36	IR36	LSD (5%)
Yield (g/m ²)	2017	575 ab (96)	558 abc (94)	596 a	49
	2018	566 abc (116)	524 cd (108)	487 d	
	2019	590 a (111)	551 abc (103)	533 bcd	
	Average	577 a (107)	544 b (101)	539 b	
Total brown rice yield (g/m ²)	2017	586 ab (96)	572 ab (94)	611 a	50
	2018	582 ab (115)	544 bc (108)	504 c	
	2019	600 a (110)	562 ab (103)	543 bc	
	Average	589 a (107)	559 b (101)	553 b	
Spikelets/panicle	2017	89.2 cd (105)	79.8 ef (94)	84.7 de	6.1
	2018	105.7 a (115)	96.1 b (105)	91.5 bc	
	2019	83.8 de (116)	75.3 fg (104)	72.1 g	
	Average	92.9 a (112)	83.7 b (101)	82.8 b	
Panicles/m ²	2017	353 c (83)	403 ab (94)	428 a	32
	2018	291 d (85)	332 c (97)	343 c	
	2019	351 c (87)	387 b (96)	404 ab	
	Average	332 c (85)	374 b (95)	392 a	
Ripened-grain percentage	2017	85.0 ab (103)	86.0 a (104)	82.7 bcd	3.3
	2018	85.9 ab (106)	80.3 d (99)	81.1 cd	
	2019	87.2 a (104)	85.6 ab (102)	84.0 abc	
	Average	86.0 a (104)	84.0 b (102)	82.6 b	
Fertilized-spikelet percentage	2017	91.8 bc (103)	92.8 ab (104)	89.2 d	1.9
	2018	94.3 a (104)	93.3 ab (103)	90.3 cd	
	2019	92.0 bc (103)	92.5 ab (104)	89.3 d	
	Average	92.7 a (103)	92.9 a (104)	89.6 b	
Percentage of ripened grains to fertilized spikelets	2017	92.6 abc (100)	92.7 abc (100)	92.7 ab	2.8
	2018	91.1 bc (101)	86.1 d (96)	89.9 c	
	2019	94.8 a (101)	92.6 abc (98)	94.0 a	
	Average	92.8 a (101)	90.4 b (98)	92.2 ab	

Values followed by the same letter within each trait are not significantly different at the 5% level, determined by the LSDs in the table.

(): Percentage of 5867-36 or Koshi-36 to IR36.

correlated with total brown rice yield ($r=0.995$, significant at the 1% level). Spikelet number per panicle was in the order $5867-36 \geq IR36 \geq Koshi-36$ ($5867-36 > Koshi-36$) in 2017, and was $5867-36 > Koshi-36 \geq IR36$ in each of 2018 and 2019. Koshi-36 was not significantly different from IR36 in each year. 5867-36 was higher than the other two line-variety in the three experimental years. The average of the three years in this trait was in the order $5867-36 > Koshi-36 \geq IR36$. In each of the three lines-variety, this trait was in the order $2018 > 2017 > \text{or} \geq 2019$. **Supplemental Table 3** shows daily maximum and minimum temperatures, and daily duration of sunshine, which were averaged for each 10-days of each of May to August, from 2017 to 2019. Daily duration of sunshine was considerably low in the first 10-days and second 10-days of July in 2019. Because this period of 20 days almost overlapped the early and middle stages of panicle development in each line/variety, suppression for generation of secondary braches and spikelets and/or degeneration of them may have been induced, more or less, resulting in the lower spikelet number per panicle in 2019 than in the other two years. Regarding panicle number per m^2 , 5867-36 was lower by 13 to 17% than IR36 in the three experimental years. Koshi-36 was 3 to 6% lower than IR36, although being not statistically significant in each year. Nevertheless, Koshi-36 was significantly lower in this trait than IR36 in the average of the three years. In 2017, it is noteworthy that the highest value of IR36 in this trait contributed to its highest yield mentioned above. In each of the three lines-variety, this trait was significantly lower in 2018 than in the other two years. According to Kamimukai *et al.* (2020), in the same paddy field, daily duration of sunshine was considerably low in the second 10-days and the third 10-days of both May and June in 2003, resulting in the decrease of panicle number per m^2 in ‘Hinohikari’ (9th August in 80%-heading), a representative middle-heading variety in southern Japan. This result supports the postulation that growth of tillers is affected by daily duration of sunshine from transplanting to the initiation of panicle development. In 2018, however, neither a considerably low daily-duration of sunshine nor unseasonably low temperatures (both maximum and minimum) were observed from the first 10-days of May to the third 10-days of June that almost overlapped the duration mentioned above. Accordingly, we cannot specify the cause of the decrease of panicle number per m^2 in 2018 at present. Nevertheless, spikelet number per panicle was higher in 2018 than in the other two years in each line/variety, as mentioned above, as if the increase of this trait compensated the decrease of panicle number per m^2 .

Ripened-grain percentage and related traits

For ripened-grain percentage and the two related traits, the effects of the lines-variety and the years were statistically significant, but the interaction was not significantly effective (**Table 2**). Regarding ripened-grain percentage, the lines-variety were in the order $Koshi-36 \geq 5867-36$

$\geq IR36$ ($Koshi-36 > IR36$) in 2017, $5867-36 > IR36 \geq Koshi-36$ in 2018, and $5867-36 \geq Koshi-36 \geq IR36$ in 2019 (**Table 3**). Thus, IR36 was the lowest, or the second lowest and not significantly different from the lowest one, while 5867-36 was the highest or the second highest and not significantly different from the highest one, in the three experimental years. In terms of fertilized-spikelet percentage, IR36 was lower than the other two lines, in each of the years, and 5867-36 and Koshi-36 were not significantly different from each other. Therefore, the low ripened-grain percentages in IR36, mentioned above, are due to the low fertilized-spikelet percentages in it. In percentage of ripened grains to fertilized spikelets, significant differences were not noticed among the three lines-variety in 2017 and 2019. However, Koshi-36 was lower than the other two line-variety in this trait in 2018, although a considerably low daily-duration of sunshine was not observed in the first 10-days to the third 10-days of August that almost overlapped its maturing duration in 2018 (**Supplemental Table 3**). This lowest value of this trait in this year caused the lowest ripened-grain percentage in Koshi-36 in this year, mentioned above.

Grain and spikelet characteristics

The effect of the lines-variety was statistically significant in the five grain and spikelet traits except grain length and palea width (**Table 2**). The effect of the years was significant in all of the six traits except grain length. The interaction between the lines-variety and years was significantly effective in 1000-grain weight and lemma length. Regarding 1000-grain weight, 5867-36 and Koshi-36 were 6 to 12%, and 2 or 7% higher than IR36, respectively, in the three experimental years (**Table 4**). The average of the three years in this trait was in the order $5867-36 > Koshi-36 > IR36$. In each of the lines-variety, this trait was higher in 2019 than in the other two years, as if the increase of this trait compensated the decrease of spikelet number per panicle in 2019 (**Table 3**). Regarding grain length, 5867-36 was significantly higher than IR36 in 2018 and the average of the three years. Koshi-36 was higher in this trait than IR36 in the average of the three years, although being not significant in each of the years. Regarding lemma length, 5867-36 was significantly higher than IR36 in 2018; Koshi-36 was significantly higher than IR36 in 2017; and both the lines were significantly higher than IR36 in the average of the three years. In this trait, Koshi-36 was the highest among the three lines-variety in 2017, while 5867-36 was the highest in the other two years. In both of this trait and grain length, Koshi-36 was not significantly different from 5867-36 in the average of the three years. In each of the lines-variety, each of these traits was the highest in 2019 among the three years, or the second highest and not significantly different from the highest one in 2019. Grain length was significantly correlated with lemma length among the nine combinations of the three lines-variety and the three years ($r=0.762$, significant at the 5% level), indicating that

Table 4. Grain and spikelet traits in 5867-36, Koshi-36 and IR36 from 2017 to 2019

Traits	Year	5867-36	Koshi-36	IR36	LSD (5%)
1000-grain weight (g)	2017	21.5 c (108)	20.2 de (102)	19.9 e	0.4
	2018	21.5 c (112)	20.5 d (107)	19.1 f	
	2019	23.0 a (106)	22.1 b (102)	21.8 bc	
	Average	22.0 a (108)	20.9 b (103)	20.3 c	
Grain length (mm)	2017	6.54 bc (100)	6.56 abc (101)	6.52 bc	0.14
	2018	6.65 ab (103)	6.54 bc (101)	6.47 c	
	2019	6.63 ab (101)	6.70 a (102)	6.58 abc	
	Average	6.61 a (101)	6.60 a (101)	6.52 b	
Grain width (mm)	2017	2.23 b (103)	2.17 c (100)	2.17 c	0.04
	2018	2.25 b (104)	2.18 c (101)	2.16 c	
	2019	2.30 a (102)	2.24 b (100)	2.25 b	
	Average	2.26 a (103)	2.19 b (100)	2.19 b	
Grain thickness (mm)	2017	1.84 bcd (102)	1.81 cde (100)	1.81 cde	0.06
	2018	1.85 bc (104)	1.78 e (100)	1.78 de	
	2019	1.94 a (104)	1.87 b (101)	1.86 bc	
	Average	1.88 a (103)	1.82 b (100)	1.82 b	
Lemma length (mm)	2017	8.35 cd (102)	8.62 a (105)	8.20 d	0.19
	2018	8.59 ab (103)	8.40 bc (101)	8.32 cd	
	2019	8.64 a (102)	8.60 a (101)	8.47 abc	
	Average	8.53 a (102)	8.54 a (103)	8.33 b	
Lemma width (mm)	2017	2.36 ab (104)	2.26 de (99)	2.28 cde	0.07
	2018	2.34 bc (105)	2.25 de (101)	2.24 e	
	2019	2.42 a (105)	2.31 bcd (100)	2.31 bcd	
	Average	2.38 a (104)	2.27 b (100)	2.28 b	
Palea width (mm)	2017	1.21 a (100)	1.18 abc (98)	1.21 ab	0.05
	2018	1.18 abc (103)	1.15 c (100)	1.15 bc	
	2019	1.20 abc (100)	1.21 a (100)	1.21 a	
	Average	1.20 a (101)	1.18 a (99)	1.19 a	

Values followed by the same letter within each trait are not significantly different at the 5% level, determined by the LSDs in the table.

(): Percentage of 5867-36 or Koshi-36 to IR36.

grain length was primarily controlled by lemma length, and the former trait is presumed to be affected by the extent of grain filling. In grain width as well as lemma width, 5867-36 was significantly higher than Koshi-36 and IR36 in each of the years, and Koshi-36 and IR36 were not significantly different from each other. In each of the lines-variety, each of these traits was higher in 2019 than in the other two years. Grain width was significantly correlated with lemma width among the nine combinations of the lines-variety and the years ($r=0.917$, significant at the 1% level), indicating that grain width was principally regulated by lemma width. Similarly, 5867-36 was significantly greater in grain thickness than Koshi-36 and IR36 in 2018, 2019 and the average of the three years, and Koshi-36 and IR36 were not significantly different from each other in each year. In each of the lines-variety, this trait was greater in 2019 than in the other two years. Grain thickness was significantly correlated with lemma width among the nine combinations of the lines-variety and the years ($r=0.689$, significant at the 5% level), indicating that lemma width was positively related with grain thickness. On the other hand, the lines-variety were not significantly different from

each other in palea length not only in each year but also in the average of the three years. In each of the lines-variety, this trait was shorter in 2018 than in the other two years.

Spikelet number per m² and sink size

Spikelet number per m² was in the order IR36 > Koshi-36 ≥ 5867-36 in 2017, but they were not significantly different from each other in 2018 and 2019 (Table 5). The highest value of IR36 in 2017 was due to its highest panicle number per m² (Table 3). The averages of the three years for this trait were in the order IR36 ≥ Koshi-36 ≥ 5867-36 (IR36 > 5867-36). In each of the lines-variety, this trait was lowest in 2019 among the three years, which is consistent with the result in spikelet number per panicle (Table 3). Regarding sink size, significant differences were not noticed among the lines-variety in each of the three years with the exception of IR36 > Koshi-36 in 2017; they were in the order 5867-36 ≥ IR36 ≥ Koshi-36 in the average of the three years. In each of 5867-36 and Koshi-36, significant differences were not noticed among the three years; however, the order in IR36 was 2017 > 2019 ≥ 2018. According to the analysis of

Table 5. Spikelets /m², sink size, and lengths of culm and panicle in 5867-36, Koshi-36 and IR36 from 2017 to 2019

Traits	Year	5867-36		Koshi-36		IR36	LSD (5%)
Spikelets/m ² (×100)	2017	315 bc	(87)	321 b	(89)	363 a	30
	2018	307 bc	(98)	318 bc	(101)	314 bc	
	2019	294 bc	(101)	291 c	(100)	292 c	
	Average	305 b	(95)	310 ab	(96)	323 a	
Sink size ¹⁾ (g/m ²)	2017	677 ab	(94)	649 bc	(90)	721 a	63
	2018	658 abc	(110)	653 bc	(109)	600 c	
	2019	676 ab	(107)	643 bc	(101)	635 bc	
	Average	671 a	(103)	648 a	(99)	652 a	
Culm length (cm)	2017	101.9 a	(170)	80.1 b	(133)	60.0 c	3.4
	2018	100.1 a	(172)	80.4 b	(138)	58.1 c	
	2019	102.3 a	(172)	81.2 b	(137)	59.3 c	
	Average	101.4 a	(172)	80.5 b	(136)	59.1 c	
Panicle length (cm)	2017	24.0 b	(110)	22.5 cd	(103)	21.8 de	0.9
	2018	25.5 a	(111)	24.0 b	(105)	22.9 c	
	2019	22.2 cd	(109)	21.2 ef	(104)	20.4 f	
	Average	23.9 a	(110)	22.5 b	(104)	21.7 c	

Values followed by the same letter within each trait are not significantly different at the 5% level, determined by the LSDs in the table.

(): Percentage of 5867-36 or Koshi-36 to IR36.

¹⁾ Single grain weight × spikelets/m².

variance for the above two traits, the effects of the lines-variety and the interaction were not significant, while the effect of the years was significant (**Table 2**).

Culm and panicle lengths

5867-36 and Koshi-36 were higher in culm length by 41.9 to 43.0 cm and 20.0 to 22.3 cm, respectively, than IR36, in the three years (**Table 5**). Accordingly, both *SDI-in* and *SDI-ja* exerted their effects on elongating culm as compared with *sd1-d*, stably among the three years, which was supported by non-significant effects of the years and the interaction in this trait (**Table 2**). Regarding panicle length, the lines-variety were in the order 5867-36 > Koshi-36 > or ≥ IR36 in each of the three years. In each line/variety, this trait was shorter in 2019 than in the other two years, probably because the low daily durations of sunshine in the early and middle stages of panicle development affected the elongations of the panicle axis and/or the uppermost primary branch in 2019 (**Supplemental Table 3**). This result was consistent with the significant effects of the lines-variety and the years in this trait (**Table 2**).

Discussion

Murai *et al.* (2002b) developed the six isogenic genotypes combining *sd1-d* and *Ur1* (Undulate rachis -1), viz. U (*SD1/SD1 Ur1/Ur1*), H (*SD1/SD1 Ur1/+*), T (*SD1/SD1 +/+*), u (*sd1-d/sd1-d Ur1/Ur1*), h (*sd1-d/sd1-d Ur1/+*), and d (*sd1-d/sd1-d +/+*) on the genetic background of *japonica* Taichung 65 (=T), in order to examine whether *Ur1* is able to enhance yielding ability by its effect of increasing spikelet number per panicle, with and without *sd1-d*. The *SD1* of *japonica* Taichung 65 is identical with *SD1-ja*,

because its sequences of all of the three exons are the same as those of *SD1-ja* (Nagano *et al.* 2005, Nagano unpublished). In the present study, yield, yield components and other traits of T and d are quoted from Murai *et al.* (2002b), the percentage of T to d is calculated in each trait; and their grain and spikelet characteristics are measured anew for the same materials by the same way as that described in the materials and methods (**Table 6**), in order to examine the effects of *SD1-ja* compared with *sd1-d* on the genetic

Table 6. Yield, yield components and other traits of T (Taichung 65) and d in 2000

Traits ¹⁾	T	d
Yield (g/m ²)	557 a (102)	546 a
Spikelets/panicle	91.1 a (109)	83.6 b
Panicles/m ²	309 b (94)	327 a
Ripened-grain percentage	81.5 b (94)	86.3 a
Fertilized-spikelet percentage	86.4 b (97)	89.5 a
Percentage of ripened grains to fertilized spikelets	94.3 a (98)	96.4 a
Spikelets/m ² (×100)	281 a (103)	273 a
Sink size (g/m ²)	684 a (108)	633 b
1000-grain weight (g)	24.3 a (105)	23.2 b
Grain length	5.22 a (105)	4.96 b
Grain width	2.97 a (102)	2.93 a
Grain thickness	2.16 a (99)	2.18 a
Lemma length	6.84 a (103)	6.66 b
Lemma width	3.00 a (101)	2.97 a
Palea width	1.44 a (100)	1.44 a

Values followed by the same letter within each trait are not significantly different at the 5% level.

(): Percentage of T to d.

¹⁾ Data in the table except those of the length, width and thickness of grain, length and width of lemma, and palea width are quoted from Murai *et al.* (2002b).

background of Taichung 65. T was higher in spikelet number per panicle than d under all of the five environmental conditions with different fertilizer levels and years (Murai *et al.* 2002a, **Table 6**); however, T was lower in panicle number per m² than d under four of the five environmental conditions. In the average of the three years, Koshi-36 (*SD1-ja*) was not significantly different from IR36 (*sd1-d*) in spikelet number per panicle, while the former was significantly lower in panicle number per m² than the latter (**Table 3**). Accordingly, it is inferred that *SD1-ja* involves higher and lower effects on spikelet number per panicle and panicle number per m², respectively, compared with *sd1-d*; however, the former effect was not exerted sufficiently on the genetic background of *indica* IR36. 5867-36 was higher and lower than IR36 regarding spikelet number per panicle and panicle number per m², respectively, in the average of the three years. Hence, *SD1-in* seems to possess higher and lower effects on producing spikelet number per panicle and panicle number per m², respectively, compared with *sd1-d*, on the genetic background of *indica* IR36.

Regarding 1000-grain weight, T was higher than d under all of the five environmental conditions (Murai *et al.* 2002a, **Table 6**). In the lengths of grain and lemma, T was higher than d in 2000. On the other hand, T was not significantly different from d in the width and thickness of grain as well as the widths of lemma and palea. Similarly, Koshi-36 was higher in 1000-grain weight, and the lengths of grain and lemma than IR36 in the average of the three years (**Table 4**). Accordingly, *SD1-ja* seems to increase grain length by producing longer lemmas, resulting in the increase of 1000-grain weight, compared with *sd1-d*. 5867-36 was higher not only in 1000-grain weight, and the lengths of grain and lemma, but also in the widths of grain and lemma, and grain thickness, than IR36, in each of the three years. Furthermore, its 1000-grain weight was higher than that of Koshi-36. Therefore, *SD1-in* seems to increase the length, width and thickness of grain by producing longer and wider lemmas, compared with *sd1-d*, resulting in the higher 1000-grain weight, on the genetic background of IR36; and the effect on 1000-grain weight seems to be higher in *SD1-in* than in *SD1-ja*. Although we cannot completely deny a close linkage between *SD1-in* and a minor gene for increasing lemma width in 5867-36, there was little possibility that such a linkage remained after 17 backcrosses. According to a result of Ogi *et al.* (1993), the *sd1-d* isogenic line of Norin 29 did not significantly different from Norin 29 in both the length and width of grain in an experiment in a year. In grain length (**Table 4**), the difference between IR36 (*sd1-d*) and Koshi-36 (*SD1-ja*) was not significant in each year, but the former was significantly lower than the latter in the average of the three years. Hence, the multi-year experiments would enable to detect a small difference in a morphological characteristic such as grain length.

Regarding ripened-grain percentage, T was lower than d under all of the five environmental conditions (Murai *et al.*

2002a, **Table 6**), because T was lower than d in both fertilized-spikelet percentage and percentage of ripened grains to fertilized spikelets in 2000. However, Koshi-36 was not significantly different from IR36 regarding ripened-grain percentage as well as percentage of ripened grains to fertilized spikelets, in the average of the three years, although the former was significantly higher in fertilized-spikelet percentage than the latter (**Table 3**). Accordingly, the effects of *SD1-ja* on ripened-grain percentage and its two related traits compared with *sd1-d* seems not to be constant between the genetic backgrounds of Taichung 65 and IR36. On the other hand, 5867-36 was higher in ripened-grain percentage than IR36, due to its higher fertilized-spikelet percentage than IR36, in the average of the three years, while the former was not significantly different from the latter in percentage of ripened grains to fertilized spikelets. Therefore, *SD1-in* seems to involve the effect of enhancing fertilized-spikelet percentage compared with *sd1-d*, resulting in the higher ripened-grain percentage, at least on the genetic background of *indica* IR36.

T was higher in yield than d under the five environmental conditions, being statistically significant under three environmental conditions, because the increases in spikelet number per panicle and 1000-grain weight exceeded the decreases in panicle number per m² and ripened-grain percentage (Murai *et al.* 2002a, **Table 6**). Koshi-36 was not significantly different from IR36 in yield, in the average of the three years, mainly because the increase of 1000-grain weight compensated the decrease of panicle number per m² in Koshi-36. Accordingly, it is inferred that *SD1-ja* increase yielding ability compared with *sd1-d* on the genetic background of *japonica* Taichung 65, while *SD1-ja* does not affect yielding ability on the genetic background of *indica* IR36. It is suggested that when *sd1-d* is employed to develop *japonica* varieties, the possibility of diminishing yield should be taken into consideration. Tabuchi *et al.* (2000) reported that the *japonica* variety 'Kinuhikari' harbors *sd1-d*; however, we don't know other varieties carrying *sd1-d* that are grown broadly in Japan. On the other hand, 5867-36 was higher in yield than IR36, in the average of the three years, which was resulted from the increases in spikelet number per panicle, ripened grain percentage and 1000-grain weight, despite the decrease in panicle number per m². Hence, it is inferred that *SD1-in* increases yielding ability compared with *sd1-d* on the genetic background of *indica* IR36; in other words, *sd1-d* decreases yielding ability compared with *SD1-in*. Nevertheless, serious lodging was observed in 5867-36 at the late stage of maturity in the three experimental years, due to the long culm of more than 1 m (**Table 5**), and higher total weight of panicle, leaves and internodes above the fifth one, and lower breaking strengths at the fourth and fifth internodes, compared with those of IR36 (Murai unpublished). On the other hand, no lodging was observed in IR36 in the three years. Therefore, it is indispensable to use *sd1-d* in breeding programs for

indica rice, particularly for developing lodging-resistant varieties adaptable to high fertilizer application. According to Murai *et al.* (1992), *sd1-d* involves a pleiotropic effect of enhancing tolerance to high-temperature damage at flowering caused by unfertilization of spikelets, which is consistent with the broad cultivation of *sd1-d*-carrying varieties in the tropics and subtropics.

It is well known that *sd1-r* originating from ‘Reimei’ (Ashikari *et al.* 2002, Futsuhara 1968, Murai and Yamamoto 2001, Murai *et al.* 2003), the *sd1* allele originating from the landrace ‘Jikkoku’ (Ashikari *et al.* 2002, Kikuchi *et al.* 1985, Nagano *et al.* 2005) and the *sd1* allele originating from Calrose 76 (Ashikari *et al.* 2002, Mackill and Rutger 1979, Spielmeyer *et al.* 2002), which were caused by the corresponding single-base substitutions in the exon 3, exon 1 and exon 2 of the *sd1* locus, respectively, have been employed to develop elite short-culm *japonica* varieties grown in Tohoku region (Toriyama *et al.* 1967, Yamazaki *et al.* 1987) and Kyushu District (Okada *et al.* 1967) both in Japan, and California (Rutger 1983, McKenzie *et al.* 1994). Besides, two isogenic lines of a high eating-quality variety Koshihikari both carrying the *sd1* allele of Jikkoku, registered as ‘Pikaichi’ (Nonaka *et al.* 1991) and ‘Hikarishinseiki’ (Tomita 2009), have been recommended in Saga Prefecture and Tottori Prefecture, respectively, in Japan. In addition, ‘Hikarikko’ (Murai and Endo 2006), in which not only *sd1-r* but also an incompletely-dominant earliness gene originating from Reimei were introduced into Koshihikari by backcrossing (Ikeda *et al.* 2018), is cultivated in Kochi Prefecture. It is suggested from the results of Toriyama *et al.* (1967) that *sd1-r* reduces culm length by about 15 cm, ranging from 5 to 26 cm, under a number of environmental conditions with different fertilizer levels and experimental locations, but involves little effects on panicle length, panicle number per hill, 1000-grain weight and yield on the genetic background of ‘Fujiminori’. In addition, the *sd1-r* isogenic line of Koshihikari was 10.5 cm shorter in culm length than Koshihikari in the same experimental field in 2018 (Murai unpublished). From the results of Takagi *et al.* (1991), Nonaka *et al.* (1991) and Tomita (2009), it is suggested that the *sd1* allele of Jikkoku decreased culm length by about 11.0 to 26.4 cm, but increased panicle number per hill, and involves little effects on 1000-grain weight and yield on the genetic background of Koshihikari. Calrose 76 was 25 cm lower in height to panicle top than the original variety ‘Calrose’ (Mackill and Rutger 1979); and the former was 20.0 and 0.9 cm lower in culm and panicle lengths, respectively, than the latter (Murai *et al.* 1995). According to Murai *et al.* (1995, 2002a, 2002b), d was lower in culm length by 25.7 to 36.7 cm (29.9 cm on average) than T, under eight environmental conditions involving different levels of fertilization, years and distant experimental sites in Japan. This difference seems to be higher than that between IR36 and Koshi-36 (21.4 cm on average, **Table 5**). Accordingly, it is inferred that 1) the effect of *sd1-d* on

reducing culm length compared with *SD1-ja* was affected by the difference between the genetic backgrounds of IR36 and Taichung 65; and 2) the reducing effect of *sd1-d* is higher than those of *sd1-r* and the *sd1* allele of Jikkoku. Koshi-36 was 20.9 cm lower in culm length than 5867-36 in the average of the three years, indicating that the effect of *SD1-ja* on elongating culm is lower than that of *SD1-in* (**Table 5**). In Koshi-36 (*SD1-ja*), the culms bent at maturity in the three years, but the non-serious bending without breaking of lower internodes did not affect yield. These results are consistent with the postulation that *japonica* varieties carrying *SD1-ja*, for example, Koshihikari and ‘Nipponbare’ (Murai *et al.* 2011), have been broadly cultivated in Japan. Consequently, it may be an appropriate way to substitute *SD1-ja* by *sd1-r* or the *sd1* allele of Jikkoku for developing short-culm *japonica* varieties, because the two alleles moderately reduce culm length without diminishing yielding ability.

Author Contribution Statement

BBR and MK performed the whole of the experiments and analyses. MB performed the whole of the experiments. LR and AM participated the experiments in 2019. HN performed the sequencing of the *sd1* locus of Taichung 65, and ascertained the descriptions regarding the polymorphisms at the *sd1* locus in the manuscript. HO performed the critical reading for the manuscript. MM developed the two tall isogenic lines of IR36, designed and performed the whole of the experiments, and wrote the manuscript.

Literature Cited

- Aquino, R.C. and P.R. Jennings (1966) Inheritance of semi dwarfism in an indica rice variety. *Crop Sci.* 6: 551–554.
- Asano, K., M. Yamasaki, S. Takuno, K. Miura, S. Katagiri, T. Ito, K. Doi, J. Wu, K. Ebana, T. Matsumoto *et al.* (2011) Artificial selection for a green revolution gene during *japonica* rice domestication. *Proc. Natl. Acad. Sci. USA* 108: 11034–11039.
- Ashikari, M., A. Sasaki, M. Ueguchi-Tanaka, H. Itoh, A. Nishimura, S. Datta, K. Ishiyama, T. Saito, M. Kobayashi, G.S. Khush *et al.* (2002) Loss-of-function of a rice gibberellin biosynthetic gene, *GA20oxidase* (*GA20ox-2*), led to the rice ‘Green revolution’. *Breed. Sci.* 52: 143–150.
- De Datta, S.K., A.C. Tauro and S.N. Balaoing (1968) Effect of plant type and Nitrogen level on the growth characteristics and grain yield of indica rice in the tropics. *Agron. J.* 60: 643–647.
- Futsuhara, Y. (1968) Breeding of a new rice variety Reimei by gamma-ray irradiation. *Gamma Field Symp.* 7: 87–109.
- Ikeda, K., C. Kawahara, J.E. Garcon, H. Nagano, Y. Koide, B.B. Rana, M. Murai and I. Takamura (2018) Genetic analysis of the early heading gene derived from rice variety Reimei. Report of the Hokkaido Branch, the Japanese Society of Breeding and Hokkaido Branch, the Crop Science Society of Japan 59: 14–15 (in Japanese).
- Kamimukai, M., T. Iwakura, T. Akaoka and M. Murai (2020) High-yielding *japonica* rice lines carrying *Ur1* (Undulate rachis-1) gene, possessing various heading times. *SABRAO J. Breed. Genet.* 52:

- 465–492.
- Kikuchi, F., N. Itakura, H. Ikehashi, M. Yokoo, A. Nakane and K. Maruyama (1985) Genetic analysis of semidwarfism in high yielding rice varieties in Japan. *Bull. Nat. Inst. Agr. Sci., Ser. D* 36: 125–145 (in Japanese with English summary).
- Mackill, D.J. and J.N. Rutger (1979) The inheritance of induced-mutant semidwarfing genes in rice. *J. Hered.* 70: 335–341.
- Maeda, H., T. Ishii, H. Mori, J. Kuroda, M. Horimoto, I. Takamura, T. Kinoshita and O. Kamijima (1997) High density molecular map of semidwarfing gene, *sd-1*, in rice (*Oryza sativa* L.). *Breed. Sci.* 47: 317–320.
- McKenzie, K.S., C.W. Johnson, S.T. Tseng, J.J. Oster and D.M. Brandon (1994) Breeding improved rice cultivars for temperate regions: a case study. *Aust. J. Exp. Agric.* 34: 897–905.
- Monna, L., N. Kitazawa, R. Yoshino, J. Suzuki, H. Masuda, Y. Maehara, M. Tanji, M. Sato, S. Nasu and Y. Minobe (2002) Positional cloning of rice semidwarfing gene, *sd-1*: Rice “Green revolution gene” encodes a mutant enzyme involved in gibberellin synthesis. *DNA Res.* 9: 11–17.
- Murai, M., S. Hirose, N. Suzuki, M. Yamane and S. Sato (1992) Effects of the dwarfing gene from Dee-geo-woo-gen and three others on high temperature tolerance at flowering. *Japan. J. Breed.* 42: 91–102.
- Murai, M., N. Shinbashi, S. Sato, K. Sato, H. Araki and M. Ehara (1995) Effect of the dwarfing gene from Dee-geo-woo-gen on culm and internode lengths, and its response to fertilizer in rice. *Breed. Sci.* 45: 7–14.
- Murai, M. and H. Yamamoto (2001) Allelic relationships and height effects of rice dwarfing genes from cvv. Dee-geo-woo-gen, Calrose 76 and Reimei determined in a constant genetic background. *SABRO J. Breed. Genet.* 33: 21–30.
- Murai, M., I. Takamura, S. Sato, T. Tokutome and Y. Sato (2002a) Effects of the dwarfing gene originating from ‘Dee-geo-woo-gen’ on yield and its related traits in rice. *Breed. Sci.* 52: 95–100.
- Murai, M., S. Sato, A. Nagayama, N. Ishii and S. Ihashi (2002b) Effects of a major gene *ur1* characterized by undulation of rachis branches on yield and its related traits in rice. *Breed. Sci.* 52: 299–307.
- Murai, M., K. Maruyama and F. Kikuchi (2003) Gene symbol registration No. 155. Gene symbol: *sd1-r*, *sd1-d*. *Rice Genet. Newsl.* 20: 5.
- Murai, M., T. Komazaki and S. Sato (2004) Effects of *sd1* and *Ur1* (Undulate rachis -1) on lodging resistance and related traits in rice. *Breed. Sci.* 54: 333–340.
- Murai, M. and Y. Endo (2006) A new rice cultivar ‘Hikarikko’: genes for short culm and earliness were introduced into ‘Koshihikari’ by backcrossing. *Breed. Res.* 8: 183–189 (in Japanese).
- Murai, M., H. Nagano, K. Onishi, A. Ogino, N. Ichikawa, H.B. KC and Y. Sano (2011) Differentiation in wild-type allele of the *sd1* locus concerning culm length between *indica* and *japonica* subspecies of *Oryza sativa* (rice). *Hereditas* 148: 1–7 (First published online on 22 Dec. 2010).
- Nagano, H., K. Onishi, M. Ogasawara, Y. Horiuchi and Y. Sano (2005) Genealogy of the “Green Revolution” gene in rice. *Genes Genet. Syst.* 80: 351–356.
- Nonaka, K., Y. Takagi, S. Matsuyuki, H. Yokoh, Y. Hirota, T. Shigyo, O. Shigetomi, H. Kishigawa, D. Nakamura, H. Kanayama *et al.* (1991) A new rice cultivar “Pikaichi”. *Kyushu Agricultural Research* 53: 1 (in Japanese).
- Ogi, Y., H. Kato, K. Maruyama and F. Kikuchi (1993) The effects on the culm length and other agronomic characters caused by semidwarfing gene at the *sd-1* locus in rice. *Japan. J. Breed.* 43: 267–275.
- Okada, M., Y. Yamakawa, K. Fujii, H. Nishiyama, H. Motomura, S. Kai and T. Imai (1967) On the new varieties of paddy rice “Hoyoku, Kokumasari and Shiranui”. *Bull. Kyushu Agr. Exp. Sta.* 12: 187–224 (in Japanese with English summary).
- Peng, S., K.G. Cassman, S.S. Virmani, J. Sheehy and G.S. Khush (1999) Yield potential trends of tropical rice since the release of IR8 and the challenge of increasing rice yield potential. *Crop Sci.* 39: 1552–1559.
- Rutger, J.N. (1983) Applications of induced and spontaneous mutation in rice breeding and genetics. *Adv. Agron.* 36: 383–413.
- Sasaki, A., M. Ashikari, M. Ueguchi-Tanaka, H. Itoh, A. Nishimura, D. Swapan, K. Ishiyama, T. Saito, M. Kobayashi, G.S. Khush *et al.* (2002) A mutant gibberellin-synthesis gene in rice. *Nature* 416: 701–702.
- Spielmeier, W., M.H. Ellis and P.M. Chandler (2002) Semidwarf (*sd-1*), “green revolution” rice, contains a defective gibberellin 20-oxidase gene. *Proc. Natl. Acad. Sci. USA* 99: 9043–9048.
- Suh, H.S. and M.H. Heu (1978) The segregation mode of plant height in the cross of rice varieties VI. Linkage analysis of the semidwarfness of the rice variety “Tongil”. *Korean J. Breed. Sci.* 10: 1–6.
- Tabuchi, H., N. Hashimoto, A. Takeuchi, T. Terao and Y. Fukuta (2000) Genetic analysis of semidwarfism of the *japonica* rice cultivar Kinuhikari. *Breed. Sci.* 50: 1–7.
- Takagi, Y., H. Kishikawa, M. Egashira, Y. Seo, H. Sonoda and T. Matsuno (1991) Transfer of semidwarf gene to rice variety Koshihikari by the backcross method. *Bull. Fac. Agr., Saga Univ.* 70: 55–60 (in Japanese with English summary).
- Tomita, M. (2009) Introgression of Green Revolution *sd1* gene into isogenic genome of rice super cultivar Koshihikari to create novel semidwarf cultivar ‘Hikarishinseiki’ (Koshihikari-sd1). *Field Crops Res.* 114: 173–181.
- Toriyama, K., K. Tsunoda, Y. Futsuhara, J. Wada, K. Fujimura and T. Nakahori (1967) On the new rice variety “Reimei”. *Bull. Aomori Agric. Exp. Stn.* 12: 6–17 (in Japanese with English summary).
- Yamazaki, K., K. Tanabu, M. Takadate, T. Mikami, K. Arima, Y. Kawamura, H. Tatsuta, M. Namioka, T. Kanazawa, K. Ono *et al.* (1987) A new rice cultivar “Mutsuhomare”. *Bull. Aomori Agric. Exp. Stn.* 30: 1–17 (in Japanese with English summary).