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学位論文全文に代わる要約
Extended Summary in Lieu of Dissertation

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学位論文題目：
Title of Dissertation

Effects of a dwarfing allele *sd1-d* at the *sd1* locus on yield and related traits, compared with tall alleles, in *indica* rice.

（イネの*sd1*座の矮性対立遺伝子*sd1-d*が*indica*品種の遺伝的背景において収量および関連形質に及ぼす作用）

学位論文要約：
Dissertation Summary

Rice (*Oryza sativa* L.) is one of the major staple food for more than 3.5 billion people in the world. Rice supplies 20% of the human intake of calorie in the world, while wheat and maize supply 19 and 5%, respectively. From this perspective, rice is the most important crop for food security globally. Increasing of rice production is a major countermeasure for the problem mention above. Hence, improvement of productivity per unit area in rice should be the key countermeasure to dissolve the problem.

In Nepal, rice is grown in three agro-ecological regions, viz. Terai, Mid Hills and High Hills by the combination of the two regimes of irrigation (irrigated and rain-fed) and the two topographic conditions (lowland and upland). Rice is the first major food crop followed by maize and wheat in the country. On the average, Nepalese people consumed about 120 kg of milled rice per person per year.

International Rice Research Institute (IRRI) in Philippines succeeded to develop the first semi-dwarf *indica* variety IR8, released in 1966, which possess high yielding ability adaptable to higher fertilizer application, and high lodging resistance. IR8 and its descendants drastically increase rice production in South East Asia and South Asia, which has been bruited as “Green revolution”.

The *sd1-d* is an allele at the *sd1* locus on chromosome 1, originating from Taiwanese variety ‘Dee-geo-woo-gen’. This allele has been playing important role for developing short-culmed and lodging-resistant *indica* varieties in rice, since the first *sd1-d*-carrying variety IR8 was released by International Rice Research Institute (IRRI) in 1966. One of IR8’s descendants, IR36 occupied the broadest cultivated area in Southeast Asia during 1980s. At present, following *sd1-d*-carrying varieties such as IR72 are grown in Southeast Asia and others tropical and subtropical areas.

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 *japonica* variety Taichung 65.

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 383 bp between the two sites of the exon 1 and exon 2, resulting in the loss of the enzymic function. The dominant allele *SD1* at the *sd1* locus is differentiated into *SD1-in* and *SD1-ja* which are harbored in *indica* and *japonica* subspecies, respectively. The effect of elongating culm was higher in *SD1-in* than in the *SD1-ja*, which could be one of the causes of intersub-specific difference in height. 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.

Murai *at al*. (2011) developed two tall isogenic lines of an *indica* variety IR36. The *sd1-d* allele of an *indica* variety IR36 was replaced with *SD1-in* or *SD1-ja* by 17 recurrent backcrosses with IR36, and two isogenic tall lines regarding the respective dominant alleles were developed by using an *indica* tall variety IR5867 and a *japonica* tall one 'Koshihikari' as donors, being denoted by "5867-36" and "Koshi-36", respectively. The present study was conducted to examine the effect of dwarfing gene *sd1-d* on yielding ability as well as lodging resistance, as compared with *SD1-in* and *SD1-ja.* The two isogenic tall lines and IR36 were grown in a paddy field in three years, not only yield and related traits but also lodging resistance and related traits were measured.

The two tall isogenic lines and IR36 were grown at the experimental paddy field of Agriculture and Marine Science, Kochi University, Nankoku, Japan (33°35′N) in 2017, 2018 and 2019. Twelve-day seedlings were transplanted with two seedlings per hill at a spacing of 30cm × 15cm (22.2 hills/m^2), on 3rd May in the three years. Randomized block design with three replications was employed. Chemical fertilizers were applied at the rates of 8.00, 6.86 and 7.62 g/m^2 in total for N, P_2O_5 and K_2O, respectively, in each of the years.

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 IR36. Grain yield of rice can be dissected into the four components: panicle number per panicle, spikelet number per panicle 1000-grain weight and ripened grain percentage.

Out 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. 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 below 1.5mm was estimated by subtracting the number of grains above 1.5mm from the number of all fertilized spikelets in each hill (Fig. 1).

Fig. 1. Classification of brown-rice grains by thickness in IR36.

The 80%-heading dates were 27th July in the two tall lines and 29th or 30th July in IR36 in both 2017 and 2018. In 2019, those of two tall lines were 28th July identically, and that of IR36 was 30th July.

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 m^2. Hence, it is inferred that *SD1-in* increases yielding ability compared with *sd1-d* on the genetic background of *indica* IR36. 5867-36 was higher in ripened-grain percentage than IR36, due to the higher fertilized-spikelet percentage than IR36, in the average of the three years. *SD1-in* seems to involve the effect of enhancing fertilized-spikelet percentage compared with *sd1-d*, resulting in the higher ripened-grain percentage, on the genetic background of *indica* IR36. *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.

Koshi-36 was not significantly different from IR36 in yield, in the average of three years, mainly because the increase of 1000-grain weight was compensated the decrease of panicle number per m^2 in Koshi-36. *SD1-ja* increase yielding ability compared with *sd1-d* on the genetic background of *japonica* Taichung 65. Hence *SD1-ja* does not affect yield on the genetic background of *indica* IR36. However, it is known that *sd1-d* decreases yielding ability compared with *SD1-ja* on the genetic background of *japonica* Taichung 65. It is suggested that when *sd1-d* is employed to develop *japonica* varieties, the possibility of diminishing yield should be taken into consideration.

5867-36 was higher in yield than Koshi-36 in the average of the three years, which was resulted from the increase in spikelets per panicle, ripened grain percentage and 1000-grain weight, despite the decrease in panicle number per m^2, compare with Koshi-36. Therefore, it is inferred that *SD1-in* increases yield ability, compared with *SD1-ja,* on the genetic background of *indica* IR36. 5867-36 was higher in ripened-grain percentage than Koshi-36, due to its higher percentage of ripened grains to fertilized spikelets than Koshi-36, in the average of the three years. *SD1-in* seems to involve the effect of enhancing percentage of ripened grains to fertilized spikelets compared with *SD1-ja*, resulting in the higher ripened-grain percentage, on the genetic background of *indica* IR36. *SD1-in* seems to increase the width and thickness of grain by producing wider lemmas, compared with *SD1-ja*, resulting in the higher 1000-grain weight, on the genetic background of IR36.

The effects of *sd1-d* on lodging resistance and related traits, compared with *SD1-in* and *SD1-ja*, were examined, using the same materials of the two tall lines and IR36 grown in 2017. 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. Lodging resistance in paddy field is lowest at about 20 to 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.

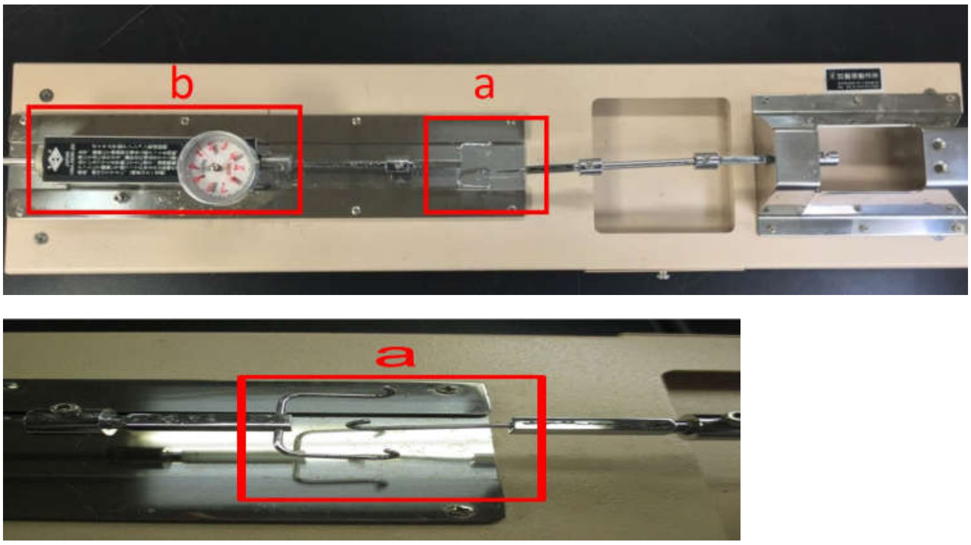

Fig. 2. Breaking Strength Meter for Cereal Culm

Note: - 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.

Seko (1962) observed that the breaking occurred mainly at the 4th or 5th internode in lodged rice plants, and it was frequently when the length of the internode was longer than 6 cm. 5867-36, Koshi-36 and IR36 were 12.9, 6.5 and 3.9 cm in 4th internode length, respectively, and 7.0, 3.9 and 2.3 cm, respectively in 5th internode length. The 5th internode length of IR36 was too small 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 measurable commonly. 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, and the 1st to 4th internodes, leaf sheaths and leaf blades) (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 (Fig. 2). Measurements were performed at the two times of ripening, viz. 10 days and 21 days after 80%-heading. At each of the times, the longest culm in each of 24 hills was sampled from each of the three replications (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.

s*d1-d* decreased culm length by 42.3 and 21.1 cm, in the average of the three years, as compared with *SD1-in* and *SD1-ja*, respectively, on the genetic background of IR36. Index of lodging (g·cm/g) was 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 the 10th day after 80%-heading. Hence, *sd1-d* enhances lodging resistance due to the decreases in the length and weight above the 4th internode inclusive, and the increase of breaking strength. The effect of *SD1-in* on lodging resistance is lower than that of *SD1-ja*. Serious lodging was observed in 5867-36 at the late stage of maturity in the three experimental years. Hence, it is crucial to use *sd1-d* in breeding programs of *indica* rice, particularly for developing lodging-resistant varieties adaptable to high fertilizer application.