Genetic Analysis of Semidwarfness and Their Significance for Breeding of High-Yielding Varieties in Rice

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A breakthrough in rice production has been attained through the exploitation of semidwarf varieties in Japan since the early 1960's. In the Northeast a semidwarf variety Reimei which was induced from Fujiminori by gamma-ray irradiation dominated fertile rice lands with its high response to an increased fertilizer level[4,5]. Likewise, in the Southwest of Japan a series of new high-yielding varieties, namely Hoyoku, Kokumasari and Shiranui were released from a cross between Zensho 26 and a native semidwarf variety, Jikkoku. The Jikkoku derivatives have changed the rather stagnant yield in the southern Japan into the most productive one since the early 1960's[14]. The two sources of semidwarfism have made up a basic frame of current varieties through subsequent hybridization of them with other varieties.

Semidwarf varieties gave more drastic impact on tropical rice cultivation than they were in Japan. Taichung Native 1(TN1) was released in 1956 in Taiwan from a cross of a dwarf Chinese variety, Dee-geo-woo-gen (DGWG), and a local Taiwanese variety, Tsai-yuan-chon. In 1962, DGWG was used in a cross with Peta, a tall vigorous variety, and resulted in a release of IR-8, which was rapidly adopted in irrigated regions across tropical Asia. Along with subsequent incorporation of disease and insect resistance into the semidwarf varieties, a series of studies have been continued to analyze the genes for the semidwarfism at the International Rice Research Institute(IRRI). As the results, a single gene partially recessive for shortness was found responsible to the height reduction in the semidwarf varieties, TN1, I-geo-tze(IGT) and DGWG[1,6,8]. Similar studies extended to collected semidwarfs by IRRI indicated that the majority of presently known semidwarfs possess the same, or allelic dwarfing genes[9,10,11]. Through the researches, a few other semidwarf sources have been reported to be nonallelic to the semidwarf gene of DGWG. A study on some American short-statured varieties showed that they have a semidwarfism with an inheritance type of a quantitative nature[8]. One of the semidwarf source different from the DGWG's was confirmed in a line from CP 231/SLO-17(CPSLO), which has been used extensively in the IRRI's hybridization program. Many of the present high-yielding rice varieties are descent of CPSLO mostly through IR127 and IR661 lines (IR24, IR26, IR28, IR36 and Miliyang 21, 22 and 23 of the Republic of Korea), although the extent to which this particular source is actually contributing to their dwarfness is not known.

The utilization of the semidwarfism has brought another breakthrough in rice breeding in the Republic of Korea and California, USA; the 'Green Revolution' in Korea is a direct achievement of an intensive use of the tropical dwarfs[2]; a new high-yielding type in California is reported to possess the dwarfing gene

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allelic to DGWG[15]. In the central regions of the main island in Japan some newly released varieties are shorter than those being replaced.

Undoubtedly, the use of the semidwarfism is one of the most brilliant successes in the area of plant breeding in this century. However, it should not be overlooked that the prevailing gene for the semidwarfism in mostly the one identified in DGWG despite the difference in the donor varieties. With a single gene dominating large crop areas there may be a potential danger of loosing a genetic diversity. Accordingly, the search for dwarfing genes which are non-allelic to the DGWG gene is in progress at IRRI and in India[10,11,18]. On the other hand, the expression of the semidwarfism gene in a different set of modifying genes has drawn researchers' interest, because such knowledge is indispensable in identifying the dwarfing genes. Diallel crosses have been made to study the genic effects to obtain more detailed information for the semidwarfism[3,15].

In Japan so far little has been known about the interrelationship between the semidwarfism genes in the japonicas and those in indicas. But the identification of the dwarfing genes becomes increasingly important, because the use of the semidwarfing gene is very closely related to the breeding for high-yielding varieties. Moreover, the frequent use of the Korean semidwarf varieties as a source for yield increase makes it necessary to determine whether the semidwarf gene in Korean varieties is allelic to those in Japanese short-statured varieties.

Genetic analysis of Japanese semidwarf rice varieties[7]

The reason why there has been few trial to identify the dwarfing genes in the two groups of rice varieties, i.e., indicas and japonicas, can be explained partly by the fact that each source for the semidwarfism is introduced independently through different native varieties or by artificial mutation, and naturally considered to be different from each other. Another reason for the scarcity of the previous work to relate the dwarfing genes in japonicas to those in indicas is the high-sterility and extraordinarily wide segregation in many characters, which always occur in the cross between indicas and japonicas.

Obviously, for the study of an identity of a gene in japonica varieties with any similar ones in indicas a particular method is needed to overcome the difficulty mentioned above. One of the approaches to study the interrelationship between a gene in japonicas and ones in indicas is provided by the use of isogenic lines. By transferring the semidwarf gene from TN1 and another semidwarf gene from Shiranui into an ordinary variety, Norin 29 through 4 time backcrosses, while retaining the semidwarf stature, two series of near isogenic lines were developed, and designated as SC 2 and 3 (TN1/5*Norin 29), and SC 4

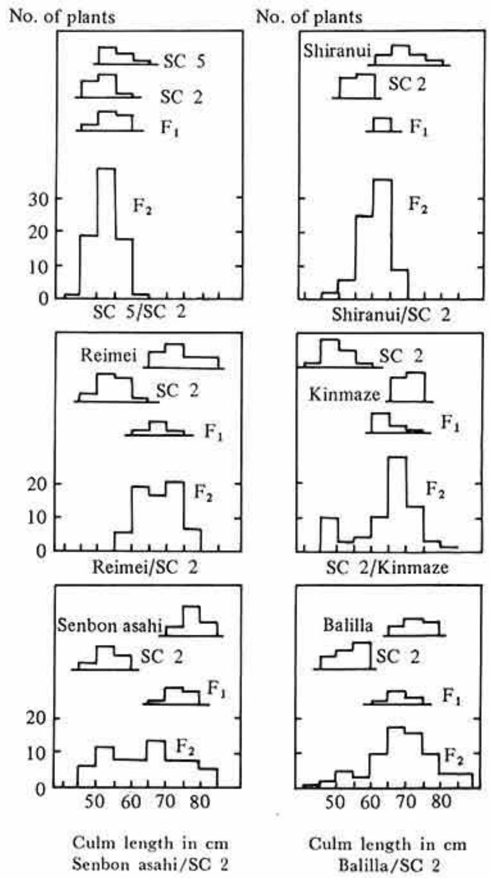

Fig. 1. Distribution of culm length in F_1, F_2 and parents

and 5 (Shiranui/5*Norin 29)[7].

In 1979 several crosses were made between the two series of the semidwarf isogenic lines. At the same time, SC 2 was crossed as a tester to some semidwarf, high-yielding varieties. In 1980 the parents, F_1 and F_2 populations for each cross were grown to measure their segregation pattern for culm length (Fig. 1).

Non-genetic segregation in the F_2 of the cross between SC 2 and SC 5 indicated that the donor of the semidwarf genes, namely DGWG and Jikkoku have an identical semidwarf gene. An attempt to identify the gene by a direct cross between TN1 and Shiranui (with Jikkoku's gene) was not successful because of the frequent sterility and the segregation in heading date which interferred with the expression of the segregation in culm length.

In the cross between Reimei and SC 2, the range of the segregation in F_2 was narrower than that between the two parents. Apparently, there was no complete recovery of the type of the shorter parent in the F_2. Therefore, it was suggested that Reimei and SC 2 have a common dwarfing gene, although there seemed to be some modifiers, of which those elongating the height appeared to be in Reimei, while those reducing the height in SC 2. Probably, few individual plants in the F_2 realized the cumulation of only those modifiers reducing the stature. This explains the non-recovery of the parent dwarf type in the experiment.

The remaining three crosses between SC 2 as a tester and Kinmaze, SC 2 and Senbon Asahi, and SC 2 and Balilla showed a significant segregation in culm length at their F_2's, possibly due to some dominant gene allelic to the recessive semidwarfism gene of DGWG.

In 1980 some other high-yielding varieties with semidwarf stature were tested by crossing them to Shiranui which was found to possess the same dwarfing gene as DGWG's. A preliminary observation suggested that at least two semidwarf varieties, Hokuriku 100 (an induced mutant from Koshihikari) and Kochihibiki (from a cross of Akibare/2* Kochikaze) have other dwarfing gene non allelic to the one in DGWG (Table 1). Although further studies are necessary to conclude that they have some other dwarfing gene, the gene would be useful as the two varieties are already noted for their high yield.

Table 1. Culm length of F_1 and parents in the crosses between semidwarf varieties

Crosses/parents	heading date	culm length
		cm
Etsu-nan 77	Aug. 17	69.3±3.4
Etsu-nan 77/Shiranui	〃 28	76.2±4.1
Shiranui	Sept. 4	64.2±4.9
Hokuriku 100	Aug 17	66.9±3.2
Hokuriku 100/Shiranui	〃 27	82.2±4.3
Shirauni	Sept. 4	67.4±4.3
Kochihibiki	Aug. 21	69.4±4.3
Kochihibiki/Shiranui	〃 29	81.0±2.9
Shiranui	Sept. 4	70.2±3.3
Balilla	Aug. 11	78.2±5.7
Balilla/Shiranui	〃 23	82.2±3.4
Shiranui	Sept. 4	68.9±4.6
Reimei	Aug. 12	72.6±4.3
Remei/Shiranui	〃 22	75.6±3.3
Shiranui	Sept. 4	68.4±4.9
Shiranui	Sept. 1	64.0±4.4
Shiranui/SC 4	Aug. 24	60.9±1.8
SC 4	〃 21	52.4±5.1
Shiranui	Sept. 1	63.9±3.1
Shiranui/Taich. N.1	〃 12	69.6±1.4
Taichung Native 1	Aug. 29	59.3±5.4

Note: Figures after "±" indicate standard deviations.

Implication of the gene identification

A recent work[18] in Korea has shown that the semidwarf gene in a variety Tongil (IR 8/ Yukara//TN1) is located in the third linkage group[18]. Presumably, this locus is liable to mutate, and to bear the semidwarfism gene which has been utilized in the breakthrough of yield level, independently in different regions of the world; in the tropics in the form of TN1 and IR 8; in the Southwest of Japan through the Jikkoku-derivatives, in the Northeast of Japan by an induced mutant; later in

Korea as the base for the green revolution; and in California, USA in the form of Calrose 76.

Although the common gene is demonstrated to be a base for yield increase in the different regions of the world, it is confirmed that there are some alternative genes which seem to be also responsible for a yield increase perhaps in some limited areas. The comparative study of the high-yielding dwarfism should be in a focus point in the genetics of rice.

On the other hand, despite the identical dwarf gene it appears that different groups of rice varieties are not uniform in their response to an increased fertilizer and in other respects. For an example, the Korean semidwarf varieties seem to be more responsive to a high input of fertilizer than some Japanese high-yielding varieties as have been shown through extensive comparative studies. One of the reasons for the high fertilizer response in Korean varieties seems to be explained by their low level of endogenous gibberellic acid (GA)[17]. According to a recent study (by Matsunaga et al.[14]) most of indica varieties are sensitive to exogenous GA suggesting their low GA level, and regardless of the semidwarf gene of DGWG all the Japanese varieties seem to have relatively high level of the endogenous GA (less sensitive to exogenous GA). Therefore, Matsunaga et al.[13] assume that the high fertilizer response in indica dwarf is complemented by the low GA level, which is perhaps controlled by a gene system independent of the dwarfism. If so, even the current Japanese varieties with the same dwarfing gene as DGWG can be improved into a type more responsive to an increased fertilizer through the incorporation of the low GA level from indica varieties.

A period of nearly twenty years has passed since the extensive use of the semidwarfism gene. However, the implication of the genic relationship is being elucidated only for the past few years, giving promising ideas for the further improvement of high-yielding varieties.

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