Semi-Dwarfing Genes and Resistance to Lodging in Japanese Wheat Varieties

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Introduction

There are two types of semi-dwarfing genes in bread wheat, *Triticum aestivum* L. The first type is characterized by the gibberellin (GA)-insensitivity whereby stem elongation is not promoted by external application of GA regardless of the growth stage of wheat. Those genes such as *Rht1* and *Rht2* of Norin 10, and *Rht3* of Tom Thumb correspond to this type. The second type of semi-dwarfing genes is characterized by the GA-sensitivity and the Akakomugi genes, *Rht8* and *Rht9*, are typical examples of this type.

Both types have been used for shortening plant height and alleviating lodging susceptibility of wheat, and concurrent increases in grain yield have been and are being recorded in various parts of the world. Japanese wheat breeders have also used these semi-dwarfing genes, and many high-yielding varieties have been developed. However, any genotype associated with the semi-dwarfism of most Japanese varieties has not been documented yet.

Although several strategies other than the modification of plant height can be adopted for improving the resistance to lodging, information on the characters related to the lodging resistance is limited.

This paper describes the results of a series of the experiments, in which the culm length, GA-responsiveness, *Rht* genotypes and lodging resistance in Japanese wheat varieties have been subjected to study.

Culm length and GA-responsiveness

The final culm length in the field and the GA-responsiveness at the seedling stage of 148 wheat varieties (Norin 1 to Norin 129 and other 19 varieties, including 11 local and 8 foreign varieties used as parents in the pedigrees of Norin varieties) were investigated[8]. The results are given in Tables 1 and 2. Out of 148 varieties, 105 and 43 varieties were GA-insensitive and GA-sensitive, respectively.

The GA-insensitive group consisted of 99 Norin varieties, comprising most of the modern varieties and 6 local varieties. The culm length of these varieties was less than 90 cm in general, and approximately 70 to 80 cm in most of the modern varieties in particular.

The GA-sensitive group consisted of 30 Norin varieties, 5 local and 8 foreign varieties. All the foreign varieties tested were GA-sensitive. The culm length of the GA-sensitive varieties mostly exceeded 100 cm. Especially, the culm length of the local and foreign varieties, which were approximately 130 to 160 cm, were generally higher than that of a majority of the GA-sensitive Norin varieties. It is likely that Japanese breeders have unconsciously selected the genotypes of either GA-insensitivity or GA-sensitivity. However, the phenotypic selection by the breeders had resulted in a continuous reduction of the wheat plant height. The varieties Norin 43, Norin 45 and Fukuwasekomugi as well as Akakomugi, all of which belong to the GA-sensitive group, had a short culm

Table 1. Culm length of GA-insensitive wheat varieties

Variety (culm length, cm)
Norin 1 (81), Norin 2 (97), Norin 4 (88), Norin 5 (73), Norin 6 (81), Norin 7 (80), Norin 9 (70), Norin 10 (62), Norin 11 (76), Norin 12 (77), Norin 13 (81), Norin 14 (84), Norin 16 (75), Norin 17 (83), Norin 18 (74), Norin 19 (86), Norin 21 (71), Norin 24 (98), Norin 25 (78), Norin 26 (85), Norin 28 (76), Norin 30 (78), Norin 32 (90), Norin 33 (102), Norin 44 (81), Norin 48 (68), Norin 49 (84), Norin 50 (74), Norin 52 (78), Norin 53 (89), Norin 54 (70), Norin 55 (81), Norin 56 (84), Norin 57 (78), Norin 58 (97), Norin 59 (75), Norin 60 (79), Norin 61 (89), Norin 63 (78), Norin 64 (71), Norin 65 (96), Norin 66 (98), Norin 67 (82), Norin 68 (71), Norin 69 (87), Norin 70 (87), Norin 71 (87), Norin 72 (91), Norin 73 (79), Norin 74 (90), Yuyakekomugi (81), Susonokomugi (87), Mutsubenkei (109), Iyokomugi (86), Aobakomugi (80), Nanbukomugi (86), Akatsukikomugi (71), Yukichabo (76), Hikarikomugi (88), Myokokomugi (84), Ebisukomugi (84), Hitsumikomugi (97), Kokeshikomugi (68), Okukomugi (105), Sakyukomugi (87), Yutakakomugi (77), Danchikomugi (87), Shirasagikomugi (81), Junreikomugi (82), Kitakamikomugi (96), Fujimikomugi (89), Hayatokomugi (87), Mikunikomugi (85), Shimofusakomugi (81), Miyaginokomugi (82), Nichirinkomugi (71), Ushiokomugi (77), Omasekomugi (77), Hiyokukomugi (72), Mukakomugi (101), Zenkojikomugi (80), Kobushikomugi (74), Sakigakekomugi (70), Hachimankomugi (77), Horoshirikomugi (87), Takunekomugi (79), Hanagasakomugi (79), Shiroganekomugi (64), Gogatsukomugi (71), Toyohokomugi (80), Setokomugi (71), Chikushikomugi (78), Shirowasekomugi (68), Asakazekomugi (66), Fukuhokomugi (77), Minaminokomugi (81), Chihokukomugi (67), Wakamatsukomugi (81), Nishikazekomugi (67), Akadaruma (81)[a], Hayakomugi (75)[a], Hiroshima Shipree (92)[a], Shirochabo (94)[a], Shirodaruma (72)[a], Yushoki 347 (73)[a]

a): Local varieties.

Table 2. Culm length of GA-sensitive wheat varieties

Variety (culm length, cm)
Norin 3 (146), Norin 8 (132), Norin 15 (106), Norin 20 (95), Norin 22 (90), Norin 23 (95), Norin 27 (94), Norin 29 (121), Norin 31 (98), Norin 34 (94), Norin 35 (116), Norin 36 (95), Norin 37 (96), Norin 38 (101), Norin 39 (111), Norin 40 (102), Norin 41 (92), Norin 42 (90), Norin 43 (87), Norin 45 (81), Norin 46 (96), Norin 47 (91), Norin 51 (91), Norin 62 (109), Norin 75 (133), Hatamasari (98), Furutsumasari (104), Haruhikari (124), Haruminori (122), Fukuwasekomugi (72), Akakawaaka (145)[a], Akakomugi (87)[a], Ejima (127)[a], Jarl Weizen (116)[b], Marquis (137)[b], Martin's Amber (148)[b], Rieti (127)[b], Sapporoharukomugi (163)[a], Shisen 1 (100)[a], Turkey Red (139)[b], Turkey Red II (132)[b], Velvet (128)[b], Wilhelmina (139)[b]

a): Local varieties.
b): Foreign varieties.

ranging from 70 to 90 cm in length. These short culms were comparable to those of the GA-insensitive varieties. Norin 43, Norin 45 and Fukuwasekomugi may bear both or either of the Akakomugi genes, *Rht8* and *Rht9*.

Identification of GA-insensitive *Rht* genes

The GA-insensitive *Rht* genes of 18 Japanese modern varieties and local varieties were identified[9].

The length of the first leaf sheath of the GA-insensitive parents and their F_1's was less than 6 cm. F_2 seedlings could be classified readily into those which responded to the gibberellin treatment and the insensitive ones (Plate 1.A-F and Fig. 1). Those varieties which responded to gibberellin showed a distinct phenotype, producing thin stems with a first leaf sheath of more than 6 cm in length and light green leaves. As shown in Plate 1.D,F and Fig. 1, the measurement of the length of the first leaf sheath showed that the insensitive F_2 population of the cross involving the *Rht3* tester line could be classified into two distinct groups; i.e., highly insensitive (below 3 cm) and insensitive (3–6 cm)

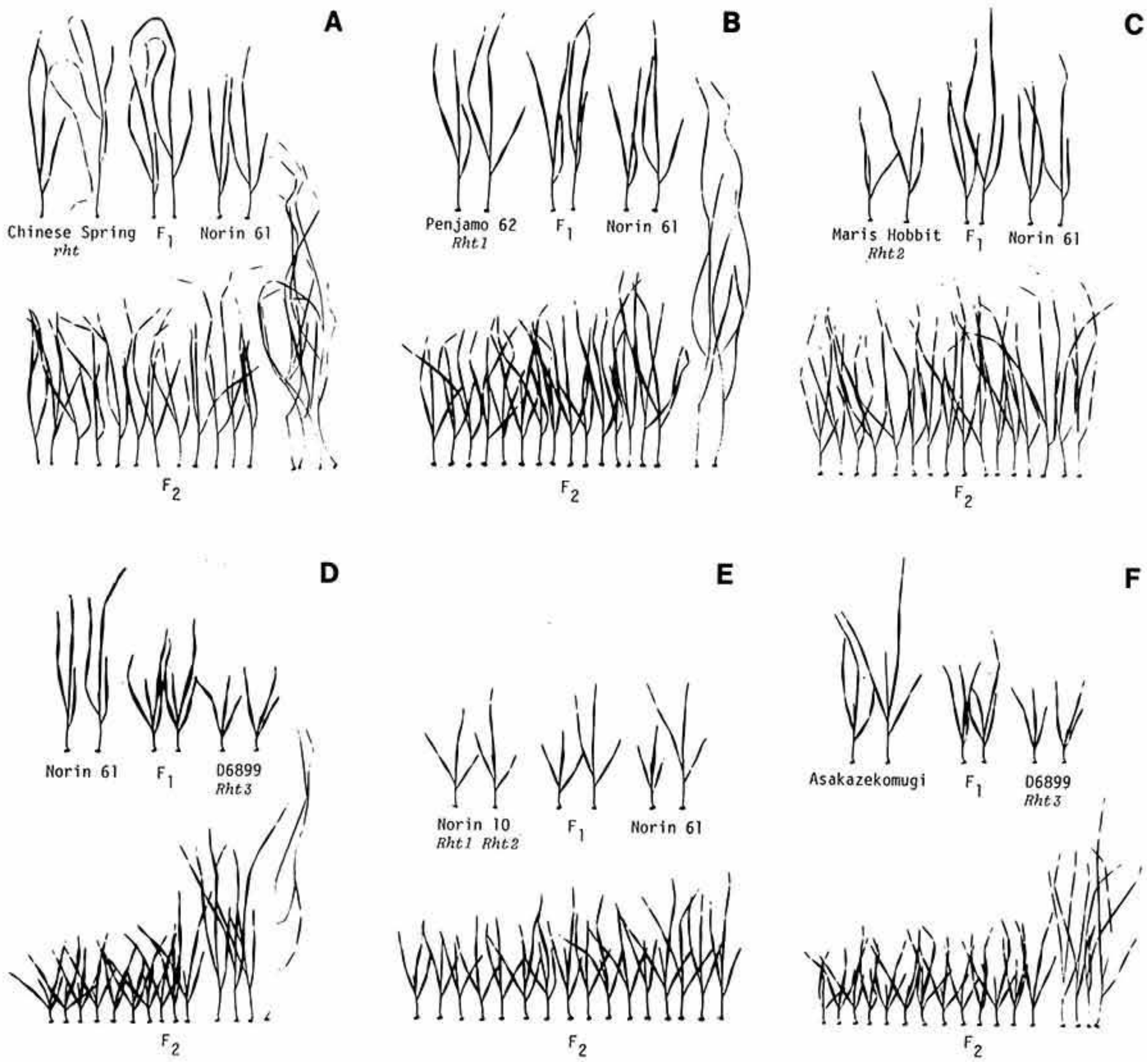

Plate 1. Seedlings after 21 days of treatment with 10 ppm gibberellic acid
A–F) P_1, P_2, F_1: left, untreated; right, treated.
A) Chinese Spring (*rht*) × Norin 61
F_2: left 12, insensitive; right 4, sensitive,
B) Penjamo 62 (*Rht1*) × Norin 61
F_2: left 15, insensitive; right 2, sensitive.
C) Maris Hobbit (*Rht2*) × Norin 61
F_2: all 16, insensitive.
D) Norin 61 × D6899 (*Rht3*)
F_2: left 10, highly insensitive; middle 3, insensitive; right 1, sensitive.
E) Norin 10 (*Rht1 Rht2*) × Norin 61
F_2: All 16, insensitive.
F) Asakazekomugi × D6899 (*Rht3*)
F_2: left 13, highly insensitive; right 4, insensitive.

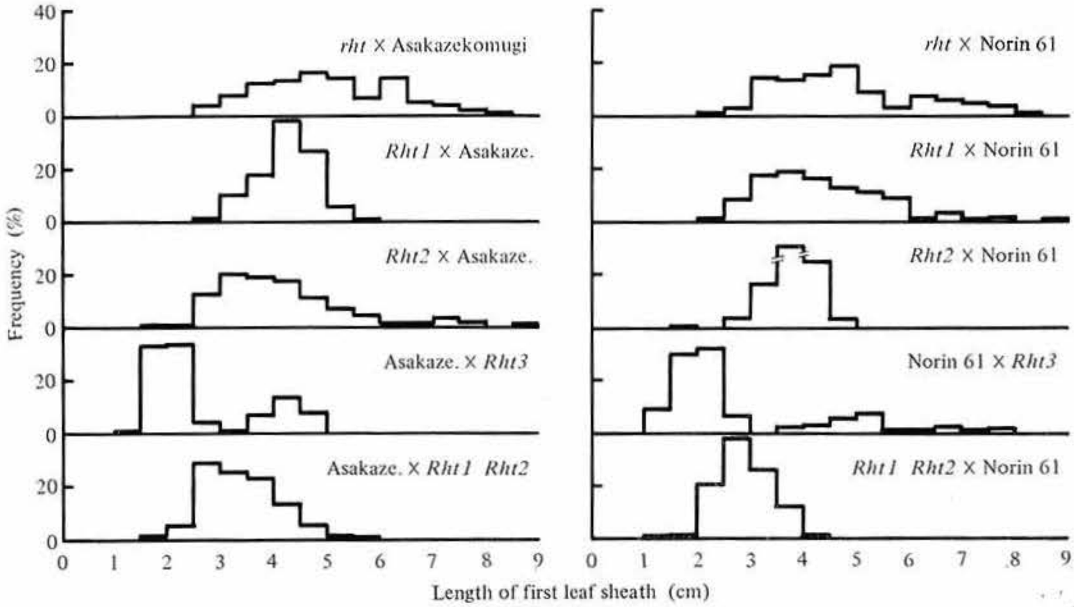

Fig. 1. Frequency distribution of the length of the first leaf sheath of F_2 seedlings derived from the crossing of Japanese wheat varieties with *Rht* tester lines (Yamada, 1989. Published with permission of Kluwer Academic Publishers, 3300 AA Dordrecht, Holland)
The leaf sheath length was measured after 21 days of treatment with 10 ppm gibberellic acid.

Table 3. Classification of *Rht* genotypes of Japanese modern and local varieties of wheat*

Genotype	Variety		
Rht1	Asakazekomugi Nishikazekomugi	Chikushikomugi Setokomugi	Fukuhokomugi Shiroganekomugi
Rht2	Akadaruma[a)] Shirochabo[a)] Chihokukomugi Nanbukomugi	Hayakomugi[a)] Shirodaruma[a)] Horoshirikomugi Norin 61	Hiroshima Shipree[a)] Yushoki 347[a)] Kitakamikomugi Takunekomugi

a): Local varieties.
* Yamada, 1989. Published with permission of Kluwer Academic Publishers, 3300 AA Dordrecht, Holland.

groups, indicating that the *Rht3* gene could be distinguished from the other *Rht* genes by the elongation test of the first leaf sheath associated with the GA_3 treatment.

As shown in Table 3, the genotype of the following six modern varieties; Asakazekomugi, Chikushikomugi, Fukuhokomugi, Nishikazekomugi, Setokomugi and Shiroganekomugi, was *Rht1*. All these six varieties are leading varieties in the central and southwestern regions of Japan, including the Kanto, Tokai, Kinki, Chugoku, Shikoku and Kyushu districts. The genotype of the other six modern varieties such as Chihokukomugi, Horoshirikomugi, Kitakamikomugi, Nanbukomugi, Norin 61 and Takunekomugi, was *Rht2*. These varieties except for Norin 61 are leading varieties in the northern part of Japan; i.e., Hokuriku, Tohoku and Hokkaido. Among the leading varieties in the central and southwestern regions of Japan, only Norin 61 has an *Rht2* genotype. These results indicate that the geographical distribution of the *Rht* genotypes in the Japanese modern varieties was clearly localized, suggesting that the varieties with the *Rht1* and *Rht2* genotypes may have a different adaptability to agro-ecological environments.

All the local varieties tested carried only *Rht2*. Among the *Rht2* modern varieties tested, all the varieties except for Norin 61 were related to the sources of the local varieties in their pedigrees. Based on pedigree studies, it is assumed that *Rht2* of Norin 61 was derived from Hizakiri although this local variety was not tested in the present study. All the *Rht1* modern varieties tested were also related to the *Rht2* local varieties in their pedigrees. However, none of these modern varieties carried *Rht2*. The gene *Rht1* of these varieties was probably derived from other sources which were not included in this study.

Among the 12 modern varieties, no variety carried both *Rht1* and *Rht2*. Allan and Pritchett[1] reported that lines with such genotypes out-yielded the corresponding tall lines but not the single-gene isogenic lines as a consequence of reduced grain size. In the course of the wheat breeding program in Japan aiming at a high yielding ability, it is very likely that the wheat breeders have unconsciously selected the genotypes carrying either the *Rht1* or *Rht2* gene.

Among all the varieties tested, no variety carried *Rht3* which significantly reduces plant height and confers a greater GA-insensitivity than *Rht1* and *Rht2*. Also in a more extensive study on culm length and GA-insensitivity[8], no Japanese wheat varieties with phenotypes comparable to those conferred by *Rht3* were observed in the local varieties and the varieties developed in the breeding program as well. Due to the extreme dwarfism conferred by *Rht3*, the varieties bearing such a genotype could not be used commercially in other countries as well[5]. In addition to their extreme dwarfism, the *Rht3* varieties which are most susceptible to heat stress are easily sterile[7] and suffer greatly from open pollination[10]. However, it was shown that the low production of alpha-amylase in the germinating *Rht3* grains corresponded to a resistance mechanism to preharvest sprouting damage[2-4]. In Japan, the preharvest sprouting damage caused by rainfall is one of the most serious problems in wheat production because the harvest time coincides with the rainy season. In their breeding programs in alleviating such a damage, some European breeders have adopted to use *Rht3*[5]. This gene would be worthwhile to be also used in the breeding program of Japan. In practice, however, an adequate strategy should be established in order to solve the problems relating to extreme dwarfism and reduced fertility associated with the *Rht3* gene.

Lodging resistance

The lodging resistance and its related characters were investigated in 12 representative varieties in the central and southwestern regions of Japan[6].

The lodging resistance within a variety decreased with the increase in grain yield. As shown in Table 4, Shiroganekomugi (*Rht* genotype: *Rht1*), Asakazekomugi (*Rht1*), Nishikazekomugi (*Rht1*) and Kanto 100 (*Rht1*, Yamada unpublished) showed a high lodging resistance. On the other hand, Norin 61 (*Rht2*), Norin 26 (*Rht1*, Yamada unpublished) and Shirasagikomugi (*Rht2*, genealogically estimated) showed a low lodging resistance. The lodging resistance of Omasekomugi (*Rht2*, Yamada unpublished), Setokomugi (*Rht1*), Chikushikomugi (*Rht1*), Fukuhokomugi (*Rht1*) and Fukuwasekomugi (Akakomugi type but genotype is unknown) was intermediate.

All the varieties with a high lodging resistance as well as a majority of the varieties which showed an intermediate lodging resistance had an *Rht1* genotype. On the other hand, all the varieties except for Norin 26 having a low lodging resistance carried an *Rht2* genotype. These results suggest that *Rht1* be intrinsically superior to *Rht2* in im-

Table 4. Average grain yield, average lodging rate and frequency of non-lodging in the range of grain yield between 5 and 7 t/ha

Variety	Average grain yield (t/ha)	Average lodging rate*	Frequency of non-lodging (%)
Norin 61	4.49	1.7	10
Norin 26	4.13	1.3	18
Shirasagikomugi	4.40	1.4	18
Omasekomugi	5.03	1.2	35
Setokomugi	5.52	1.1	38
Chikushikomugi	5.14	0.6	50
Fukuhokomugi	4.84	0.6	59
Fukuwasekomugi	4.17	0.7	64
Kanto 100	5.02	0.3	68
Nishikazekomugi	4.94	0.4	70
Asakazekomugi	4.60	0.2	76
Shiroganekomugi	4.68	0.2	77

The above results were obtained in the performance tests for recommendable varieties carried out during the period 1978 to 1984 throughout Japan.
* 0 (no lodging) – 5 (complete lodging).

Table 5. Varietal variation of characters related to the lodging resistance

Variety	Culm length (cm)	CW (g/culm)	CW/TW (%)	BM	LI	BR	SR	No. of roots per culm	ND
Norin 61	90	0.14	7.0	604	129	14	1.02	9.0	9.5
Fukuhokomugi	84	0.15	6.7	636	106	78	1.21	10.9	9.7
Shiroganekomugi	76	0.16	8.3	679	68	168	1.67	10.5	10.9
Nishikazekomugi	77	0.14	7.8	656	77	162	1.65	9.6	10.1
Kanto 100	78	0.16	8.7	726	74	157	1.57	9.9	13.0

CW: Culm weight of basal 10 cm part.
TW: Top dry weight.
BM: Bending moment of culm at breaking.

LI: Lodging index $= \frac{(\text{Culm length})^2 \times (\text{Top fresh weight})}{(\text{Dry weight of culm}) \times \text{BM}} \times 100$

BR: Bending rigidity of culm.

$$SR = \frac{\text{BR} \times (\text{Culm length}) + (\text{Whole fresh weight}) \times (\text{Height of the centroid at weighing})}{(\text{Whole fresh weight}) \times (\text{Height of the centroid})}$$

ND = (No. of roots per culm) × (Diameter of root).

proving the lodging resistance.

As shown in Table 5, the varieties having a high lodging resistance showed a shorter culm and a greater bending rigidity of culm, or a stronger culm. They also showed a higher root index represented by the product of the number of roots per culm and the diameter of root. As a consequence, all of those varieties showed a stronger bearing capacity of roots.

In improving lodging resistance and yielding ability of the Japanese bread wheat, the breeding strategy adopted by the breeders has generally placed emphasis on shortening of the plant height by using the semi-dwarfing genes. Recent studies have indicated that these semi-dwarfing genes exhibit pleiotropic effects on other plant characters including grain quality, and phenotypic expressions of those genes are affected by their interactions with the components of agricultural environments as well as by other major genes. The accumulated information on these genes will certainly be useful for the breeders in establishing their strategies to develop high yielding wheat varieties with a better quality in the future.

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