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Classification of GA response, *Rht* genes and culm length in Japanese varieties and landraces of wheat

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Summary

The GA response, *Rht* genes and culm length of 133 Norin varieties, 6 breeding lines and 16 landraces of Japanese wheat were investigated. Out of 133 Norin varieties tested, 103 were GA-insensitive and 30 GA-responsive. The 6 breeding lines were all GA-insensitive. Out of 16 landraces tested, 10 were GA-insensitive and 6 GA-responsive. Among the 10 GA-insensitive landraces, only Daruma had a *Rht1* genotype. The other 9 had a *Rht2* genotype. None of the landraces tested carried both *Rht1* and *Rht2* or *Rht3*. Out of the 103 GA-insensitive Norin varieties, 22 carried only *Rht1*, another 79 carried only *Rht2*, and only Norin 10 and Kokeshikomugi carried both *Rht1* and *Rht2*. No tested variety carried *Rht3*. Some Norin varieties carrying *Rht2* showed tall culms comparable to that of the *rht* tester line Chinese Spring. These results suggest that these varieties had a nullifier or modifier gene(s) or height promoting genes in the background controlling the height-reducing effect of *Rht2*. Conversely, six GA-responsive Norin varieties were as short as Akakomugi which carries the GA-responsive *Rht* genes, *Rht8* and *Rht9*. They also seemed to carry a GA-responsive *Rht* gene or genes, and moreover all but one may carry gene(s) other than the Akakomugi genes. The origin of *Rht1* and *Rht2* of Norin 10 was speculated on the GA-response and *Rht* genotypes of its related varieties and landraces.

Introduction

In bread wheat, *Triticum aestivum* L., two main sources of semi-dwarfing genes have been successfully used for reducing plant height and lodging susceptibility of wheat. Concurrent increases in grain yield have been and are being recorded in various parts of the world. These two sources are the Norin 10 genes *Rht1* and *Rht2* which are characterized by gibberellin (GA) insensitivity and the Akakomugi genes *Rht8* and *Rht9* which are GA sensitivity.

Rht1 is carried on chromosome 4B (Gale & Marshall, 1976; see later – chromosome designation), while *Rht2* is localized at a homeologous position on the short arm of chromosome 4D (Gale et al., 1975; McVittie et al., 1978). *Rht3,* a stronger GA insensitive gene (Zeven, 1969) carried by Tom Thumb wheats (Morris et al., 1972) is allelic to *Rht1* (Gale & Marshall, 1976). *Rht8* and *Rht9* are carried on chromosomes 2D and 7B, respectively (Law et al., 1981). Although the GA-responsive *Rht* genes are difficult to detect, the *Rht1, Rht2* and *Rht3* genes can readily be detected at the seedling stage by their insensitivity to GA (Gale & Law, 1977). Gale et al. (1981) identified and classified these genes in a number of international varieties, and Worland (1986) surveyed European wheats for the presence of GA-insensitive dwarfing genes.

Japanese wheat breeders released 133 Norin varieties between 1929, when Norin 1 was first developed and 1988. Gale et al. (1981) reported that Norin 2 and Norin 10 carried both *Rht1* and *Rht2*, while Aobakomugi carried only *Rht2*. Yamada (1989) identified the GA-insensitive *Rht* genes of 18 Japanese modern varieties and landraces. However, the dwarfing genes of the other Japanese wheats have not been documented yet.

This paper reports the results of a series of experiments in which the GA response, *Rht* genotypes and culm length of 155 Japanese wheats have been studied.

Materials and methods

The 133 Norin varieties, six breeding lines and 16 landraces together with the 15 tester lines were subjected to a seedling GA response test and a field trial to determine final culm length. The tester lines which are shown in Table 1 with their genotypes, were kindly supplied by Dr. M.D. Gale, Cambridge Laboratory, Institute of Plant Science Research, Cambridge.

For the GA response test, seeds were germinated in Petri dishes for 2 days at 20° C then transplanted to a seed trays in a mixture of vermiculite, soil and sand in the ratio of 2:2:1 volume. A proper quantity of compound manure and slaked lime in 323(L) × 233(W) × 52(H) mm was added. The seedlings were grown at the density of 204 individuals/tray in a growth chamber under controlled light and temperature conditions. After 21 days of cultivation at 20/15° C (day/night) for 16/8 hours and applications of irrigating water containing 10 ppm gibberellic acid (GA_3) every other day, the length of the first leaf sheath (LS) was measured. By this time the growth of the first leaf sheath had ceased. Under these conditions it was possible to distinguish three phenotypes, i.e., fully and partially insensitive to GA and responsive to GA. In the case of the varietal GA response test, control GA-untreated seedlings which received an equal quantity of irrigating water without GA_3 were grown at the same time as the cultivation of the GA-treated seedlings. These GA-treated and GA-untreated tests were made with 3 replications in which each replication contained 12 seedlings for each variety. The GA response index (GRI) of each variety was calculated using the following numerical expression: (LS of GA-treated seedlings/LS of GA-untreated seedlings) × 100.

The GA-insensitive Japanese varieties, breeding lines and landraces were hybridized with the *rht, Rht1, Rht2, Rht3* and *Rht1 Rht2* tester lines. The F_1 hybrids were then selfed to produce F_2 populations. A number of 200–800 F_2 seedlings/cross, 6–12 F_1 seedlings/cross were subjected to the GA response test. χ^2 tests were performed to examine the goodness of fit between expected and observed segregations in the F_2 populations from the test crosses. Thereafter the genotypes of the Japanese wheats were identified.

For the measurement of the final culm length, the plants were grown in a field at a spacing of 10 cm within the row and 60 cm between rows in a randomized block design with 2 replications. One replication contained 170 plots, with one plot for each variety. Each plot contained 10 plants of each variety. At the ripening stage, the culm length of 5 plants/plot was measured at the level of the highest culm of the tillers of each plant.

Results and discussion

The GRI value of the GA-responsive tester line Chinese Spring was 240 (Table 1). The GA-treated seedlings of Chinese Spring also showed the distinct phenotype characterized by thin stems with light green leaves and leaf sheaths. The GRI values of the GA-insensitive *Rht1* and *Rht2* tester lines ranged from 142 to 179, and those of the *Rht3* tester lines ranged from 101 to 108 indicating that these lines showed a high level of insensitivity. The GRI values of two *Rht1 Rht2* tester lines were 116 and 104. These values were lower than those of the tester lines with single gene *Rht1* and *Rht2* indicating that these genes additively reduced the GRI value as well as the culm length. Especially in Olesen, the GRI value was comparable to those of the *Rht3* tester lines. Fick and Qualset (1973) reported that Olesen carried a third dwarfing gene in addition to *Rht1* and *Rht2*. The third gene of Olesen may also induce the reduction of the GRI value.

The GRI values of 155 Japanese wheats ranged from 101 in D. W. sel. No. 71 to 302 in Eshima and Haruhikari (Tables 2 and 3). The frequency distribution of the GRI values was discontinuous at 200–210 (Fig. 1). The wheats having GRI values below 200 did not show the characteristic phenotype such as thin stems with light green leaves and leaf sheaths presented in the GA-responsive wheat plant. Thus the 103 Norin varieties, 6 breeding lines and 10 landraces with GRI values below 200 were classified into the GA-insensitive group (Tables 2 and 3).

The results of the *Rht* gene analysis obtained from the test crosses are shown in Tables 2 and 3. Among the 10 GA-insensitive landraces, only Daruma had a *Rht1* genotype and the other 9 had a *Rht2* genotype. None of the tested landraces carried both *Rht1* and *Rht2* or *Rht3*.

As mentioned above, among the 133 Norin varieties 103 (77%) and 30 (23%) were GA-insensitive and GA-responsive, respectively, indicating that the majority of them were GA-insensitive. Of the 103 GA-insensitive Norin varieties 22 (21%) carried only *Rht1*, 79 (77%) carried only *Rht2*, and only 2 (2%), Norin 10 and Kokeshikomugi, carried both *Rht1* and *Rht2*. None of the Norin varieties tested carried *Rht3*. These results indicated that the majority of the GA-insensitive Norin varieties carried only *Rht2*.

Gale et al. (1981) reported that Norin 2 and Norin 10 carried both *Rht1* and *Rht2*, while Aobakomugi carried only *Rht2*. The *Rht* genotypes of Norin 10 and Aobakomugi identified in this study agreed with their results. However, it was found that Norin 2 carried only *Rht2* as shown in Table 3. It is unlikely that the Norin 2 variety tested in this study carried both *Rht1* and *Rht2* because its culm length, 111 cm, was comparable to that of the single gene *Rht2* tester lines or was rather slightly taller.

Among the Norin varieties, the four varieties identified as carriers of *Rht1*; Norin 11, Shirasagikomugi, Mikunikomugi and Gogatsukomugi, and one variety identified as carrying *Rht2*, Norin 52, showed no connections with the recognised sources of the corresponding *Rht* genes in their pedigrees (Fig. 2). Based on pedigree studies, it would be expected that these 4 varieties, Norin 11, Shirasagi-

Table 1. GA response index, GA reactions, *Rht* genotypes and culm length of tester lines

Tester line	GRI[1] (%)	GA reaction[2]	Genotypes	Culm length (cm)
Chinese Spring	240	R	*rht*	127
SD1	174	I	*Rht1*	87
Highbury	172	I	*Rht1*	86
Penjamo 62	179	I	*Rht1*	95
Sona 227	166	I	*Rht1*	91
SD2	165	I	*Rht2*	92
Maris Hobbit	165	I	*Rht2*	76
Maris Fundin	142	I	*Rht2*	72
Pitic 62	148	I	*Rht2*	101
Sonora	163	I	*Rht2*	80
Tom Thumb[3]	101	MI	*Rht3*	45
D6899	105	MI	*Rht3*	33
Minister Dwarf	108	MI	*Rht3*	41
Norin 10/Brevor 14	116	I	*Rht1 Rht2*	65
Olesen	104	I	*Rht1 Rht2*	39

[1] GA response index: (Length of the first leaf sheath (LS) of GA-treated seedlings/LS of GA-untreated seedlings) × 100.
[2] R: responsive, I: insensitive, MI: markedly insensitive.
[3] Synonymous to Tom Pouce.

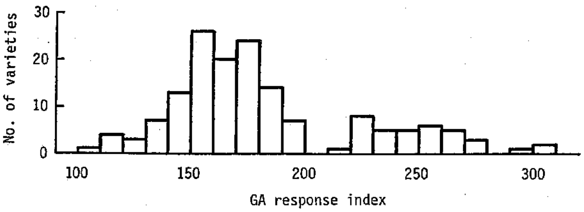

Fig. 1. Frequency distribution of GA response index of Japanese Norin varieties, breeding lines and landraces.

komugi, Mikunikomugi and Gogatsukomugi, should carry *Rht2* and Norin 52 would be predicted to be GA-responsive. The *Rht1* gene of two breeding lines, Saitama 27 and Saitama 29, must have been derived from the landrace Hayakomugi because they were not related to the other possible *Rht1* gene sources in their pedigree, i.e., California/Sojukuakage//Hayakomugi. Both California and Sojukuakage were the GA-responsive varieties whose GRI values were 262 and 233, respectively. These facts supported the above speculation. However since the genotype of Hayakomugi tested in this study was identified as *Rht2,* it is reasonable to assume that a different Hayakomugi carrying the *Rht1* gene had existed.

Worland (1986) reported that, although clearly insensitive, Saitama 27 and its derivatives were less insensitive than would have been expected for materials homozygous for either of the Norin 10 genes. Worland & Petrovic (1988) also reported that the new weak source of GA insensitivity derived from Saitama 27 was controlled by a single gene located on chromosome 4B (see later – chromosome designation) and allelic to *Rht1* and *Rht3,* and it was proposed to temporarily refer to the Saitama 27 allele as *Rht1S* to distinguish it from *Rht1.* However, in this study the GRI value of Saitama 27 was 118 which was lower than those of the *Rht1* tester lines. As mentioned above Saitama 29 has the same pedigree as Saitama 27 and based

Table 2. GA response index, GA reactions, *Rht* genotypes and culm length of Japanese landraces

Landrace	GRI[1] (%)	GA reaction[2]	Genotype	Culm length (cm)
Akadaruma	150	I	*Rht2*[3]	91
Akadaruma 7	113	I	*Rht2*	88
Akakawaaka	252	R	–	162
Akakomugi	243	R	*Rht8 Rht9*[4]	98
Daruma	190	I	*Rht1*	103
Daruma 2	223	R	–	109
Eshima[5]	302	R	–	134
Hayakomugi	162	I	*Rht2*[3,6]	90
Hiroshima Shipree	149	I	*Rht2*[3]	102
Sapporoharukomugi	258	R	–	160
Shirochabo	144	I	*Rht2*[3]	105
Shirodaruma	150	I	*Rht2*[3]	78
Shirodaruma Sai 1	117	I	*Rht2*	80
Shisen 1	227	R	–	109
Shou Fultz	136	I	*Rht2*	101
Yushoki 347	156	I	*Rht2*[3]	80

[1] GA response index: (Length of the first leaf sheath (LS) of GA-treated seedlings/LS of GA-untreated seedlings) × 100.

[2] R: responsive, I: insensitive.

[3] Cited from Yamada (1989).

[4] Cited from Law et al. (1981).

[5] Synonymous to Ejima.

[6] This may not be correct as many Southern European wheats carry a weak GA insensitive allele from Saitama 27 (Worland & Petrovic, 1988). This allele located at the same position as *Rht1*/*Rht3* on 4B (see later – chromosome designation) appears to originate from Hayakomugi. Therefore this should not carry *Rht2.*

–: Genes not identified.

Table 3. GA response index, GA reactions, *Rht* genotypes and culm length of Japanese Norin varieties and breeding lines

Norin No.	Variety and breeding line	GRI[1] (%)	GA reaction[2]	Genotypes	Culm length (cm)
1	Norin 1	167	I	*Rht2*	97
2	Norin 2	159	I	*Rht2*	111
3	Norin 3	276	R	–	153
4	Norin 4	159	I	*Rht2*	90
5	Norin 5	149	I	*Rht2*	81
6	Norin 6	157	I	*Rht2*	90
7	Norin 7	168	I	*Rht2*	87
8	Norin 8	250	R	–	143
9	Norin 9	145	I	*Rht2*	80
10	Norin 10	115	I	*Rht1 Rht2*[3]	72
11	Norin 11	172	I	*Rht1*[4]	92
12	Norin 12	145	I	*Rht2*	92
13	Norin 13	150	I	*Rht2*	89
14	Norin 14	158	I	*Rht1*	100
15	Norin 15	253	R	–	111
16	Norin 16	146	I	*Rht2*	84
17	Norin 17	140	I	*Rht2*	90
18	Norin 18	139	I	*Rht2*	84
19	Norin 19	144	I	*Rht2*	92
20	Norin 20	228	R	–	103
21	Norin 21	157	I	*Rht2*	88
22	Norin 22	223	R	–	109
23	Norin 23	233	R	–	109
24	Norin 24	177	I	*Rht2*	107
25	Norin 25	150	I	*Rht2*	89
26	Norin 26	181	I	*Rht1*	94
27	Norin 27	237	R	–	112
28	Norin 28	141	I	*Rht2*	75
29	Norin 29	278	R	–	125
30	Norin 30	151	I	*Rht2*	79
31	Norin 31	221	R	–	126
32	Norin 32	161	I	*Rht1*	95
33	Norin 33	158	I	*Rht2*	120
34	Norin 34	233	R	–	103
35	Norin 35	224	R	–	128
36	Norin 36	225	R	–	107
37	Norin 37	226	R	–	109
38	Norin 38	266	R	–	113
39	Norin 39	265	R	–	123
40	Norin 40	242	R	–	123
41	Norin 41	216	R	–	102
42	Norin 42	238	R	–	88
43	Norin 43	246	R	–	93
44	Norin 44	155	I	*Rht2*	91
45	Norin 45	241	R	–	88
46	Norin 46	254	R	–	98
47	Norin 47	266	R	–	98
48	Norin 48	162	I	*Rht2*	77
49	Norin 49	173	I	*Rht1*	94
50	Norin 50	139	I	*Rht2*	84

Table 3. Continued

Norin No.	Variety and breeding line	GRI[1] (%)	GA reaction[2]	Genotypes	Culm length (cm)
51	Norin 51	231	R	–	100
52	Norin 52	158	I	*Rht2*[4]	87
53	Norin 53	163	I	*Rht1*	96
54	Norin 54	151	I	*Rht2*	84
55	Norin 55	157	I	*Rht2*	99
56	Norin 56	159	I	*Rht2*	94
57	Norin 57	153	I	*Rht2*	89
58	Norin 58	139	I	*Rht2*	110
59	Norin 59	177	I	*Rht2*	90
60	Norin 60	167	I	*Rht2*	96
61	Norin 61	188	I	*Rht2*[5]	92
62	Norin 62	248	R	–	117
63	Norin 63	163	I	*Rht2*	95
64	Norin 64	142	I	*Rht2*	85
65	Norin 65	164	I	*Rht2*	102
66	Norin 66	163	I	*Rht2*	104
67	Norin 67	152	I	*Rht2*	97
68	Norin 68	142	I	*Rht2*	86
69	Norin 69	170	I	*Rht1*	101
70	Norin 70	160	I	*Rht2*	104
71	Norin 71	162	I	*Rht2*	103
72	Norin 72	157	I	*Rht2*	92
73	Norin 73	158	I	*Rht2*	89
74	Norin 74	169	I	*Rht2*	97
75	Norin 75	292	R	–	131
76	Yuyakekomugi	192	I	*Rht2*	101
77	Susonokomugi	166	I	*Rht2*	101
78	Mutsubenkei	177	I	*Rht2*	124
79	Iyokomugi	182	I	*Rht2*	93
80	Hatamasari	263	R	–	109
81	Aobakomugi	163	I	*Rht2*[3]	97
82	Nanbukomugi	169	I	*Rht2*[5]	97
83	Akatsukikomugi	182	I	*Rht2*	85
84	Yukichabo	170	I	*Rht2*	88
85	Hikarikomugi	172	I	(*Rht2*)[6]	94
86	Myokokomugi	156	I	*Rht2*	99
87	Ebisukomugi	173	I	*Rht2*	90
88	Hitsumikomugi	172	I	*Rht2*	104
89	Kokeshikomugi	135	I	*Rht1 Rht2*	77
90	Okukomugi	174	I	*Rht2*	115
91	Sakyukomugi	164	I	*Rht2*	96
92	Yutakakomugi	193	I	*Rht2*	92
93	Danchikomugi	177	I	*Rht2*	93
94	Furutsumasari	276	R	–	112
95	Shirasagikomugi	188	I	*Rht1*[4]	92
96	Junreikomugi	184	I	*Rht1*	89
97	Kitakamikomugi	169	I	*Rht2*[5]	101
98	Fujimikomugi	183	I	*Rht1*	94
99	Hayatokomugi	162	I	*Rht2*	95
100	Mikunikomugi	179	I	*Rht1*[4]	93

Table 3. Continued

Norin No.	Variety and breeding line	GRI[1] (%)	GA reaction[2]	Genotypes	Culm length (cm)
101	Shimofusakomugi	152	I	*Rht2*	88
102	Miyaginokomugi	151	I	*Rht2*	91
103	Nichirinkomugi	168	I	*Rht2*	89
104	Haruhikari	302	R	–	130
105	Ushiokomugi	173	I	*Rht2*	90
106	Omasekomugi	183	I	*Rht2*	84
107	Hiyokukomugi	196	I	*Rht1*	81
108	Mukakomugi	158	I	*Rht2*	112
109	Zenkojikomugi	181	I	*Rht2*	86
110	Kobushikomugi	188	I	*Rht2*	86
111	Haruminori	257	R	–	115
112	Sakigakekomugi	187	I	*Rht2*	83
113	Hachimankomugi	180	I	*Rht2*	85
114	Horoshirikomugi	176	I	*Rht2*[5]	96
115	Takunekomugi	153	I	*Rht2*	88
116	Hanagasakomugi	171	I	*Rht2*	92
117	Shiroganekomugi	172	I	*Rht1*[5]	72
118	Gogatsukomugi	192	I	*Rht1*[4]	80
119	Toyohokomugi	178	I	*Rht2*	88
120	Setokomugi	199	I	*Rht1*[5]	85
121	Chikushikomugi	193	I	*Rht1*[5]	84
122	Shirowasekomugi	171	I	*Rht1*	73
123	Asakazekomugi	176	I	*Rht1*[5]	78
124	Fukuhokomugi	188	I	*Rht1*[5]	83
125	Minaminokomugi	177	I	*Rht1*	84
126	Chihokukomugi	176	I	*Rht2*[5]	86
127	Wakamatsukomugi	177	I	*Rht2*	84
128	Fukuwasekomugi	264	R	–	80
129	Nishikazekomugi	173	I	*Rht1*[5]	79
130	Haruyutaka	127	I	*Rht1*	103
131	Shiranekomugi	134	I	*Rht2*	86
132	Airakomugi	126	I	*Rht2*	85
133	Koyukikomugi	130	I	(*Rht2*)[6]	92
	Chugoku 131	144	I	*Rht1*	79
	D.W. sel. No. 71	101	MI	*Rht1 Rht2*	65
	Kanto 100	180	I	*Rht1*	80
	Saitama 27	118	I	*Rht1*	98
	Saitama 29	144	I	*Rht1*	87
	Sanin 1	129	I	*Rht2*	95

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[1] GA response index: (Length of the first leaf sheath (LS) of GA-treated seedlings/LS of GA-untreated seedlings) × 100.

[2] R: responsive, I: insensitive, MI: markedly insensitive.

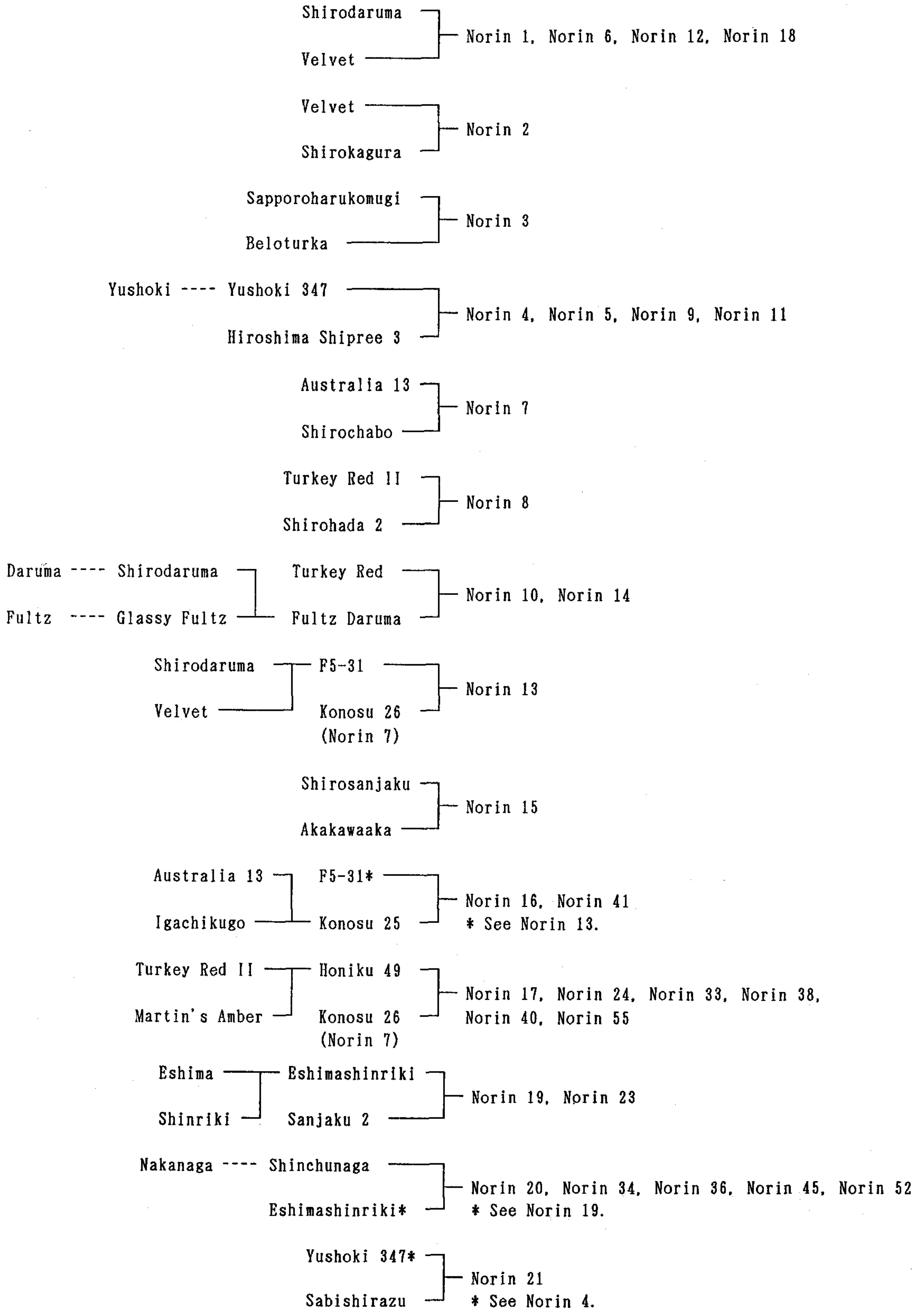
[3] After Gale et al. (1981).

[4] Aberrant genotypes based on their pedigrees.

[5] Cited from Yamada (1989).

[6] Estimated from their pedigrees.

–: Genes not identified.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Yushoki ---- Yushoki 347
Hiroshima Shipree 3
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Australia 13
Shirochabo
Norin 7
Turkey Red II
Shirohada 2
Norin 8
Daruma ---- Shirodaruma
Fultz ---- Glassy Fultz
Turkey Red
Fultz Daruma
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Shirodaruma
Velvet
F5-31
Konosu 26
(Norin 7)
Norin 13
Shirosanjaku
Akakawaaka
Norin 15
Australia 13
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F5-31*
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* See Norin 13.
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Martin's Amber
Honiku 49
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(Norin 7)
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Norin 40, Norin 55
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Shinriki
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Sanjaku 2
Norin 19, Norin 23
Nakanaga ---- Shinchunaga
Eshimashinriki*
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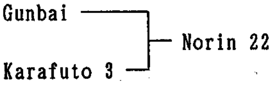
Yushoki 347*
Sabishirazu
Norin 21
* See Norin 4.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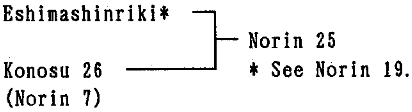
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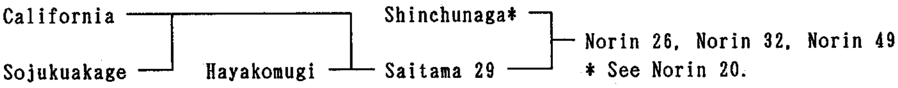
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Hayakomugi
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Saitama 29
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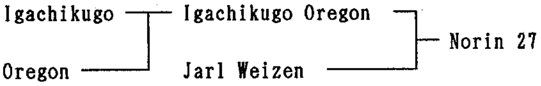
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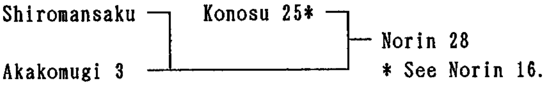
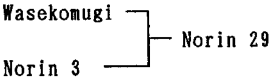
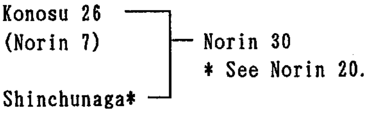
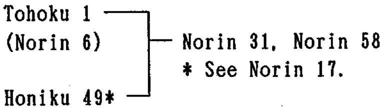
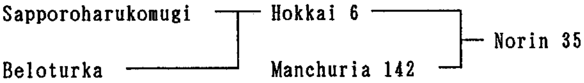
Oregon
Igachikugo Oregon
Jarl Weizen
Norin 27

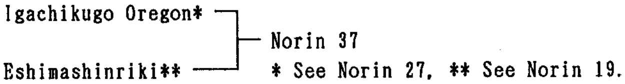

Shiromansaku
Akakomugi 3
Konosu 25*
Norin 28
* See Norin 16.

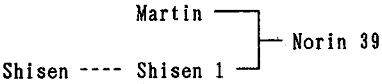

Wasekomugi
Norin 3
Norin 29

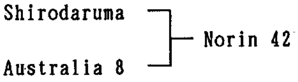

Konosu 26
(Norin 7)
Shinchunaga*
Norin 30
* See Norin 20.

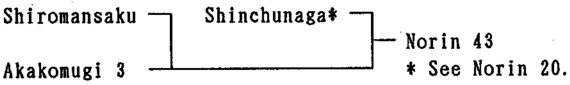

Tohoku 1
(Norin 6)
Honiku 49*
Norin 31, Norin 58
* See Norin 17.

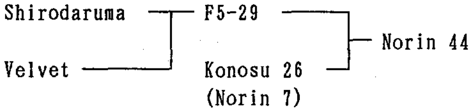

Sapporoharukomugi
Beloturka
Hokkai 6
Manchuria 142
Norin 35

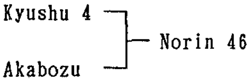

Igachikugo Oregon*
Eshimashinriki**
Norin 37
* See Norin 27, ** See Norin 19.

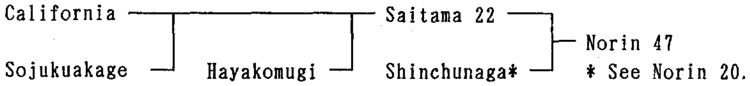

Martin
Shisen ---- Shisen 1
Norin 39

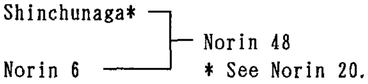

Shirodaruma
Australia 8
Norin 42

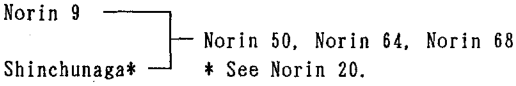

Shiromansaku
Akakomugi 3
Shinchunaga*
Norin 43
* See Norin 20.

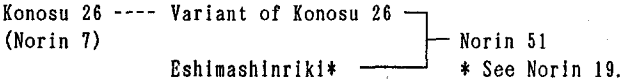

Shirodaruma
Velvet
F5-29
Konosu 26
(Norin 7)
Norin 44

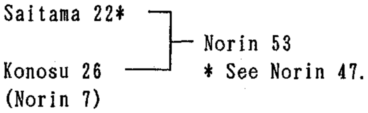

Kyushu 4
Akabozu
Norin 46

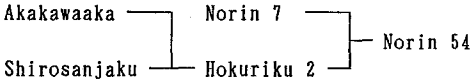

California
Sojukuakage
Hayakomugi
Saitama 22
Shinchunaga*
Norin 47
* See Norin 20.

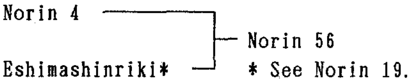

Shinchunaga*
Norin 6
Norin 48
* See Norin 20.

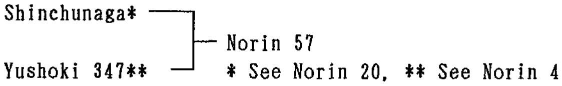

Norin 9
Shinchunaga*
Norin 50, Norin 64, Norin 68
* See Norin 20.

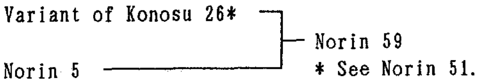

Konosu 26 ---- Variant of Konosu 26
(Norin 7)
Eshimashinriki*
Norin 51
* See Norin 19.

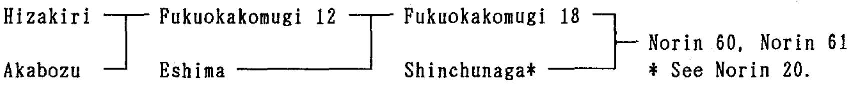

Saitama 22*
Konosu 26
(Norin 7)
Norin 53
* See Norin 47.

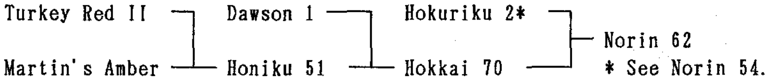

Akakawaaka
Shirosanjaku
Norin 7
Hokuriku 2
Norin 54

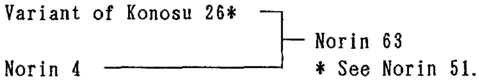

Norin 4
Eshimashinriki*
Norin 56
* See Norin 19.

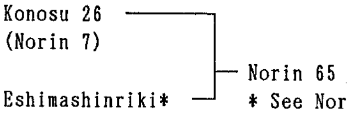

Shinchunaga*
Yushoki 347**
Norin 57
* See Norin 20, ** See Norin 4


Variant of Konosu 26*
Norin 5
Norin 59
* See Norin 51.

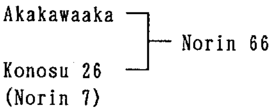

Hizakiri
Akabozu
Fukuokakomugi 12
Eshima
Fukuokakomugi 18
Shinchunaga*
Norin 60, Norin 61
* See Norin 20.

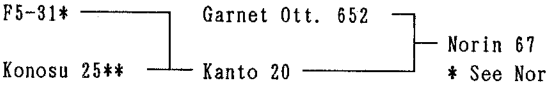

Turkey Red II
Martin's Amber
Dawson 1
Honiku 51
Hokuriku 2*
Hokkai 70
Norin 62
* See Norin 54.


Variant of Konosu 26*
Norin 4
Norin 63
* See Norin 51.

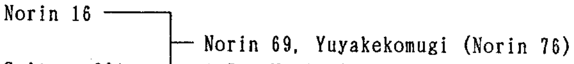


* See Norin 19.

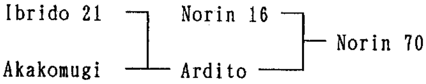


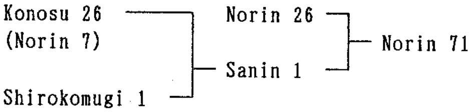


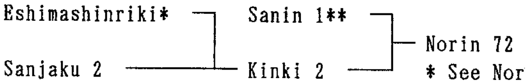
* See Norin 13, ** See Norin 16.



* See Norin 26.

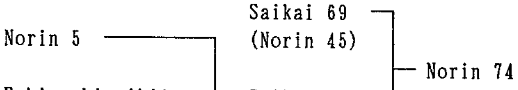




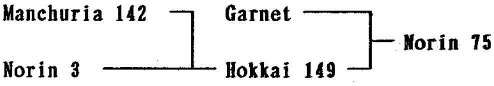


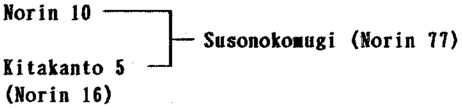
* See Norin 19, ** See Norin 71.

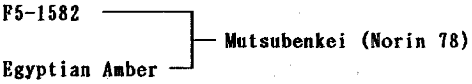
* See Norin 20.

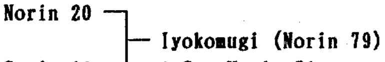


* See Norin 19.

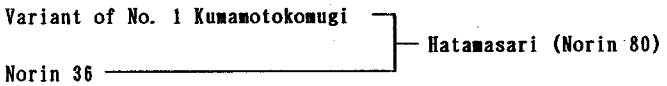


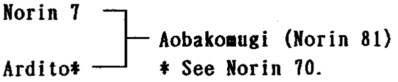


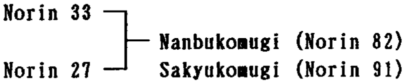


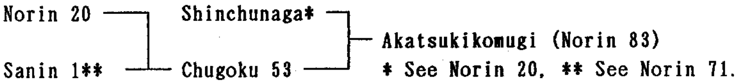


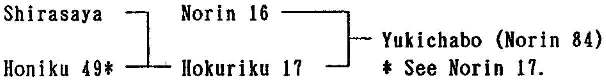
* See Norin 71.

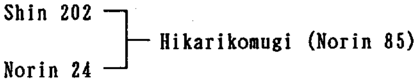

Variant of No. 1 Kumamotokomugi
Norin 36
Hatamasari (Norin 80)

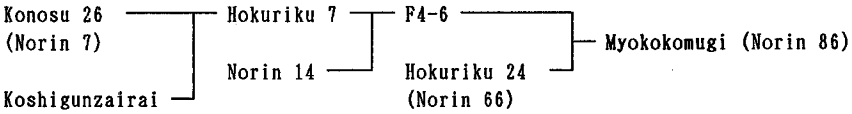

Norin 7
Ardito*
Aobakomugi (Norin 81)
* See Norin 70.

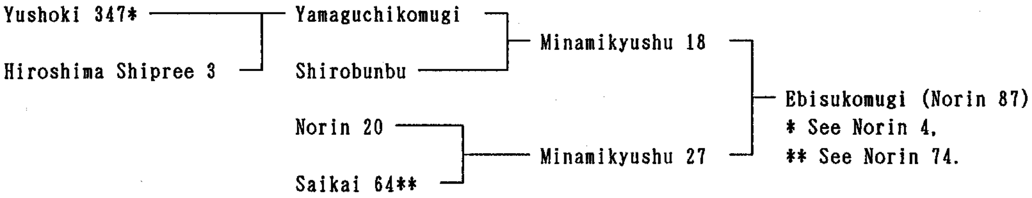

Norin 33
Norin 27
Nanbukomugi (Norin 82),
Sakyukomugi (Norin 91)

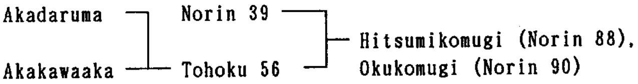

Norin 20
Sanin 1**
Shinchunaga*
Chugoku 53
Akatsukikomugi (Norin 83)
* See Norin 20, ** See Norin 71.

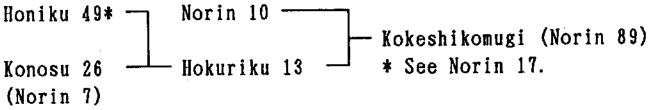

Shirasaya
Honiku 49*
Norin 16
Hokuriku 17
Yukichabo (Norin 84)
* See Norin 17.

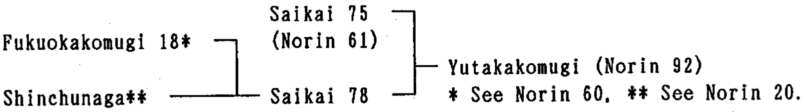

Shin 202
Norin 24
Hikarikomugi (Norin 85)

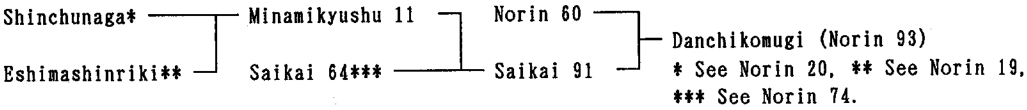

Konosu 26
(Norin 7)
Koshigunzairai
Hokuriku 7
Norin 14
F4-6
Hokuriku 24
(Norin 66)
Myokokomugi (Norin 86)

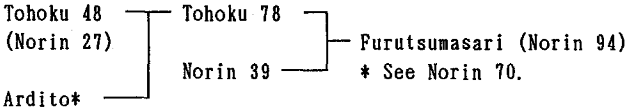

Yushoki 347*
Hiroshima Shipree 3
Yamaguchikomugi
Shirobunbu
Minamikyushu 18
Norin 20
Saikai 64**
Minamikyushu 27
Ebisukomugi (Norin 87)
* See Norin 4,
** See Norin 74.


Akadaruma
Akakawaaka
Norin 39
Tohoku 56
Hitsumikomugi (Norin 88),
Okukomugi (Norin 90)

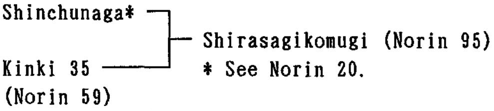

Honiku 49*
Konosu 26
(Norin 7)
Norin 10
Hokuriku 13
Kokeshikomugi (Norin 89)
* See Norin 17.


Fukuokakomugi 18*
Shinchunaga**
Saikai 75
(Norin 61)
Saikai 78
Yutakakomugi (Norin 92)
* See Norin 60, ** See Norin 20.

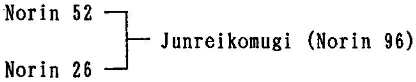

Shinchunaga*
Eshimashinriki**
Minamikyushu 11
Saikai 64***
Norin 60
Saikai 91
Danchikomugi (Norin 93)
* See Norin 20, ** See Norin 19,
*** See Norin 74.

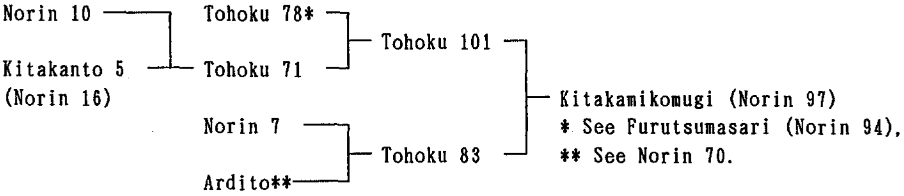


* See Norin 70.

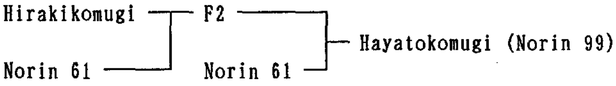


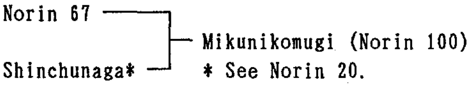
* See Norin 20.



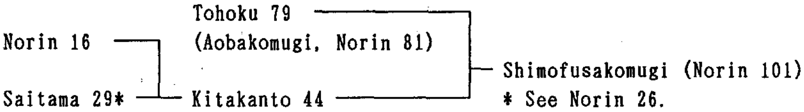


* See Furutsumasari (Norin 94),
** See Norin 70.

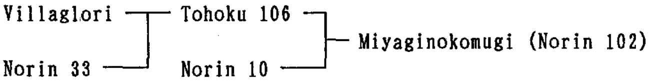


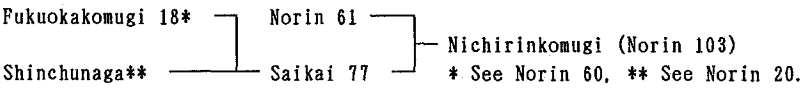


* See Norin 20.

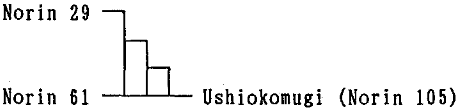


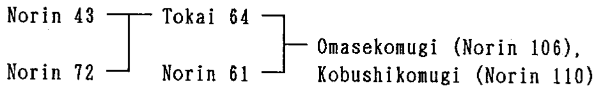
* See Norin 26.

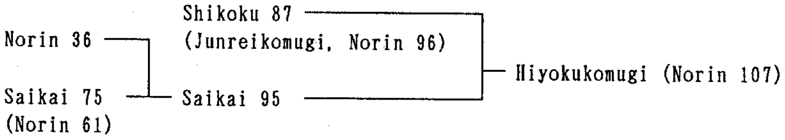


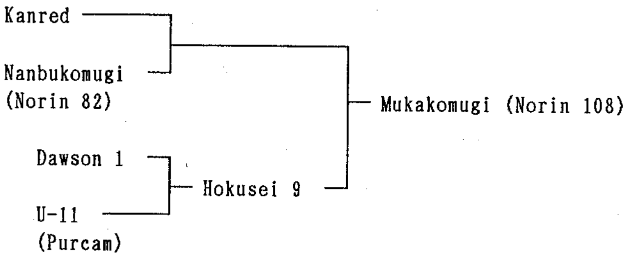


* See Norin 60. ** See Norin 20.



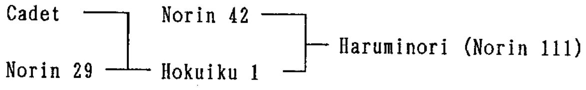


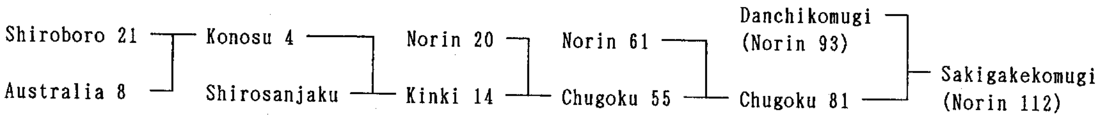


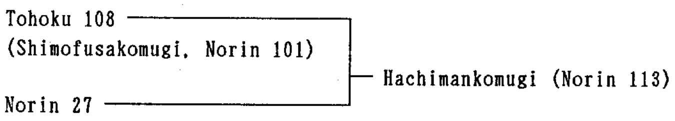


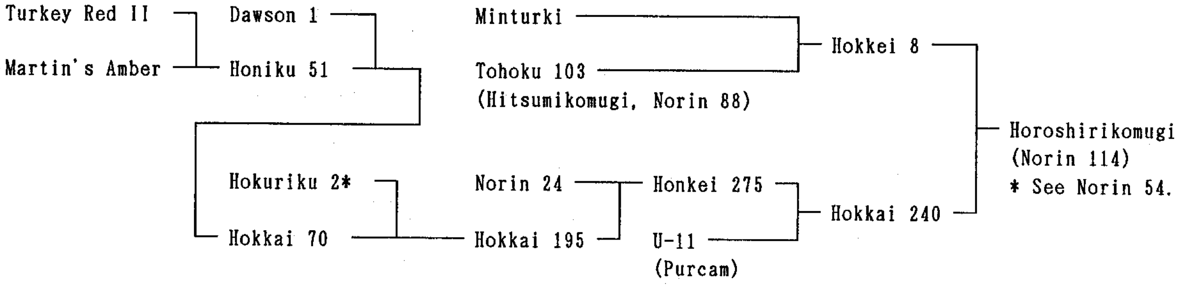
Igachikugo Oregon* ---- Mutant iduced by γ irradiation ---- Zenkojikomugi (Norin 109)

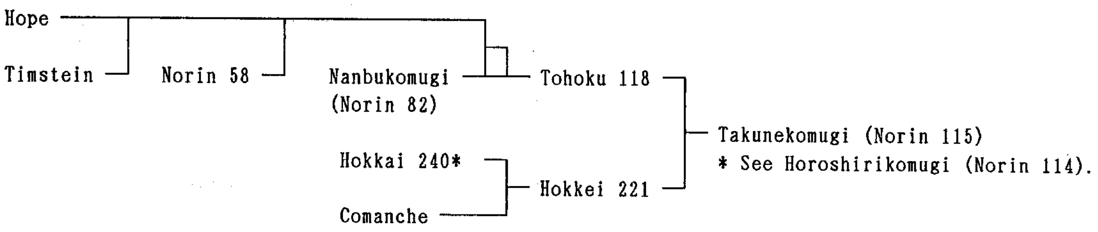
* See Norin 27.

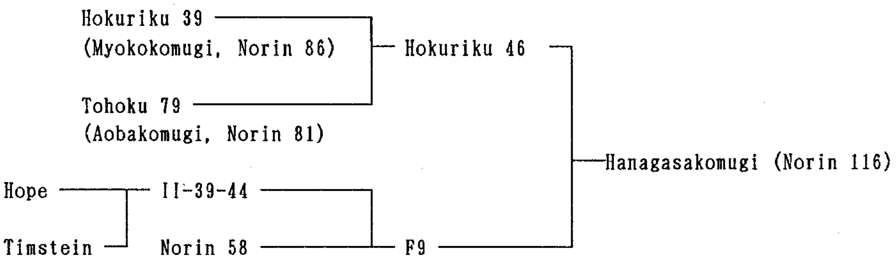


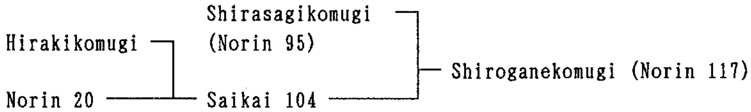


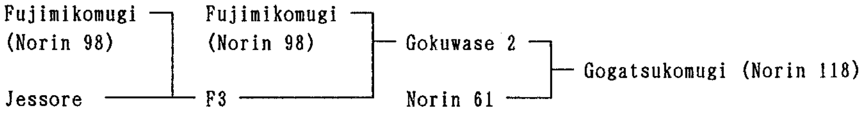


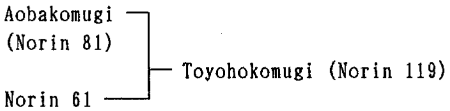


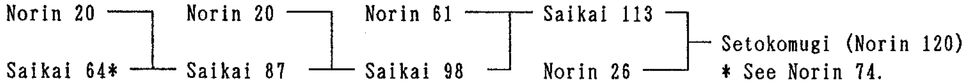


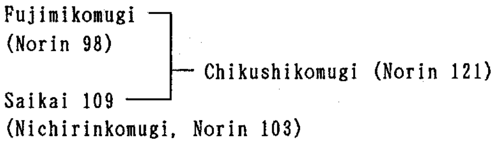




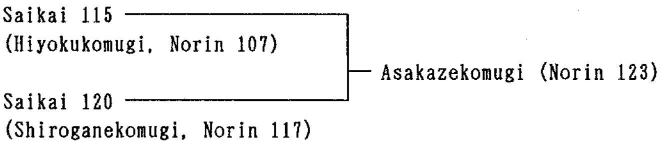


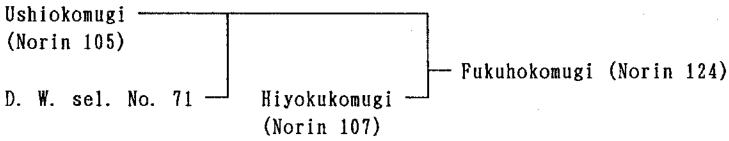


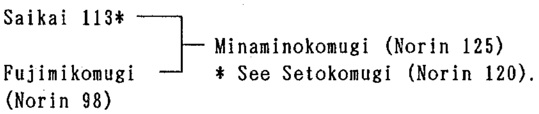


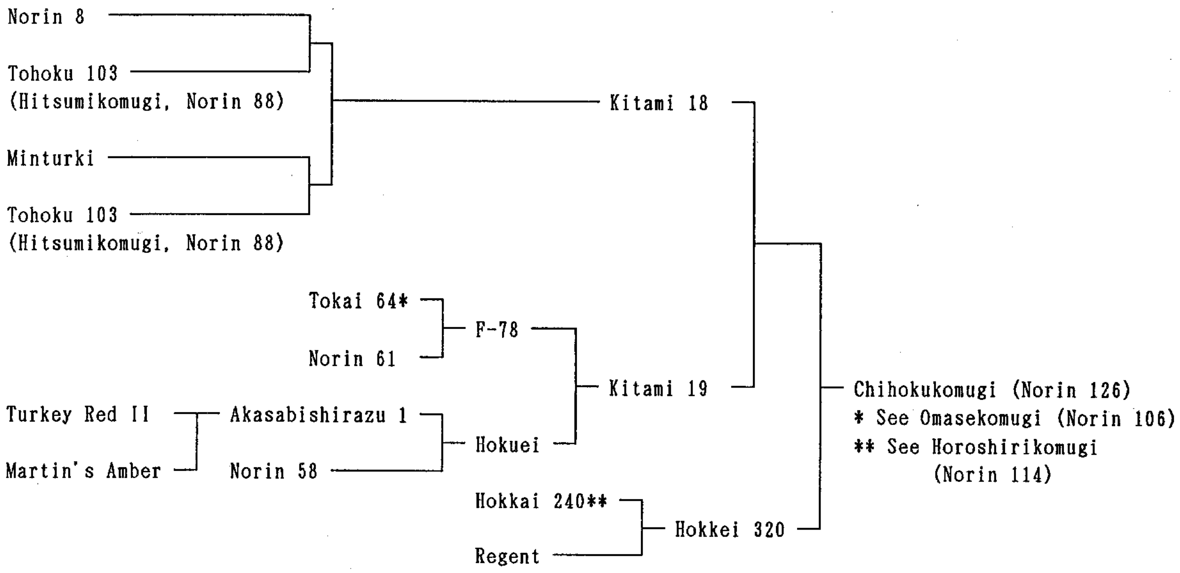


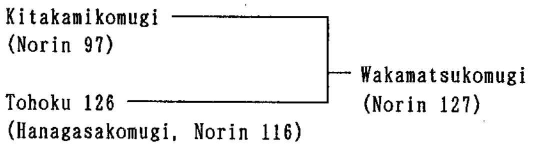
Saikai 120 ---- Mutant induced by γ irradiation ---- Shirowasekomugi (Norin 122)
(Shiroganekomugi, Norin 117)

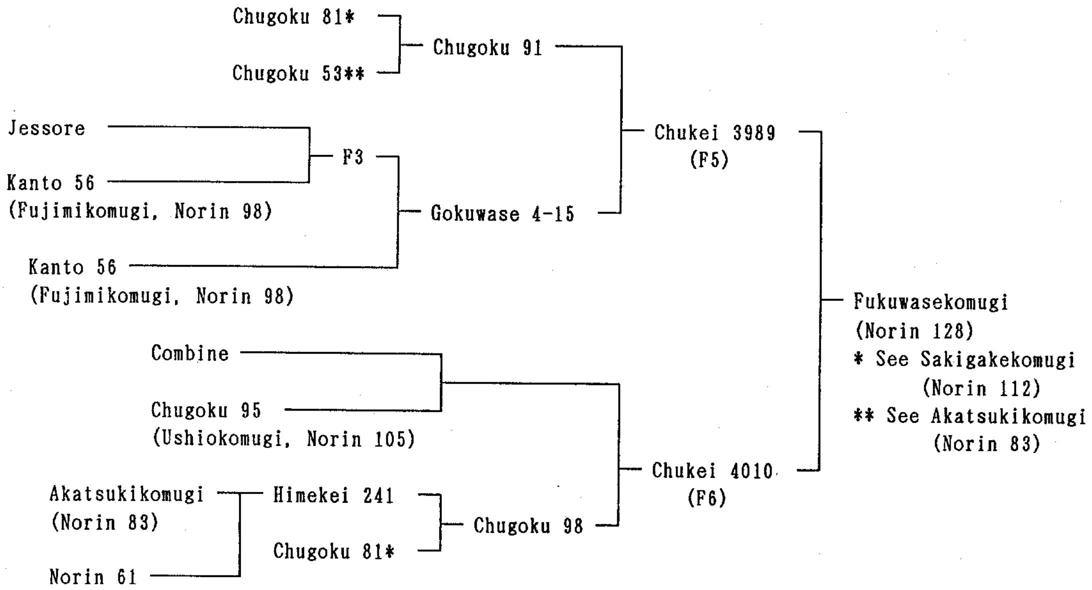


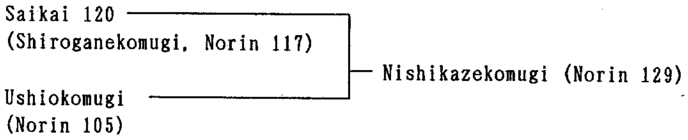





Norin 8
Tohoku 103
(Hitsumikomugi, Norin 88)
Minturki
Tohoku 103
(Hitsumikomugi, Norin 88)
Kitami 18
Tokai 64*
Norin 61
F-78
Kitami 19
Turkey Red II
Martin's Amber
Akasabishirazu 1
Norin 58
Hokuei
Hokkai 240**
Regent
Hokkei 320
Chihokukomugi (Norin 126)
* See Omasekomugi (Norin 106)
** See Horoshirikomugi
(Norin 114)


Kitakamikomugi
(Norin 97)
Tohoku 126
(Hanagasakomugi, Norin 116)
Wakamatsukomugi
(Norin 127)


Chugoku 81*
Chugoku 53**
Chugoku 91
Jessore
Kanto 56
(Fujimikomugi, Norin 98)
F3
Kanto 56
(Fujimikomugi, Norin 98)
Gokuwase 4-15
Chukei 3989
(F5)
Combine
Chugoku 95
(Ushiokomugi, Norin 105)
Akatsukikomugi
(Norin 83)
Norin 61
Himekei 241
Chugoku 81*
Chugoku 98
Chukei 4010
(F6)
Fukuwasekomugi
(Norin 128)
* See Sakigakekomugi
(Norin 112)
** See Akatsukikomugi
(Norin 83)


Saikai 120
(Shiroganekomugi, Norin 117)
Ushiokomugi
(Norin 105)
Nishikazekomugi (Norin 129)

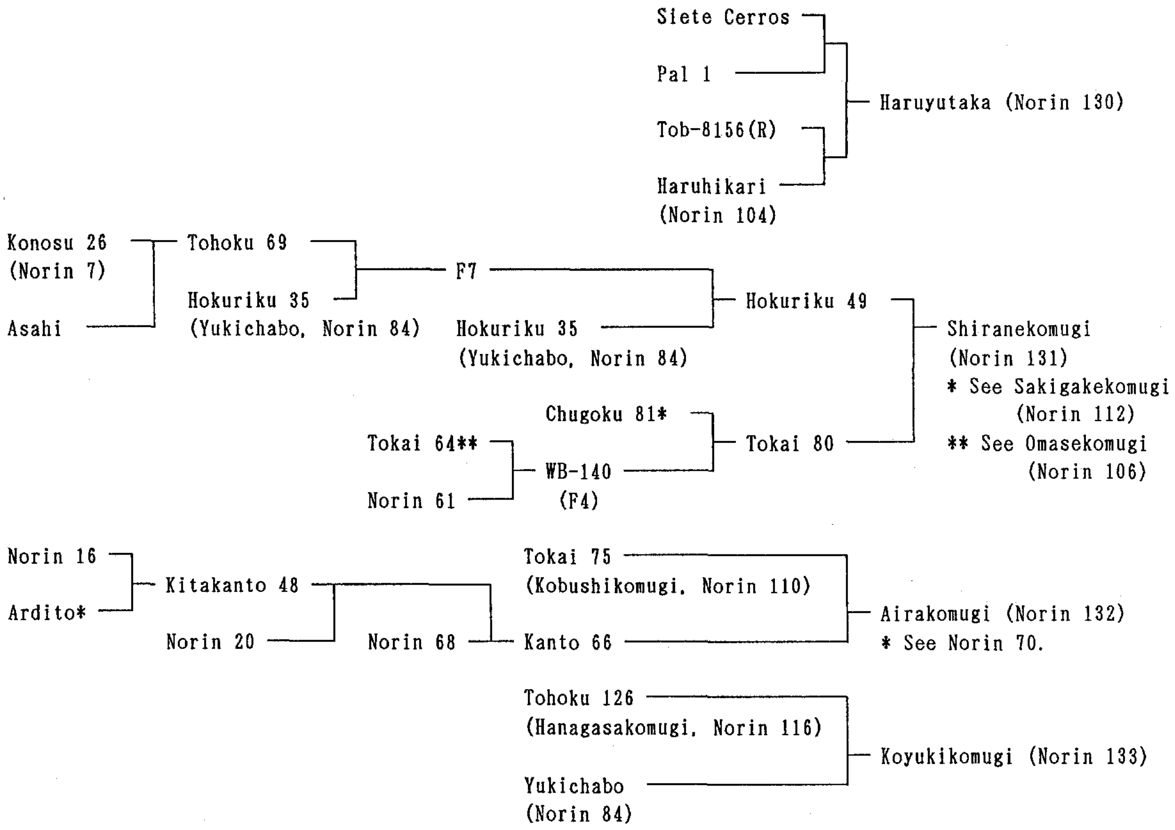


Fig. 2. Pedigrees of Norin varieties.
The upper side of each cross combination is the female parent and the lower side is the male parent.
Synonym: Nakanaga = Chunaga, Eshima = Ejima, Eshimashinriki = Ejimashinriki,
Shinriki = Shinrikimugi = Shinrikikomugi.

on pedigree studies the *Rht1* gene of 10 varieties, Norin 26, Norin 32, Norin 49, Norin 69, Junreikomugi, Fujimikomugi, Hiyokukomugi, Setokomugi, Chikushikomugi and Minaminokomugi, must have been derived from Saitama 29 (Fig. 2). The GRI value of Saitama 29 was 144. Out of the 10 descendants of Saitama 29 mentioned above, indeed the GRI values of the 6 varieties, Norin 26, Junreikomugi, Fujimikomugi, Hiyokukomugi, Setokomugi and Chikushikomugi, were above 180, and especially the GRI value of Setokomugi was 199 which was the highest value among the GRI values recorded in the GA-insensitive wheats. However, the GRI values of the other 4 descendants were not as high but comparable to those of the *Rht1* tester lines. Thus the results in this study did not necessarily provide consistent evidence that the weak GA-insensitive allele occurred at the *Rht1* locus in the Japanese wheats tested.

According to Inazuka (1971), Norin 10 was developed from the cross between Turkey Red and Fultz Daruma. Fultz Daruma is a breeding line which was developed from the cross between Shirodaruma and Glassy Fultz. Shirodaruma and Glassy Fultz are considered to have been derivatives of Daruma and Fultz (GRI = 224), respectively (Fig. 2). The *Rht* genes of Norin 10 must have been derived from Fultz Daruma because the female parent Turkey Red was GA-responsive (GRI = 271) and a tall variety with a culm length of 139 cm. Although the existing Fultz Daruma was not GA-insensitive (GRI = 279) and moreover a tall variety with a culm length of 123 cm, Fultz Daruma which had been used as the parent of Norin 10 appeared to carry both *Rht1* and *Rht2* based on the photograph of Fultz Daruma and Norin 10 taken by Matsumoto (1968). The photograph shows that the culm of Fultz Daruma is clearly shorter than that of Norin 10. As shown in Table 2, Daruma carried only *Rht1* and Shirodaruma carried only *Rht2*. Therefore one of the Norin 10 genes must have been derived from Glassy Fultz. The variety called Glassy Fultz was not tested in this study. However, Shou Fultz identified as an *Rht2* carrier (Table 2) seems to be identical with Glassy Fultz because 'Shou' in Japanese corresponds to 'glassy' in English. If this assumption is valid, the following speculation can be made about the sources of the genes of Norin 10: The *Rht1* gene of Norin 10 may not have been derived from the existing Shirodaruma but from the existing Daruma, the *Rht2* gene of Norin 10 might have been derived from Glassy Fultz, and the *Rht2* gene of Glassy Fultz might have arisen by an outcrossing or a spontaneous mutation. The latter phenomenon could actually occur. For example, the *Rht10* gene of the dwarf mutant Aibian 1 (Wang et al., 1982) is located on the short arm of chromosome 4D (Sasakuma & Izumi, 1983), at the same locus as *Rht2* (Börner & Mettin, 1988).

The culm lengths of most of the wheats carrying GA-insensitive *Rht* gene or genes were less than 105 cm (Tables 1, 2 and 3, Fig. 3). However, there were 7 Norin varieties, Norin 2, Norin 24, Norin 33, Norin 58, Mutsubenkei, Okukomugi and Mukakomugi, whose culm lengths exceeded 105 cm though all of them carried the *Rht2* gene. Norin 33 and Mutsubenkei especially had tall culms comparable to that of the *rht* tester line Chinese Spring. These varieties may have a nullifier or modifier gene(s) or height promoting genes in the background (Gale & Youssefian, 1985) controlling the height-reducing effect of *Rht2*. On the other hand, there were 6 GA-responsive Norin varieties, Norin 42, Norin 43, Norin 45, Norin 46, Norin 47 and Fukuwasekomugi, that were as short as Akakomugi which carries the GA-responsive *Rht* genes, *Rht8* and *Rht9* (Worland et al., 1984). They therefore appear to carry GA-responsive dwarfing gene or genes. As all of them except for Norin 43 are not related to Akakomugi they may carry previously unidentified height reducing genes. In its pedigree Norin 43 is related to Akakomugi 3 which is probably a derivative of Akakomugi. Therefore Norin 43 may carry the same genes as Akakomugi.

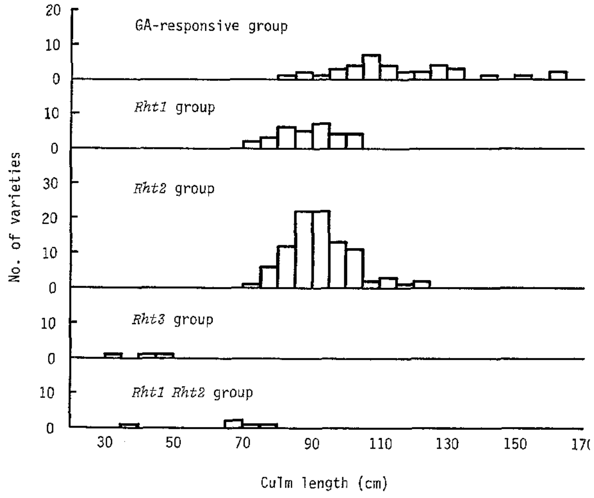


Fig. 3. Frequency distribution of culm length of every *Rht* genotype group containing *Rht* tester lines, Japanese Norin varieties, breeding lines and landraces.

The results of this study show that the *Rht1* and *Rht2* genes have been successfully used by Japanese wheat breeders unconsciously selecting for GA insensitive gneotypes. These two genes will certainly also be useful in the future. The increased knowledge of the GA insensitive genotype is obviously useful for the selection of parents, especially when wheat breeders are trying to incorporate some *Rht* gene or genes into their breeding materials or avoid major segregation for culm length. Gale & Gregory (1977) reported that in the case of the incorporation of the Norin 10 genes the breeding method combining the GA seedling response test with the single seed descent technique could remove most of the unwanted tall genotypes as F_2 seedlings by completely omitting the F_2 field sowing. Recent studies have indicated that the Norin 10 genes exhibit pleiotropic effects on other plant characters including grain quality, and that the phenotypic expression of those genes is affected by their interactions with the components of agricultural environments as well as by other major genes (Gale & Youssefian, 1985; Allan, 1989). Yamada (1989) reported that the geographical distribution of the *Rht* genotypes in the Japanese modern varieties was clearly localized suggesting that *Rht1* and *Rht2* genotypes have a different adaptability to agro-ecological environments. Such accumulated information on these genes will certainly be useful for the breeders in devising their strategies to develop high yielding wheat varieties with improved quality.

Chromosome designation

It was approved at the Seventh International Wheat Genetics Symposium that the chromosome designations of 4A and 4B were interchanged (Gale & Snape, 1988).

Acknowledgement

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