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PLEIOTROPIC EFFECTS OF DWARF GENES FOR GRAIN CHARACTERS IN RICE[1)]

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Introduction

Pleiotropic effects of different dwarf genes have been extensively studied[4,8,9,10)]. The present paper deals with their effects for grain characters involving physico-chemical properties by using a series of near-isogenic dwarf lines having the genetic background of the Hokkaido cultivar Shiokari. It is known that various grain shapes can be expressed by different dwarf genes[4)]. Therefore the authors have attempted to utilize dwarf genes to explore diverse usages of rice and surveyed the pleiotropic effects of dwarf genes as a basis of rice breeding.

Before going further, the authors wish to express their sincere thanks to the staff of Hokkaido Prefectural Kamikawa Agricultural Experiment Station.

Materials and Methods

According to KINOSHITA and SHINBASHI[5)], 21 dwarf genes were introgressed from mutants to the genetic background of Shiokari by successive backcrossings. In this experiment, 19 dwarf lines listed in Table 1 were used together with the recurrent parent, Shiokari.

Rice lines were grown at the facility in the Faculty of Agriculture, Hokkaido University. Seeds were sown at the end of April, 1991 in the greenhouse and transplanted to 2.0 l pots at the end of May with two replications. The remnant materials were transplanted to the paddy field with a single plant per hill spaced at 30.2 cm × 14.5 cm. Culture procedures followed the conventional method. Details on the measurement and analysis of characters are shown in Table 2.

Principal component analysis was made by the use of SPSS (Statistical

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Table 1. List of dwarf near-isogenic lines of shiokari used

Line	Gene symbol	Name	Chromosome	Generation of backcrossings
d_1-line	*d-1*	daikoku dwarf	5	B_{11}
d_2-line	*d-2*	ebisu dwarf	1	B_9
d_6-line	*d-6*	ebisumochi dwarf	7	B_7
d_7-line	*d-7*	heiei-daikoku dwarf	7	B_9
d_{10}-line	*d-10*	toyohikari-bunwai tillering dwarf	1	B_9
d_{11}-line	*d-11*	nohrin 28 dwarf	4	B_9
d_{12}-line	*d-12*	yukara dwarf		B_7
d_{13}-line	*d-13*	short grained dwarf		B_7
d_{14}-line	*d-14*	kamikawa-bunwai tillering dwarf	3	B_{10}
d_{17}-line	*d-17*(t)	slender dwarf		B_8
$d_{18}{}^k$-line	*d-18*^{k}	kotaketamanishiki dwarf	1	B_{11}
d_{19}-line	*d-19*(t)	kamikawa dwarf		B_9
d_{27}-line	*d-27*	bunketsuto tillering dwarf	11	B_9
d_{30}-line	*d-30*	waisei-shirasasa dwarf	2	B_7
d_{35}-line	*d-35*(t)	tanginbozu dwarf		B_{10}
d_{42}-line	*d-42*	liguleless dwarf	4	B_6
d_{47}-line	*sd-1*	dee-geo-woo-gen dwarf	1	B_7
d_{51}-line	*d-51*	dwarf Kyushu-8	8	B_7
d_{52}-line	*d-52*	dwarf Kyushu-2	3	B_6
Shiokari		recurrent parent		

Table 2. List of characters examined

Character	Measurement or analysis
Culm length (cm)	measured at harvest time
Panicle number	measured at harvest time
Heading date (days)	days from sowing to heading
Rate of hull-cracked rice (%)	counted by visual observation at harvest time
Spikelet length (mm)	measured with micrometer, mean of 20 kernels
Spikelet width (mm)	measured with micrometer, mean of 20 kernels
Spikelet shape index	calculated from spikelet lengh/spikelet width
1000 kernel weight (g)	weighed after hulling with a SATAKE machine
Rates of brown, milled and broken rice (%)	measured after hulling in rate of brown rice, and measured after milling in rates of milled and broken rice
Rates of chalky, cracked, notched, green, damaged, rusty and opaque kernels (%)	counted due to visual observation of kernel appearance
Alkali spreading value	1.7% KOH solution was used following LITTLE *et al.*[6]
Amylose content (%)	Small samples were analyzed by an autoanalyser (Technicon Instruments Corp) following INATSU[3]
Protein content (%)	measured according to KJELDAHL's method
Gel consistency (mm)	measured according to CAGAMPANG *et al.*[1]

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Results

1. Estimation of variance components

Variance analyses are shown in Table 3. Variances for treatment (greenhouse vs. field) and line were highly significant in most of the characters examined except the rates of impaired kernels. Interaction (treatment × line) was also significant in 17 characters and dwarf lines responded diversely to the treatment.

2. Character expression of dwarf lines

22 characters were surveyed in 19 dwarf lines and Shiokari under both greenhouse and field cultivating conditions. Deviations from the mean of Shiokari in 22 characters are shown in Table 4 and 5. Culm length and panicle number can be used as good indicators for the feature of dwarf lines. For example, the culm length of d_1-line was the smallest among dwarf lines used. Further, tillering dwarfs such as d_{10}-, d_{14}-, d_{17}- and d_{27}- were characterized by profuse panicle numbers and reduced culm lengths. There was no discrimination in culm length between dwarf and semidwarf types in the genetic background of Shiokari. Heading dates of d_{10}- and d_{51}- lines were delayed remarkably compared with Shiokari in the greenhouse condition. There were many small grained dwarfs as seen in the reduction of spikelet characters. Genetic features characterized by dwarf types were consistent regardless of the culture conditions. It is noted that d_{12}-, d_{18}^{k}- and d_{35}- lines increased 1000 kernel weight from Shiokari in the greenhouse condition. As for milling recovery and grain appearances, a wide range of variation occurred due to the differences of dwarf lines and the cultivating conditions. High rates of notched kernel in d_1-, d_7- and d_{11}- lines in both conditions may be related to the actions of dwarf genes involved.

Rates of impaired kernels, alkali spreading value and gel consistency were scarcely affected by dwarf genes.

Amylose content is the most important criterion for predicting the cooking and eating quality. There was a general tendency for dwarf lines to reduce amylose content in comparinon with that of Shiokari. Especially small grained dwarf lines (d_1-, d_7- and d_{11}-) were markedly lower in amylose content than Shiokari under both conditions. Protein content of dwarf lines varied from Shiokari within a range of +4.9% and −4.2% in both conditions.

3. Fluctuation of characters by cultivating conditions

It was evident that growth and maturation are accelerated in the greenhouse condition due to higher temperature during the growing season as indicated by

Table 3. Analysis of variance for 22 characters in dwarf near-isogenic lines

Source of variation	d. f.	Mean square of characters							
		Culm length	Panicle No.	Heading date	Rate of hull-cracked rice	Spikelet length	Spikelet width	Shape index	1000 kernel weight
Treatment (T)	1	*127.51***	*192.20***	*5661.61***	*2645.00***	*0.007*	*0.039***	*0.012***	*2.09***
Lines (S)	19	397.59**	483.39**	117.70**	3329.20**	2.323**	0.138**	0.163**	69.96**
S x T	19	3.53	4.04	25.11**	169.31**	0.012**	0.016**	0.003**	1.46**
Error	39	3.59	2.94	2.20	5.10	0.003	0.001	0.001	0.18
		Rate of brown rice	Rate of milled rice	Rate of broken rice	Rate of chalky kernel	Rate of cracked kernel	Rate of notched kernel	Rate of green kernel	Rate of damaged kernel
Treatment (T)	1	99.68**	4.11**	0.08**	1185.80**	64.80**	115.20**	750.31**	0.80
Lines (S)	19	17.96**	34.36**	3.43**	833.04**	31.25**	2158.46**	99.03**	3.48**
S x T	19	3.07**	3.47**	0.98**	77.58**	23.85**	108.98**	19.44**	4.37**
Error	39	0.66	0.74	0.01	6.58	1.18	2.25	4.37	1.43
		Rate of rusty kernel	Rate of opaque kernel	Alkali spreading value	Amylose content	Protein content	Gel consistency		
Treatment (T)	1	0.45	0.20	0.88**	270.59**	3.50**	891.10**		
Lines (S)	19	0.13	0.27	0.02*	20.59**	14.37**	77.40**		
S x T	19	0.13	0.09	0.02*	4.82**	0.98**	32.00		
Error	39	0.15	0.20	0.01	0.06	0.28	25.90		

*, ** : Significant at 1% and 5% levels, respectively.

Table 4. Deviations of 22 characters from those of Shiokari in dwarf near-isogenic lines (greenhouse condition)

Name of isoline	Culm length (cm)	Panicle No.	Heading date (days)	Rate of hull-cracked rice (%)	Spikelet length (mm)	Spikelet width (mm)	Spikelet shape index (legth/width)	1000 kernel weight (g)
d_{1}-line	-42.0**	-3.0	-5.0**	73.0**	-2.29**	-0.23**	-0.61**	-12.9**
d_{2}-line	-15.5**	-5.0**	4.0*	0.0	-0.47**	0.33**	-0.26**	-1.9**
d_{6}-line	-30.0**	-4.5*	-3.0	25.0**	-0.04	0.20**	-0.10**	-0.5
d_{7}-line	-12.0**	-4.0*	1.0	2.0	-1.13**	0.40**	-0.44**	-3.8**
d_{10}-line	-29.5**	17.5**	11.0**	37.0**	-0.31**	-0.18**	-0.01	-5.1**
d_{11}-line	-24.0**	-3.5	7.5**	97.0**	-2.25**	-0.02	-0.62**	-10.3**
d_{12}-line	-20.5**	-2.0	4.0*	1.0	0.05	0.02	0.01	1.4**
d_{13}-line	-32.0**	-2.5	-6.5**	21.0**	-0.85**	0.20**	-0.31**	-3.9**
d_{14}-line	-30.5**	25.0**	9.0**	76.0**	-0.86**	-0.18**	-0.17**	-5.6**
d_{17}-line	-28.0**	24.0**	6.5**	70.0**	-0.37**	-0.07*	-0.07**	-4.9**
d_{18}^{k}-line	-29.0**	0.5	-2.0	0.0	0.23**	0.31**	-0.07**	2.9**
d_{19}-line	-14.5**	-1.5	-5.0**	16.0**	-0.39**	0.29**	-0.23**	-0.3
d_{27}-line	-27.5**	24.5**	3.5	29.0**	-0.40**	-0.39**	0.08**	-4.0**
d_{30}-line	-19.5**	-2.5	0.5	73.0**	-1.10**	-0.05	-0.29**	-4.7**
d_{35}-line	-26.0**	-4.5*	-8.0**	52.0**	0.21**	0.09**	0.02	1.4**
d_{42}-line	-29.5**	0.0	0.5	18.0**	0.14**	0.03	0.03	0.2
d_{47}-line	-24.5**	0.5	-6.0**	-1.0	0.04	0.03	0.00	0.5
d_{51}-line	-27.5**	-4.5*	13.0**	30.0**	0.14**	0.05	0.02	0.8
d_{52}-line	-30.5**	-2.0	-4.5*	2.0	-0.17**	0.05	-0.07**	-0.2
Shiokari[1)]	61.0	13.0	85.5	3.0	5.96	3.63	1.64	23.7

*, ** : Significant at 1% and 5% levels, respectvely.
1) Actual value.

Table 4. Continued

Name of isoline	Rate of brown rice (%)	Rate of milled rice (%)	Rate of broken rice (%)	Rate of chalky kernel (%)	Rate of cracked kernel (%)	Rate of notched kernel (%)	Rate of green kernel (%)	Rate of damaged kernel (%)
d_{1}-line	-5.2**	-6.7**	-0.3*	-4.0	-2.0*	33.0**	14.0**	-2.0
d_{2}-line	-0.7	1.4*	0.0	0.0	-2.0*	2.0	-1.0	-2.0
d_{6}-line	-0.1	2.6**	0.0	8.0**	0.0	5.0**	-1.0	1.0
d_{7}-line	-3.8**	-2.5**	0.0	-2.0	-1.0	29.0**	-1.0	0.0
d_{10}-line	1.9**	1.7*	0.7**	-4.0	-2.0*	0.0	-1.0	-2.0
d_{11}-line	-2.2**	-7.2**	0.7**	16.0**	-2.0*	94.0**	8.0**	-2.0
d_{12}-line	-1.8**	-1.2	0.1	43.0**	-2.0*	0.0	-1.0	-1.0
d_{13}-line	-2.4**	-1.9**	0.3*	-8.0**	0.0	9.0**	-2.0	-2.0
d_{14}-line	0.6	1.1	0.3*	11.0**	-2.0*	0.0	-1.0	-1.0
d_{17}-line	0.6	1.5*	0.2*	-2.0	-2.0*	0.0	0.0	0.0
d_{18}^{k}-line	-1.0	0.0	0.0	41.0**	-1.0	0.0	3.0	3.0*
d_{19}-line	-0.2	2.3**	-0.2*	28.0**	0.0	0.0	-1.0	1.0
d_{27}-line	0.1	2.0**	0.1	-4.0	-2.0*	0.0	-1.0	-2.0
d_{30}-line	1.7*	4.0**	-0.1	-6.0*	0.0	0.0	0.0	-2.0
d_{35}-line	0.4	1.7*	1.3**	3.0	0.0	0.0	-1.0	-2.0
d_{42}-line	-0.4	-0.8	0.2*	1.0	1.0	0.0	-1.5	1.0
d_{47}-line	-3.1**	-1.5*	0.2*	3.0	1.0	0.0	-1.5	-2.0
d_{51}-line	0.3	-0.7	1.1**	20.0**	6.0**	0.0	3.0	-2.0
d_{52}-line	-0.4	-0.1	2.1**	12.0**	1.0	0.0	1.0	1.0
Shiokari[1)]	83.0	69.9	0.3	9.0	2.0	0.0	3.0	2.0

*, ** : Significant at 1% and 5% levels, respectively.
1) Actual value.

Table 4. Continued

Name of isoline	Rate of rusty kernel (%)	Rate of opaque kernel (%)	Alkali spreading value	Amylose content (%)	Protein content (%)	Gel consistency (mm)
d_{1}-line	0.0	0.0	0.2	-5.3**	4.9**	-0.5
d_{2}-line	0.0	0.0	-0.4**	-2.7**	-0.3	-10.5
d_{6}-line	0.0	0.0	0.1	-0.7	-0.8	-2.5
d_{7}-line	0.0	0.0	0.1	-3.3**	1.4*	-1.0
d_{10}-line	0.0	0.0	0.1	0.7	-2.2**	-5.0
d_{11}-line	0.0	1.0	0.0	-4.6**	1.4*	-6.0
d_{12}-line	0.0	0.0	-0.2	-2.3**	0.5	-1.5
d_{13}-line	0.0	0.0	0.1	-3.0**	2.4**	-6.5
d_{14}-line	0.0	0.0	0.0	-2.1**	-2.3**	1.0
d_{17}-line	0.0	0.0	0.0	0.4	-2.5**	0.0
d_{18}^{k}-line	1.0	0.0	-0.3*	-1.3**	2.0**	2.0
d_{19}-line	0.0	0.0	-0.2	-1.4**	-1.2*	-1.5
d_{27}-line	0.0	0.0	0.2	3.5**	-1.4*	-11.5*
d_{30}-line	1.0	0.0	0.1	0.3	-0.1	4.5
d_{35}-line	0.0	0.0	-0.1	-0.1	-0.3	1.0
d_{42}-line	1.0	0.0	-0.1	-3.8**	1.9**	0.5
d_{47}-line	0.0	0.0	-0.1	-1.9**	-0.1	0.5
d_{51}-line	0.0	0.0	0.1	-0.3	-0.4	3.0
d_{52}-line	0.0	0.0	0.0	-1.7**	3.0**	2.5
Shiokari[1)]	0.0	0.0	6.8	18.6	9.3	87.5

*, ** : Significant at 1% and 5% levels, respectively.
1) Actual value.

Table 5. Deviations of 22 characters from those of Shiokari in dwarf near-isogenic lines (field condition)

Name of isoline	Culm length (cm)	Panicle No.	Heading date (days)	Rate of hull-cracked rice (%)	Spikelet length (mm)	Spikelet width (mm)	Spikelet shape index (legth/width)	1000 kernel weight (g)
d_{1}-line	-42.0**	-3.0	-2.5	41.0**	-2.43**	-0.19**	-0.62**	-13.3**
d_{2}-line	-16.5**	-4.0*	3.5*	0.0	-0.66**	0.09*	-0.22**	-5.2**
d_{6}-line	-27.5**	-3.0	2.0	7.0**	-0.04	0.12**	-0.06**	-1.6**
d_{7}-line	-13.0**	-2.5	1.0	-1.0	-1.32**	0.28**	-0.46*	-6.6**
d_{10}-line	-30.0**	21.0**	14.0**	35.0**	-0.38**	-0.20**	-0.02	-6.6**
d_{11}-line	-25.0**	-2.0	12.5**	98.0**	-2.43**	-0.10*	-0.64*	-14.6**
d_{12}-line	-33.0**	-1.0	-1.0	-1.0	0.04	0.05	-0.01	0.5
d_{13}-line	-19.0**	0.5	6.5**	7.0**	-0.79**	-0.02	-0.20*	-5.0**
d_{14}-line	-28.0**	33.0**	11.0**	61.0**	-0.72**	-0.32**	-0.06*	-5.9**
d_{17}-line	-28.0**	24.0**	11.0**	63.0**	-0.48**	-0.26**	-0.03	-7.1**
d_{18}^{k}-line	-28.0**	4.0*	4.0**	-1.0	0.11*	0.34**	-0.12*	2.7**
d_{19}-line	-12.0**	-2.0	4.0**	6.0*	-0.45**	-0.02	-0.12*	-2.2**
d_{27}-line	-26.0**	26.0**	11.0**	27.0**	-0.50**	-0.33**	0.01	-6.0**
d_{30}-line	-15.5**	-2.0	1.0	24.0**	-1.34**	-0.30**	-0.26*	-7.8**
d_{35}-line	-28.0**	-3.0	-2.0	32.0**	0.07	0.06	-0.01	-1.4**
d_{42}-line	-24.0**	2.0	-7.5**	4.0	0.06	0.02	0.01	-1.0*
d_{47}-line	-25.0**	0.0	0.5	-1.0	-0.11*	0.03	-0.04*	-1.0*
d_{51}-line	-28.0**	-1.0	8.0**	8.0**	-0.01	0.10*	-0.05*	-2.8**
d_{52}-line	-28.5**	-2.5	0.5	2.0	0.04	0.20**	-0.08*	-1.3*
Shiokari[1)]	62.5	14.5	99.5	2.0	6.00	3.66	1.65	25.2

*, ** : Significant at 1% and 5% levels, respectively.
1) Actual value.

Table 5. Continued

Name of isoline	Rate of brown rice (%)	Rate of milled rice (%)	Rate of broken rice (%)	Rate of chalky kernel (%)	Rate of cracked kernel (%)	Rate of notched kernel (%)	Rate of green kernel (%)	Rate of damaged kernel (%)
d_{1}-line	-7.6*	-9.0**	0.0	-1.0	-4.0**	27.0**	22.0**	4.0**
d_{2}-line	-1.8	-2.2	0.0	-2.0	-3.0*	6.0**	5.0*	0.0
d_{6}-line	0.3	0.3	0.2	8.0**	-1.0	2.0	11.0**	1.0
d_{7}-line	-6.3*	-7.8**	0.2	0.0	-1.0	73.0**	0.0	1.0
d_{10}-line	1.3	1.9	0.5**	-2.0	-4.0**	-1.0	9.0**	3.0*
d_{11}-line	-7.2*	-8.8**	0.5**	5.0*	-3.0*	88.0**	21.0**	1.0
d_{12}-line	0.4	0.7	0.2	51.0**	3.0*	-1.0	10.0**	1.0
d_{13}-line	-2.9*	-2.6*	0.0	-2.0	-4.0**	17.0**	4.0	3.0*
d_{14}-line	2.0	1.4	0.2	2.0	-4.0**	-1.0	9.0**	3.0*
d_{17}-line	0.3	-0.1	0.3*	1.0	-4.0**	-1.0	8.0**	1.0
d_{18}^{k}-line	-1.0	-1.6	1.8**	48.0**	3.0*	-1.0	12.0**	0.0
d_{19}-line	0.6	1.4	0.0	2.0	-3.0*	-1.0	4.0	2.0
d_{27}-line	0.0	0.6	0.3*	-1.0	-3.0*	-1.0	1.0	1.0
d_{30}-line	-0.6	-0.1	0.4**	-3.0	7.0**	-1.0	4.0	0.0
d_{35}-line	0.7	-1.0	1.4**	-1.0	-1.0	-1.0	-1.0	1.0
d_{42}-line	-0.8	-1.1	-0.1	9.0**	-4.0**	-1.0	-1.0	1.0
d_{47}-line	-0.2	0.2	-0.1	1.0	-1.0	-1.0	2.0	1.0
d_{51}-line	-1.2	-0.5	0.4**	2.0	-2.0	-1.0	5.0*	1.0
d_{52}-line	-1.4	-3.5**	6.0**	5.0*	16.0**	-1.0	13.0**	4.0**
Shiokari[1)]	81.3	71.7	0.1	3.0	4.0	1.0	3.0	0.0

*, ** : Significant at 1% and 5% levels, respectively.
1) Actual value.

Table 5. Continued

Name of isoline	Rate of rusty kernel (%)	Rate of opaque kernel (%)	Alkali spreading value	Amylose content (%)	Protein content (%)	Gel consistency (mm)
d_1-line	0.0	1.0	0.0	-6.3**	4.3**	-3.5
d_2-line	0.0	0.0	0.0	-3.3**	0.6	-3.0
d_6-line	0.0	0.0	0.0	-0.6	-0.9	-4.0
d_7-line	0.0	0.0	0.0	-5.7**	2.0**	4.5
d_{10}-line	0.0	0.0	0.0	3.5**	-4.2**	1.0
d_{11}-line	0.0	1.0	0.0	-4.5**	0.5	0.0
d_{12}-line	0.0	0.0	0.0	-0.1	-0.8	-2.5
d_{13}-line	0.0	0.0	0.0	-0.8	0.9	-6.0
d_{14}-line	0.0	0.0	0.0	3.1**	-2.9**	-5.0
d_{17}-line	0.0	0.0	0.0	2.9**	-2.4**	-2.0
d_{18}^k-line	0.0	0.0	0.0	0.9	0.1	-10.5
d_{19}-line	0.0	0.0	0.0	-1.1	-1.7**	-11.0*
d_{27}-line	0.0	0.0	0.0	3.0**	-1.8**	-7.5
d_{30}-line	0.0	0.0	0.0	-3.9**	1.4*	5.0
d_{35}-line	0.0	0.0	0.0	-1.4	1.0	6.0
d_{42}-line	0.0	0.0	0.0	-2.8**	1.3*	8.5
d_{47}-line	0.0	0.0	0.0	-0.7	0.5	4.5
d_{51}-line	0.0	0.0	0.0	-2.5**	0.6	8.0
d_{52}-line	0.0	1.0	0.0	-3.5**	2.9**	7.5
Shiokari[1)]	0.0	0.0	7.0	22.0	9.1	79.0

*, ** : Significant at 1% and 5% levels, respectively.
1) Actual value.

Table 6. Comparison of 11 characters between greenhouse and field conditions expressed as an increase from the value in greenhouse

	Near-isogenic line																				
	S	d_1	d_2	d_6	d_7	d_{10}	d_{11}	d_{12}	d_{13}	d_{14}	d_{17}	d_{18}^k	d_{19}	d_{27}	d_{30}	d_{35}	d_{42}	d_{47}	d_{51}	d_{52}	Mean
Heading date (days)	14.0	16.5	13.5	19.0	14.0	17.0	19.0	9.0	27.0	16.0	18.5	20.0	23.0	21.5	14.5	20.0	6.0	20.5	9.0	19.0	16.85
Rate of hull-cracked rice (%)	-1.0	-33	-1	-19	-4	-3	0	-3	-15	-16	-8	-2	-11	-3	-50	-21	-15	-1	-23	-1	-11.5
Spikelet length (mm)	0.04	-0.10	-0.15	0.04	-0.15	-0.03	-0.14	0.03	0.10	0.18	-0.07	-0.08	-0.02	-0.06	-0.20	-0.10	-0.04	0.19	-0.11	0.25	-0.021
Spikelet width (mm)	0.03	0.07	-0.21	-0.05	-0.09	0.01	-0.05	0.06	-0.19	-0.11	-0.16	0.06	-0.28	0.09	-0.22	0	0.02	0.03	0.08	0.18	-0.037
1000 kernel weight (g)	1.5	1.1	-1.8	0.4	-1.3	0	-2.8	0.6	0.4	1.2	-0.7	1.3	-0.4	-0.5	-1.6	-1.3	0.3	0	-2.1	0.4	-0.27
Rate of chalky kernel (%)	-6.0	-3.0	-8.0	-6.0	-4.0	-4.0	-5.0	2.0	0	-15.0	-3.0	1.0	-32.0	-3.0	-3.0	-2.0	2.0	-8.0	-24.0	-13.0	-6.7
Rate of cracked kernel (%)	2.0	0	1.0	1.0	2.0	0	1.0	7.0	-2.0	0	0	6.0	-1.0	1.0	9.0	1.0	-3.0	0	-6.0	17.0	1.8
Rate of notched kernel (%)	1	-5	5	-2	45	0	-5	0	9	0	0	0	0	0	0	0	0	0	0	0	2.4
Rate of green kernel (%)	0	8.0	6.0	12.0	1.0	10.0	13.0	11.0	6.0	10.0	8.0	9.0	5.0	2.0	4.0	0	0.5	3.5	2.0	12.0	6.15
Amylose content (%)	3.4	2.4	2.8	3.5	1.0	6.2	3.5	5.6	5.6	8.6	5.9	5.6	3.7	2.9	-0.8	2.1	4.4	4.6	1.2	1.6	3.69
Protein content (%)	-0.2	-0.8	0.7	-0.3	0.4	-2.2	-1.1	-1.5	-1.7	-0.8	-0.1	-2.1	-0.7	-0.6	1.3	1.1	-0.8	0.4	0.8	-0.3	-0.4

earlier headings. Response of rice lines to cultivating conditions are shown in Table 6 as an increase from the value in the greenhouse condition. Both heading date and amylose content indicated high susceptibility as a whole. Rates of chalky rice in d_{19}- and d_{51}- lines decreased in the field condition. While rates of cracked and notched kernels increased conspicuously in d_{52}-, and d_7- lines, respectively. An increase of amylose content in d_{14}- line was the highest showing 8.6%. A slight fluctuation was recognized in protein content.

4. Interrelations with amylose or protein contents

Three kinds of important relations are indicated in Figs. 1, 2 and 3. Amylose content was correlated with spikelet length in both greenhouse and field conditions. A significant correlation was also recognised between amylose content and heading date in the field condition. Four dwarf lines (d_{10}-, d_{14}-, d_{17}- and d_{27}-) agreed in having high amylose content and late heading in the field condition. In the correlations between protein content and heading date, most of dwarf lines were plotted differently between greenhouse and field conditions. Negative correlations were recognized beween protein content and heading date in both conditions.

5. Principal component analysis

Interrelationships among 19 characters were examined by principal component analysis, as shown in Tables 7 and 8. Cumulative loadings were 71.7% in the first four in the greenhouse condition and 72.7% in the first three in the field

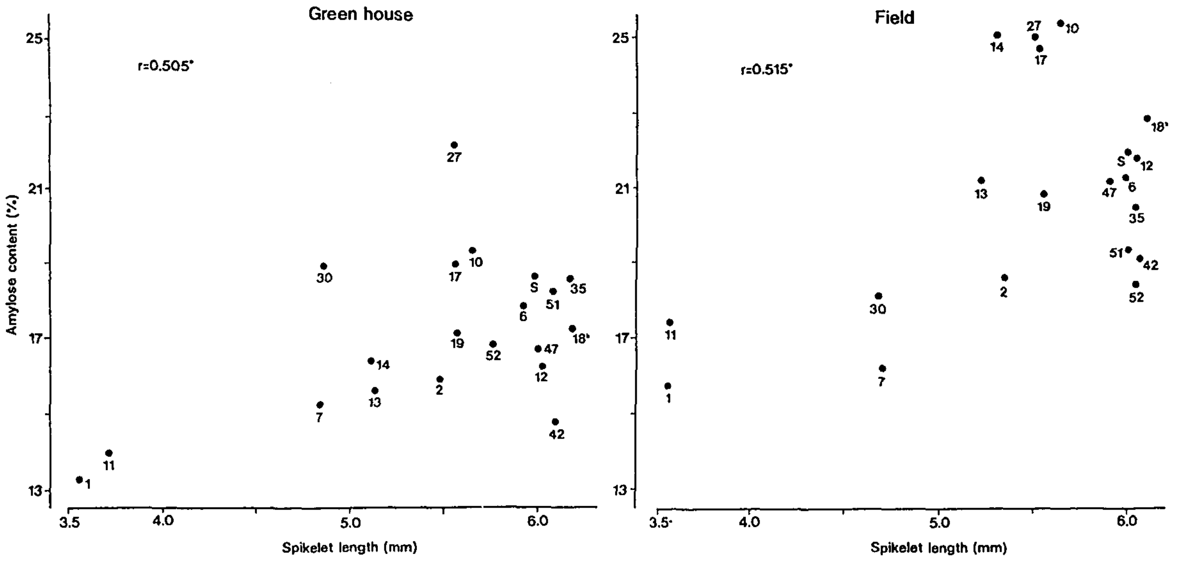

Fig. 1. Relationships between amylose content and spikelet length in the two conditions. S means Shiokari and the number means each dwarf line, for example, 1 refers to d_1-line.

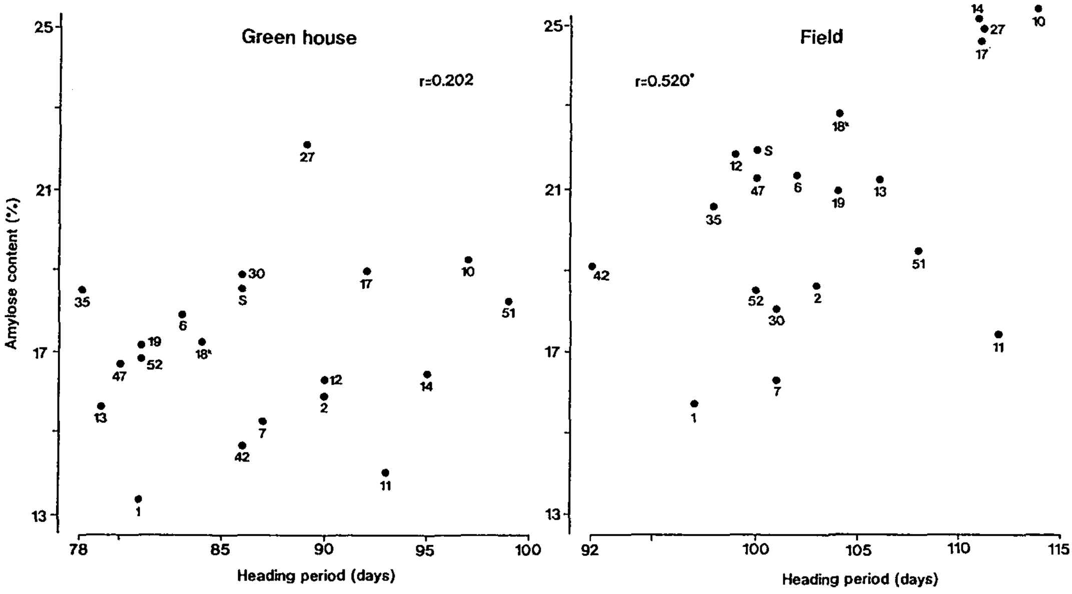

Fig. 2. Relationships between amylose content and heading period in the two conditions. S and numbers are identical with those of Fig. 1.

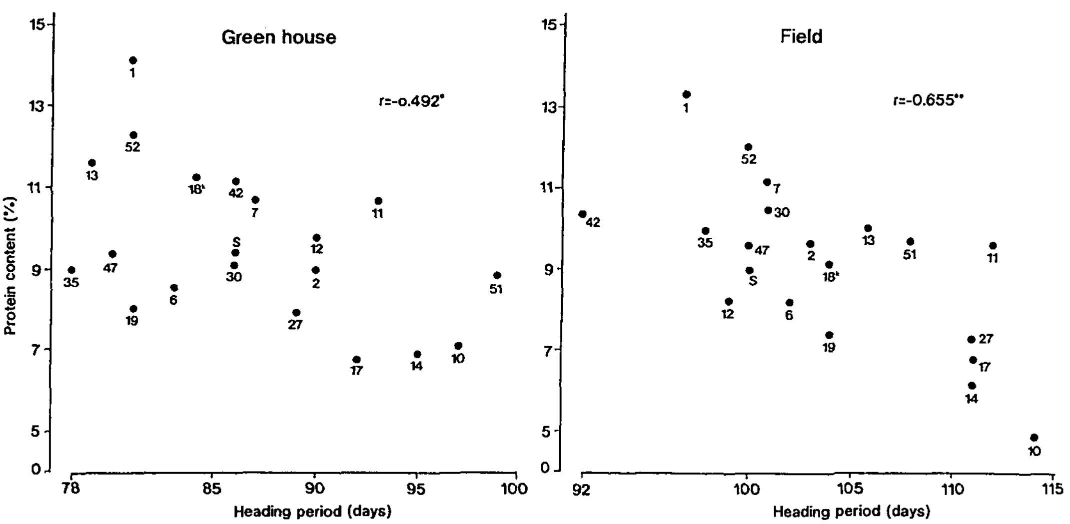

Fig. 3. Relationships between protein content and heading period in the two conditions. S and numbers are identical with those of Fig. 1.

Table 7. Structure vector of the four components extracted in dwarf near-isogenic lines (greenhouse)

Character	Factor 1	Factor 2	Factor 3	Factor 4
Culm length	0.3820	0.2082	-0.3687	-0.2344
Panicle number	0.1764	-0.8155	-0.1110	0.2425
Heading date	0.0205	-0.5540	0.0406	0.5134
Rate of hull-cracked rice	-0.5395	-0.5831	0.1635	0.2216
Spikelet length	0.9356	0.1839	0.1252	0.0073
Spikelet width	0.1891	0.7788	-0.3212	-0.0194
Spikelet shape index	0.8877	-0.1435	0.2190	0.0047
1000 kernel weight	0.8586	0.4725	0.0710	0.0155
Rate of brown rice	0.6869	-0.4956	0.0810	0.1887
Rate of milled rice	0.8337	-0.2985	-0.1384	-0.0858
Rate of broken rice	0.1846	0.0378	0.6273	0.0083
Rate of chalky kernel	0.2120	0.4659	0.0279	0.7358
Rate of cracked kernel	0.3219	0.3000	0.7045	-0.1715
Rate of notched kernel	-0.8286	0.0555	-0.0862	0.1717
Rate of green kernel	-0.7933	0.0748	0.2996	0.2502
Rate of damaged kernel	0.3392	0.4905	-0.0398	0.4072
Alkali spreading value	-0.3510	-0.5024	0.4602	-0.3780
Amylose content	0.6765	-0.5597	0.0515	-0.1217
Protein content	-0.5779	0.6205	0.2629	-0.1612
Gel consistency	0.1723	0.2916	0.6116	0.1975
Contribution	0.3315	0.2084	0.1011	0.0761
Cumulative	0.3315	0.5399	0.6410	0.7171

condition.

As shown in Table 7, the first component was loaded with a large value, for size characters, rates of brown and milled rice, rates of notched and green kernel (negative value) and amylose content. In the second component, panicle number (negatire value) and spikelet width showed a large value. As shown in Table 8, the first component loaded positively for spikelet length, spikelet shape index, 1000 kernel weight, rates of brown and milled rice and amylose content, and negatively for notched kernel. In the second component, panicle number, heading date, and rate of hull-cracked rice loaded negatively, while only spikelet width loaded positively. In the third component, rate of broken rice loaded positively.

In the scatter diagrams given by the first and second components, 19 dwarf lines were classified into four groups, i. e. group A (including Shiokari) with relatively small pleiotropic effects ; group B with broad grain and higher rates of

Table 8. Structure vector of the three components extracted in dwarf near-isogenic lines (field)

Character	Factor 1	Factor 2	Factor 3
Culm length	0.3015	0.3696	-0.5921
Panicle number	0.3734	-0.8040	0.1785
Heading date	0.0402	-0.8141	0.1468
Rate of hull-cracked rice	-0.4158	-0.7352	0.0772
Spikelet length	0.8943	0.3503	0.1156
Spikelet width	0.0080	0.7938	0.0666
Spikelet shape index	0.9656	0.0512	0.0861
1000 kernel weight	0.7774	0.5677	0.0761
Rate of brown rice	0.9537	-0.1174	0.0672
Rate of milled rice	0.9441	-0.1744	-0.0283
Rate of broken rice	0.0031	0.4009	0.7714
Rate of chalky kernel	0.2415	0.2806	0.3074
Rate of cracked kernel	0.0529	0.5838	0.5772
Rate of notched kernel	-0.8258	-0.0628	-0.2139
Rate of green kernel	-0.5766	-0.2400	0.5932
Rate of damaged kernel	-0.2721	-0.2328	0.6344
Amylose content	0.7652	-0.5700	0.1479
Protein content	-0.6266	0.6805	0.0474
Gel consistency	-0.2497	0.4366	-0.0073
Contribution	0.3543	0.2517	0.1207
Cumulative	0.3543	0.6060	0.7267

notched kernel ; group C (d_1- and d_{11}- lines) with small grain, low amylose and high protein contents, higher rates of green and notched kernels ; group D (d_{10}-, d_{14}-, d_{17}- d_{27}- and d_{30}- lines) with large panicle number and narrow grain (Fig. 4). Dwarf lines belonging to group A, B and D were plotted differently when grown in greenhouse and field. In the greenhouse, d_{35}- and d_{51}- lines were close to Shiokari, while d_{12}-, d_{18}^{k}-, d_{35}- and d_{47}- lines were close to Shiokari in the field.

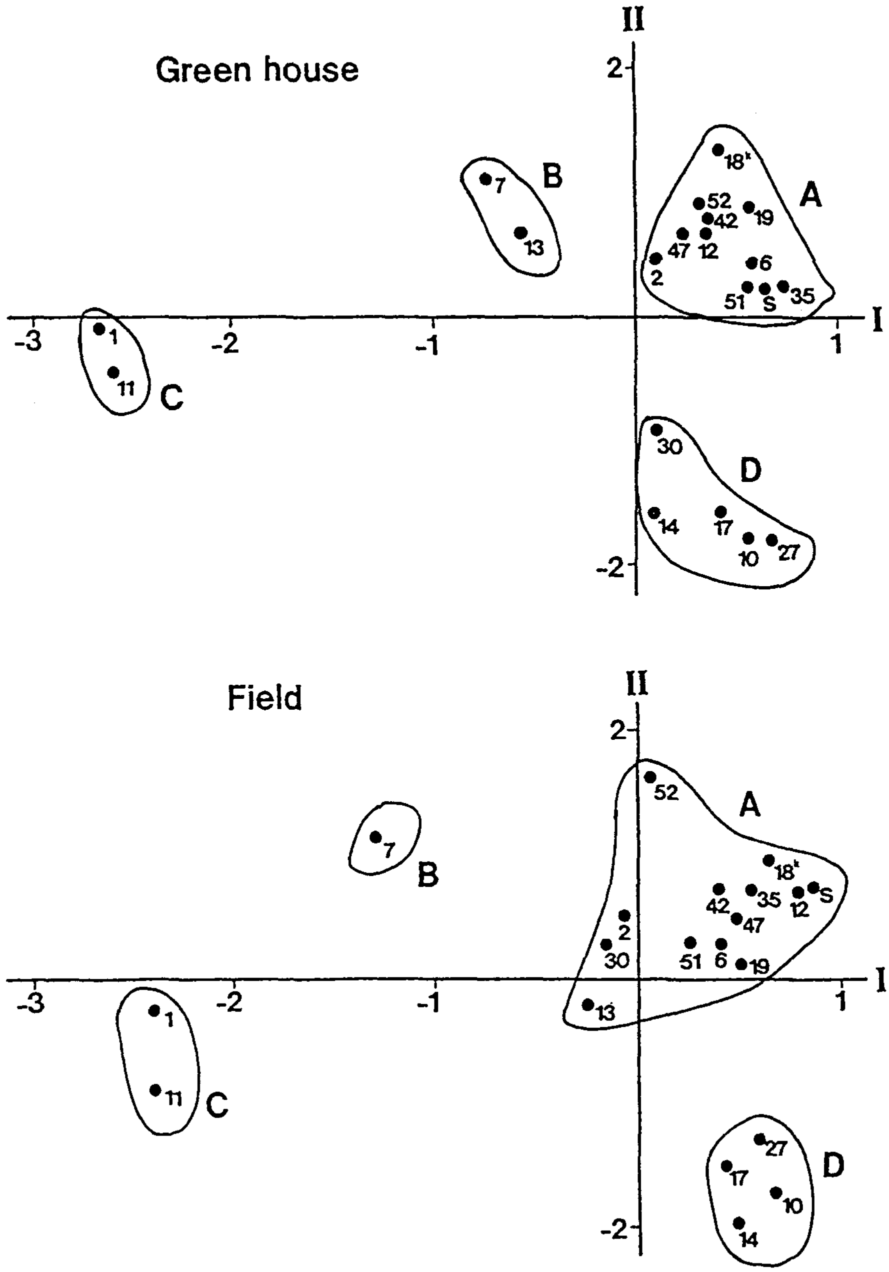

Fig. 4. 19 dwarf near-isogenic lines and Shiokari scattered in the plane defined by the first two components (I and II) in the two conditions. S means Shiokari and the number means each dwarf line.

Discussion

In recent years, rice quality and chemical composition have become an important issue and consumers are more concerned with the quality of rice[1,2,3]. In the meantime, semidwarf varieties have gained worldwide importance as a result of intensive cultivation, because of their high nitrogen response and resistance to lodging[10]. Although there have been many studies on the pleiotropic effects of dwarf genes for plant and grain characters[4,8,9], information on grain quality and composition is rather limited in normal genotypes[2,7]. Near-isogenic dwarf lines used in this experiment are appropriate to examine the effects of dwarf genes under the identical genetic background except the respective single dwarf genes. Therefore the pleiotropic effects of the respective genes can be reflected in their character expression. Thus pleiotropic effects of dwarf genes on culm length, panicle number and spikelet (grain) shape were confirmed again throughout the different culture conditions. Further it was found that the genes for small grained dwarfs such as *d-1, d-7* and *d-11* contribute to an outstanding increase of hull-cracked rice and notched kernel. As pointed out by TAKEDA and TAKAHASHI[12,13], imbalance between the development of glume and caryopsis played an important role in the small spikelets derived from those genes. Amylose content was also reduced conspicuously by the effects of small grained dwarf genes (*d-1, d-7* and *d-11*). It is noticeable that *d-1* (daikoku dwarf) indicated its pleiotropic effects to low amylose and high protein contents.

It is evident that delay of heading date and increase of amylose content can be caused by low temperature during growing and maturation periods[11]. Therefore, the pleiotropic effects caused by *d-13* (short grained dwarf) and *d-14* (kamikawa-bunwai) promoted the alteration to late heading and high amylose content in the field condition, respectively. In most characters, diverse effects of different dwarf genes were demonstrated in various degrees. Positive correlations were obtained between amylose content and spikelet length and between amylose content and heading date in the field. On the other hand, negative correlations existed between protein content and heading date in both conditions.

According to the principal component analysis, 19 dwarf genes were classified into four groups, i. e. group A (including Shiokari) with small pleiotropic effects, and groups B, C and D showing diversified effects on various characters. It was shown from the field experiment that the pleiotropic effects of so-called semidwarf genes such as *d-12* (yukara dwarf), *d-35*(t) (tanginbozu dwarf) and *sd-1*=*d-47* (dee-geo-woo-gen dwarf) are close to those of normal genotype represented by Shiokari.

Summary

Pleiotropic effects of dwarf genes on rice grain quality and composition were

investigated by using 19 near-isogenic dwarf lines having the genetic background of a Hokkaido cultivar, Shiokari, in greenhouse and field conditions. Variances for line and treatment (culture conditions) were significant in most of the characters examined except rates of impaired kernels. Line × treatment interactions were significant in these characters indicating that the pleiotropic effects of dwarf genes varied with environmental conditions.

The main effects of dwarf genes were confirmed from the variation of culm length, panicle number and spikelet shape, and the effects of dwarf genes were stable throughout the cultivating conditions. Although diverse effects of dwarf genes were observed in grain characters, it is noted that the effects of *d-1, d-7* and *d-11* (small grained dwarfs) showed an outstanding increase of hull-cracked rice and notched kernel, due to imbalance between the development of glume and caryopsis. There were scarce or no effects for rates of impaired kernels, alkali spreading value and gel consistency. In amylose content, most of the dwarf genes were responsible for reducing the contents, while bidirectional alteration from Shiokari caused by dwarf genes was recognized in protein content. Both heading date and amylose content were largely affected by low temperature condition in the field. Degrees of alteration in both characters were also affected by different dwarf genes. Correlations between amylose content and spikelet length or heading date were intensified in the field condition, producing a group of d_{10}-, d_{14}-, d_{17}- and d_{27}- lines showing high amylose content and late heading. Negative correlations were recognized between protein content and heading date in both conditions.

The principal components of the data for 19 characters gave 71.7% cumulative contribution by the first four (greenhouse) or 72.7% by the first three (field) factors. In the greenhouse, the first component comprised size traits, rates of brown and milled rice, rates of notched and green kernel and amylose content, and the second component had large loadings on panicle number and spikelet width. In the field condition, the first component comprised spikelet size, shape index, 1000 kernel weight, rates of brown and milled rice, rate of notched kernel and amylose content, and the second component had negative loadings on panicle number, heading date and rate of hull-cracked rice, and positive large loading on spikelet width. The pleiotropic effects of dwarf genes, if represented by principal component analysis, seem to be influenced by environmental conditions.

In the scatter diagrams given by the first and second components, 19 dwarf lines were classified into four groups according to the pleiotropy of the respective dwarf genes on the characters, i. e. group A (including Shiokari) with relatively small pleiotropic effects ; group B with broad grain and higher rates of notched kernel ; group C (d_1- and d_{11}- lines) with small grain, low amylose and high protein contents, higher rates of green and notched kernels ; and group D (d_{10}, d_{14}-, d_{17}- and d_{27}- lines) with large panicle number and narrow grain. Dwarf lines belonging to group A, B and D differed when grown in greenhouse and field conditions.

In the greenhouse, d_{35}- and d_{51}- lines were closer to Shiokari, while d_{12}-, d_{18}^{k},- d_{35},- and d_{47}- lines were close to Shiokari in the field condition.

Thus it was demonstrated that so-called semidwarf genes such as *d-12* (yukara dwarf), *d-35* (t) (tanginboze dwarf) and *sd-1=d-47* (dee-geo-woo-gen dwarf) have no malformed effects and resemble the grain characters of the normal genotype represented by Shiokari.

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