INFLUENCES OF ENVIRONMENTAL FACTORS FOR THE CHARACTER EXPRESSION OF THE NINETEEN KINDS OF NEAR-ISOGENIC DWARF LINES

—Genetical studies on rice plant, LXXXV*—

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Introduction

It is generally accepted that the quantitative characters of dwarf plants are markedly affected by various kinds of environmental factors. In addition, there are diverse forms of interaction between genotypes and environments. Following the studies on the character expression of the near-isogenic dwarf lines which were produced by backcrossing procedures a trial classification was made due to the relative elongation pattern of the upper and lower internodes and the reduction of the second internode[6]. In this paper, the authors examined the influence of enviromental factors such as fertilizing levels and density of planting for the character expressions of the dwarf genes. This information may be useful for the practice of breeding using dwarf types of rice.

Materials and Methods

The nineteen kinds of near-isogenic dwarf lines were developed by the backcrossing method[4]. By using them, thirty four days old seedlings were grown in the vinyl-house and transplanted to the paddy field with single plant per hill on May 29th, 1980. Three kinds of fertilization levels, non-treatment, standard (N : 7.2 kg, P_2O_5 : 7.2 kg, K_2O : 4.5 kg per 10 a) and double (N : 14.2 kg, P_2O_5 : 14.2 kg, K_2O : 9 kg) quantities were applied before planting as a basal dressing, respectively.

In these three conditions, plants were spaced at 14.5 cm $\times$ 30.2 cm. Also,

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a dense planting spaced at 7.3 cm × 30.2 cm was applied for evaluating the effect of density under the standard fertilization. In each condition, the dwarf lines and the recurrent parent, Shiokari were arranged in the order of plant height to prevent mutual shading between lines in two replications. At maturity, four plants were sampled for the survey omitting border lines in each plot. The lengths of panicle, culm, internodes, leaf sheaths and blades, the number of spikelets per panicle, and the panicle number per plant were measured. Upper internode elongation index was expressed as the arctangent of the first internode length to the third one[6]. The length of the fifth internode which showed below 10 mm was not included in the measurement.

Principal component analysis was made by the use of SPSS (Statistical Package for Social Sciences) program in Hokkaido University Computing Center.

Results

1. Principal component analysis for the length of panicle, internodes, leaf sheaths and blades

Principal component analysis was attempted using the dwarf lines for the lengths of panicle, four kinds of internodes, and leaf sheaths and blades from uppermost to the third leaf in the respective environmental conditions. As shown in Table 1, the first component was loaded positively for all characters irrespective of environmental conditions. The second component was loaded negatively for the lengths of the first internode and the first leaf sheath, and positively for the lengths of the third and fourth internodes in all of the conditions. The third component was loaded for the second internode length through the four conditions, while the other relations partly differed in each condition. Thus, as mentioned in the previous paper[6], the dwarf genes assert their effects strongly to reduce the culm and leaf lengths accompanying the diverce patterns of relative elongation of the upper and lower internodes and the conspicuous reduction of the second internode in some genotypes. In this experiment, it may be infered that the fundamental relation among the different internode lengths was stable through the three environmental conditions used.

2. Effects of fertilizer and planting density

Variance components in the nine characters were estimated as shown in Table 2. Variance analyses were carried out in the assumption of the

TABLE 1. Factor loadings of the first three principal components calculated by the lengths of panicle, internodes, leaf sheaths and blades

Length of	Non-fertilization			Standard			Double fertilization			Dense planting		
	Factor			Facter			Factor			Factor		
	I	II	III	I	II	III	I	II	III	I	II	III
Panicle	.70	−.22	.37	.58	−.05	.76	.72	−.11	.11	.53	−.08	.77
1st internode	.70	−.32	.20	.69	−.54	−.22	.69	−.46	.12	.65	−.38	−.43
2nd 〃	.55	.61	.39	.58	.15	−.46	.61	.05	.70	.56	.44	−.40
3rd 〃	.60	.70	.28	.68	.46	.31	.68	.44	.41	.66	.61	.26
4th 〃	.59	.72	−.16	.47	.78	−.14	.53	.74	−.10	.55	.72	−.08
1st leaf sheath	.85	−.41	.28	.85	−.44	.01	.86	−.44	−.05	.86	−.40	.05
2nd 〃	.95	−.20	.10	.96	−.16	−.08	.96	−.20	−.05	.96	−.17	−.02
3rd 〃	.92	.09	−.34	.94	.10	−.12	.96	.09	−.19	.96	−.02	−.04
1st leaf blade	.89	−.37	.04	.91	−.26	.10	.91	−.26	−.10	.88	−.30	.02
2nd 〃	.91	−.06	−.36	.93	.07	−.05	.93	.14	−.19	.92	−.03	−.04
3rd 〃	.85	.04	−.47	.86	.29	−.04	.87	.30	−.30	.89	.07	−.01
Eigen value	6.79	1.88	1.00	6.79	1.53	0.98	7.13	1.40	0.86	6.74	1.52	1.01
Contribution (%)	61.8	17.1	9.1	61.7	13.9	8.9	64.8	12.7	7.8	61.2	13.8	9.2
Cumulated (%)		78.9	88.0		75.6	84.5		77.5	85.4		75.0	84.3

TABLE 2. Variance components due to lines, fertilizer or planting density, and their interaction expressed by percentages to the total of the three kinds of variance components

Character	Percentage of variance component due to			Percentage of variance component due to		
	Lines	Fertilizer	L×F	Lines	Density	L×F
Panicle length	75.8**	10.0**	14.2**	95.8**	4.2**	0.0
Culm length	81.3**	14.5**	4.2**	99.3**	0.4**	0.3
1st internode length	90.4**	6.3**	3.3**	97.9**	1.8**	0.3
2nd 〃	91.2**	5.2**	3.6**	99.1**	0.4**	0.4
3rd 〃	79.2**	13.9**	6.9**	98.4**	0.2	1.4
4th 〃	82.6**	9.6**	7.8**	94.7**	1.5	3.8
Upper internode[1)] elongation index	88.2**	6.8**	5.0**	95.9**	1.4**	2.8*
Number of spikelets	82.5**	16.7**	0.8	72.7**	24.4**	2.9**
Panicle number	92.7**	6.3**	1.0**	70.3**	19.4**	10.3**

1) Expressed by the arctangent of the first internode length to the third one.
*, ** Significant at the 0.05 and 0.01 levels, respectively.

fixed-effect model. Interactions between lines and replications in each condition were pooled and used as error. The effects of fertilizers and planting density were significant in most of the characters. The percentage of variance component due to lines occupied the largest parts, showing more than 70%. The variance components due to fertilizer levels and their interactions were also significant except the number of spikelets, while planting density showed a considerable effect in both the number of spikelets and the panicle number and the interaction between line and density was significant in both characters.

TABLE 3. Nine characters of panicle, culm and spikelet in Shiokari and the nineteen near-isogenic dwarf linse in 1980

Name of isoline	Panicle length (cm)	Culm length (cm)	Internode length (cm)				Upper inter. elong. index (degree)	Number of spikelets	Panicle number
			1st	2nd	3rd	4th			
Shiokari	16.8	67.5	28.9	23.2	13.2	2.4	68.1	110.1	24.7
d_1-	10.0	21.8	16.9	1.4	2.9	0.3	79.2	94.2	27.9
d_2-	15.4	38.1	17.7	14.0	6.6	0.8	69.6	81.3	25.3
$d_{3,4,5}$-[1)]	12.4	28.2	14.7	9.8	3.5	1.4	76.1	51.4	106.0
d_6-	10.4	30.4	25.5	1.5	2.2	0.6	85.2	85.8	43.5
d_7-	12.8	59.0	24.2	23.0	11.4	1.4	64.9	114.9	22.0
d_{10}-	13.3	36.8	17.4	11.3	5.6	1.9	72.2	71.6	105.2
d_{11}-	26.8	34.4	16.5	0.6	15.1	2.2	70.8	90.7	20.9
d_{12}-	17.3	51.5	25.7	18.5	5.8	1.2	77.4	103.7	32.2
d_{13}-	11.9	43.4	17.5	12.0	9.1	4.1	62.5	89.6	25.5
d_{14}-	14.1	34.4	15.2	10.9	5.0	2.5	71.6	88.4	118.9
d_{17}-	13.0	37.9	16.7	12.0	5.8	3.1	70.8	74.9	107.8
d_{18}^h-[2)]	6.7	7.1	5.5	1.0	0.5	0.2	84.6	30.1	47.9
d_{18}^k-[2)]	14.2	35.4	18.5	11.9	5.2	0.5	74.4	64.3	37.4
d_{27}-	13.9	39.8	17.2	13.1	6.1	2.7	70.6	78.7	104.8
d_{30}-	12.5	55.3	17.1	17.6	14.9	6.3	48.8	123.5	24.9
d_{35}-	14.0	42.2	13.5	17.3	10.2	1.7	53.0	85.8	26.4
d_{47}-	15.2	41.1	18.8	14.2	6.2	1.4	74.1	89.4	21.5
d_a-[3)]	13.1	34.2	7.8	14.5	10.3	1.7	37.2	137.7	19.4
d_b-[4)]	15.1	35.6	15.9	13.4	5.8	1.0	69.9	82.5	23.6

1) Triplicate genes.
2) Multiple alleles in the order of $+ > d_{18}^k > d_{18}^h$ (Shinbashi *et al.*[8)]).
3), 4) Single recessive genes named tentatively.

The characteristics of the nineteen dwarf lines and Shiokari in the standard coondition were shown in Table 3. The fluctuation of the characters from those of the standard cultivation with a moderate fertilization and a normal density, were examined in the three conditions (Figs. 1 and 2). Generally, the effects by non-fertilizing condition were prominent in most of the characters, especially in the lengths of culm and the internodes above the third internode, the number of spikelets and the panicle number. However, the differences from the standard cultivation fluctuated depending on the genotype of dwarfness. In the panicle length, d_{11}- line was significantly affected by the three conditions, while the other genotypes showed variable modifications. In the culm length, nonfertilizing condition brought a significant decrease in most of the genotypes, while the other two conditions showed variable effects among the genotypes. It is noted that d_7- and d_{12}-

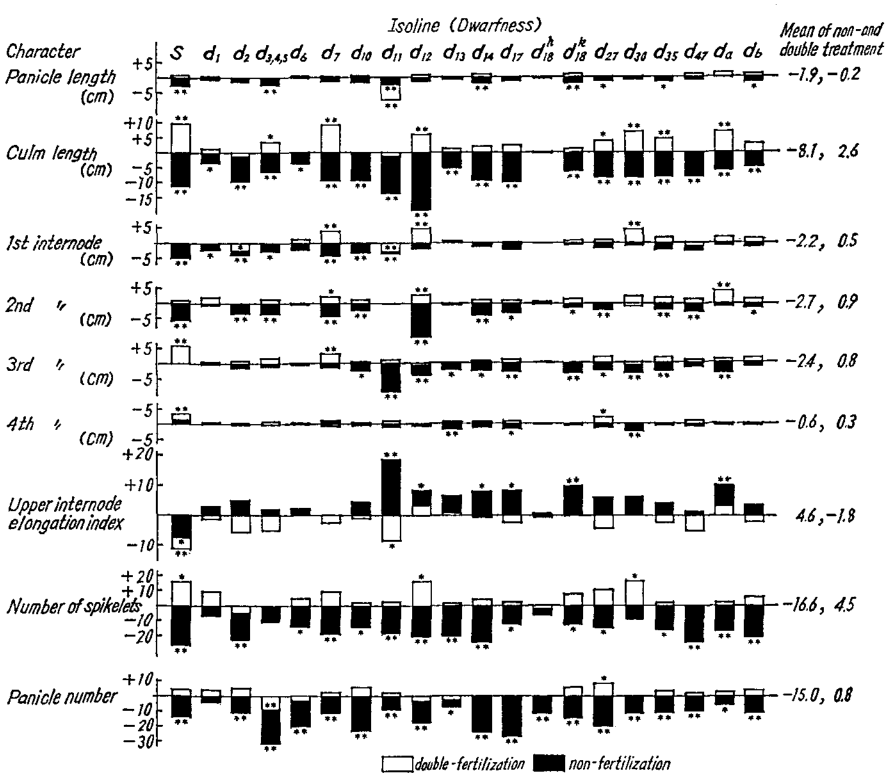

Fig. 1. Comparison of nine characters between non- or double-fertilization and standard condition with a moderate fertilization in the cultivar, Shiokari (S) and 19 kinds of dwarf isolines; * and ** indicate significances at the 0.05 and 0.01 levels, respectively.

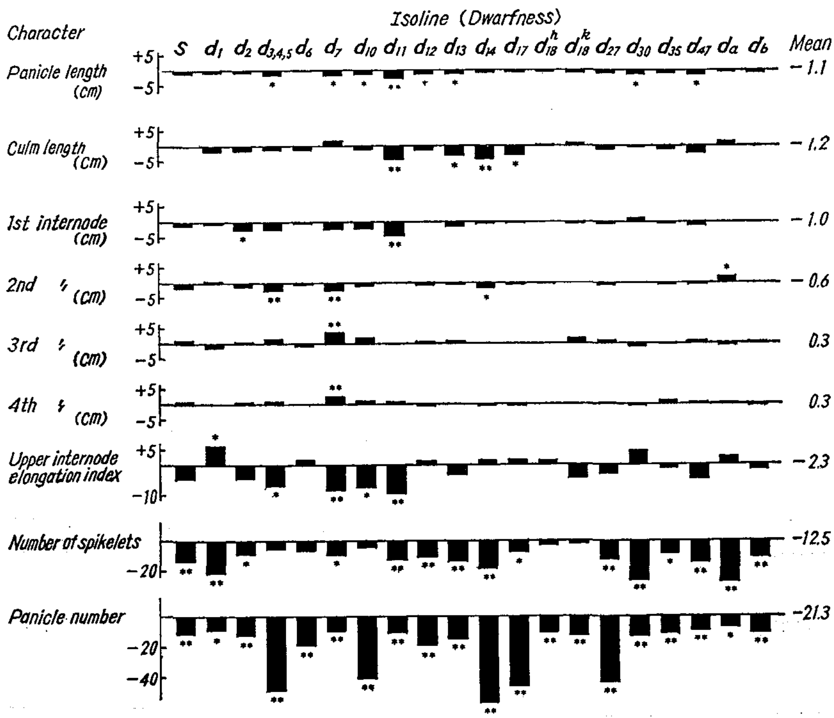

Fig. 2. Comparison of nine characters between dense planting and standard condition with a normal density in the cultivar, Shiokari (S) and 19 kinds of dwarf isolines; * and ** indicate significances at the 0.05% and 0.01% levels, respectively.

lines showed a significant fluctuation in the culm length for the fertilizer conditions as well as that of Shiokari. In addition, d_{27}, d_{30}-. d_{35}- and d_a- lines showed a similar tendency in the culm length though the degrees of response were smaller. The effect of dense planting were shown to decrease the characters though the decrement was not so prominent except the number of spikeletes and the panicle number. As to the internodes, the fluctuation of the second and third internodes were prominent under non-fertilizing condition. The responses of the internode lengths from the first to third in the other conditions were variable depending on the dwarf genotypes. A similar tendency was obtained in the lengths of leaf sheaths and blades though their data are omitted here. In the upper internode elongation index, Shiokari showed a significant decrease both in non- and double fertilizations, while d_{11}-, d_{12}-, d_{14}-, d_{17}-. d_{18}^k- and d_a- lines showed a significant increment in non-treatment of fertilizer. In the number of spikelets, most of the lines decreased in non-fertilization, while Shiokari, d_{12}- and d_{30}- lines showed a significant increase in the double fertilization. More than half of the dwarf lines showed a significant decrement in the dense planting. In the panicle number, all lines including Shiokari decreased prominently in both non-fertilization and dense planting. The five tillering dwarfs, namely $d_{3,4,5}$-, d_{10}-, d_{14}, d_{17}- and d_{27}- lines indicated a prominient decrease in the dense planting. Through the expreiment, it is remarkable that the non-fertilizing condition showed a decrease in most of the characters, though the degrees were variable among the genotypes. The effect of plant density was prominent in both the number of spikelets and the panicle number.

3. Correlations among the responses of the dwarf lines for the fertilizer treatment

In the previous section, it was shown that the difference between the non- and the standard fertilization was most prominent as the response to fertilization. Thus, the increment of the characters was considered as a

TABLE 4. Correlation coefficients among the increased values from the non- to the standard fertilization in the nine characters

	Panicle length	Culm length	Internode length				Upper inter. elong. index	Number of spikelets	Panicle number[1)]		
			1st	2nd	3rd	4th					
Panicle length		−.01	.34	−.14	.78**	.03	.09	.15	−.08	(−.12,	.36)
Culm length			.33	.91**	.21	.12	−.62**	.47*	.28	(.36,	−.40)
1st internode length				.28	.04	−.53*	.17	.30	.04	(−.01,	.34)
2nd 〃					−.03	−.11	−.79**	.43	.35	(.43,	.54)
3rd 〃						.39	−.01	.08	−.14	(−.11,	−.45)
4th 〃							−.11	−.14	.15	(−.11,	−.18)
Upper internode elongation index								−.18	−.48*	(−.46,	−.37)
Number of spikelets									−.09	(.08,	−.41)
Correlation between the increments and the values of the standard condition	.85**	.69**	.56*	.59**	.54*	.77**	−.02	.33	.86**	(.59*,	−.01)

1) Correlation coefficients calculated by the five tillering dwarfs (right) and those calculated by the dwarf lines and Shiokari except the tillering dwarfs (left) in the parentheses, respectively.

*, ** Significant at the 0.05 and 0.01 levels, respectively.

result of fertilization. Therefore the correlation coefficients were calculated using the increased values of the dwarf lines and Shiokari from the non-fertilization to the standard condition (Table 4). A close correlation was obtained between the culm length and the length of the second internode. In addition, the culm length was negatively correlated with the upper internode elongation index, indicating that the increment in the culm length is related to the reduction of the index. A significant negative correlation was also recognized between the first and fourth internode lengths. Furthermore, the increments of the characters were significantly correlated with the actual values in the standard condition, except the upper internode elongation index and the number of spikelets. Principal component analysis was applied to detect the correlations among the increase of the lengths of the respective internodes. As shown in Table 5, the first component contributing 43.2% to the total variation was negatively loaded for the lengths of the first and the second internodes and positively for the lengths of the third and fourth internodes. It is implied that a large part of the variation due to the fertilizer response may be explained by the relation between upper and lower internodes elongation.

TABLE 5. Factor loadings of the first three principal components calculated by the increments of the length of internodes from the non- to the stanard fertilization

Length of	I	II	III
1st internode	−.77	.41	−.35
2nd 〃	−.44	.52	.73
3rd 〃	.43	.79	−.37
4th 〃	.86	.24	.25
Eigen value	1.73	1.12	.85
Contribution (%)	43.2	28.0	21.1
Cumulated (%)		71.2	92.4

4. Regression analysis

It was assumed that the dwarf lines can respond to various environments in a different manner. Therefore, the regression analysis was applied using the data of the five different conditions, namely the non-, standard and double fertilizations and the dense planting condition in 1980 and the standard condition in 1979. In the analysis, the response of Shiokari was used as the standard to the respective lines and the regression coefficients were calculated

TABLE 6. The regressions of the responses to the five environmental conditions in the nineteen dwarf lines on those in Shiokari; the regression coefficients and the coefficients of determination (%) in the parentheses

Name of isoline	Panicle length	Culm length	Internode length				Upper inter. elong. index	Number of spikelets	Panicle number
			1st	2nd	3rd	4th			
d_1-	.31 (53)	.23 (89)*	.42 (69)	.30 (48)	.15 (17)	.09 (69)	.10 (2)	.45 (48)	.55 (56)
d_2-	.37 (80)*	.38 (53)	.28 (6)	.65 (43)	.16 (6)	.01 (0)	.26 (8)	.67 (54)	1.03 (90)*
$d_{3,4,5}$-	.80 (84)*	.45 (97)*	.39 (29)	.77 (80)*	.33 (49)	.04 (1)	.35 (10)	.15 (31)	2.32 (72)
d_6-	.22 (44)	.15 (61)	.37 (29)	.01 (0)	−.04 (5)	.03 (3)	−.14 (33)	.35 (79)*	1.25 (74)
d_7-	.67 (61)	.89 (96)**	.32 (35)	.97 (82)*	.57 (39)	−.35 (13)	.01 (0)	.85 (81)*	.82 (99)**
d_{10}-	.69 (77)	.41 (45)	.44 (40)	.52 (46)	.21 (10)	−.04 (1)	−.04 (0)	.37 (85)*	2.36 (77)*
d_{11}-	2.33 (27)	.58 (57)	.25 (60)	.02 (34)	.71 (16)	.35 (32)	.36 (2)	.54 (94)**	.76 (94)**
d_{12}-	.68 (78)*	1.23 (88)*	.91 (49)	2.19 (92)*	.21 (7)	−.15 (39)	−.38 (17)	.85 (98)**	1.19 (86)*
d_{13}-	.26 (30)	.31 (61)	−.10 (9)	.16 (39)	.17 (13)	.14 (3)	−.15 (3)	.54 (86)*	.63 (57)
d_{14}-	.92 (80)*	.48 (62)	−.13 (7)	.79 (91)*	.30 (36)	.15 (5)	.05 (0)	.65 (83)*	2.61 (58)
d_{17}-	.43 (47)	.54 (68)	.21 (7)	.61 (85)*	.35 (35)	.31 (21)	.07 (0)	.35 (92)**	2.48 (76)
d_{18}^{h}-	.25 (80)*	.00 (0)	−.04 (2)	.08 (71)	.00 (0)	−.03 (90)*	−.01 (0)	.12 (55)	1.10 (68)
d_{18}^{k}-	.88 (88)*	.38 (73)	.16 (64)	.44 (95)**	.09 (1)	−.01 (2)	−.38 (9)	.47 (96)**	1.22 (91)*
d_{27}-	.61 (76)	.51 (73)	.06 (0)	.47 (83)*	.42 (48)	.54 (45)	.28 (7)	.62 (94)**	2.38 (72)
d_{30}-	.32 (23)	.71 (97)**	.61 (40)	.42 (72)	.27 (20)	−.03 (0)	−.56 (89)*	.75 (54)	.86 (93)**
d_{35}-	.59 (91)*	.61 (97)**	.42 (45)	.55 (94)**	.56 (59)	−.09 (2)	.18 (24)	.39 (92)**	.91 (97)**
d_{47}-	.65 (70)	.38 (72)	.22 (16)	.59 (99)**	.23 (32)	.11 (7)	.35 (24)	.61 (84)*	.79 (99)**
d_a-	.27 (4)	.57 (96)**	.20 (16)	.70 (63)	.45 (37)	−.02 (1)	−.34 (11)	.60 (59)	.61 (99)**
d_b-	.75 (97)**	.34 (14)**	.30 (39)	.40 (93)**	.38 (57)	.03 (1)	.22 (7)	.67 (97)**	.93 (99)**
Mean	.63 (63)	.48 (73)	.28 (30)	.57 (69)	.29 (26)	.06 (18)	.01 (13)	.53 (77)	1.31 (82)
Correlation[1]	.87**[2]	.78**		.63**[3]				.75**	.98**[4]

1) The correlation coefficient between the regression coefficients and the actual values in the standard condition.
2) $r=0.58$*, calculated with the exception of d_{11}-line.
3) $r=0.85$*, calculated with the exception of d_1-, d_6-, d_{11}- and d_{18}^{h}-lines.
4) $r=0.72$**, calculated with the exception of the five tillering dwarfs, and $r=0.92$*, calculated in the tillering dwarfs, respectively.

by using the five values of Shiokari obtained in the five kinds of conditions as the independent variable and those of the respective dwarf lines as the dependent variable, as shown in Table 6. Most of the dwarf lines showed a good fitness to the regressions in the panicle and the culm lengths, the length of the second internode and the number of spikelets and the panicle number, while a poorer fitness was recognized in the lengths of the first, third and fourth internodes and the upper internode elongation index. In the paincle length, the d_{11}- line showed a larger value due to the occurrence of additional neck leaf. It is also noted that d_{12}-line showed a larger response than that of Shiokari in the culm length and the length of the second internode. The dwarf lines possessing the extremely reduced second internode such as d_6-, d_{11}- and d^h_{18}-lines showed a feeble response. In these lines, the environmental conditions used in this study scarcely affected the second internode. In the panicle number, the five kinds of tillering dwarfs, $d_{3,4,5}$-, d_{10}-, d_{14}-, d_{17}- and d_{27}-lines showed a remarkable response. In addition, d_2, d_{12} and d^k_{81}-lines indicated somewhat weaker responses. The extreme dwarf type, d^h_{18}-line showed no or little response throughout the characters except the panicle number. As shown in the table, significant correlations were shown between the regression coefficients and the actual values of the respective dwarf lines in the standard condition in 1980. The correlation coefficient between the regression coefficients of the culm length and the length of the second internode was highly signifiant ($r=0.81^{**}$ including all dwarf lines and $r=0.85^{**}$ in the 15 dwarf lines except d_1-, d_6-, d_{11} and d_{12}-lines).

Discussion

There are several papers[1,2,3,5,9] on the influences of environmental conditions for the character expression of dwarf lines. However, most of the dwarf lines used, consisted of different origins and possessed different genetic backgrounds. In the present experiment, the near-isogenic dwarf lines possessing the genetic background of Shiokari were used for examining the environmental effects. From the results of principal component analysis under the four kinds of different environmental conditions, the fundamental relations among the different internode lengths were maintained through the all conditions showing the strong effects of dwarf genes. In addition, the increased values of the internodes from non-fertilizing to the standard condition in the dwarf lines and Shiokari were explained by the compensative relation between upper and lower internodes. In the standard cultivation, it is evident that d_1, d_6, d_{11} and d^h_{18} genes exert their actions to diminish the second internode. This genic action was hardly affected by the environmental conditions used in this study.

According to several papers[1,2,9] the extreme reduction of the second internode caused by d_1 was maintained through the long day and the low temperature conditions during panicle formation, while the short day and the high temperature conditions affected significantly. The near-isogenic lines used in this experiment, possessed the genetic background of Shiokari. The panicle formation in Shiokari and most of the isogenic lines proceeded in the relatively long day (more than 14 hours) and the low temperature (about 19°C) conditions in July. Thus, it is supposed that the climatic condition in Sapporo was favourable to maintain the reduction of the second internode.

Depending on the regression analysis, most of the dwarf lines showed a parallel and smaller response than those of Shiokari in the panicle and the culm lengths, the length of the second internode and the number of spikelets. In the respective characters, the regression coefficients correlated with the actual values in the standard condition. In addition, a close correlation was found between the responses of the culm length and the length of the second internode.

From this study, it is concluded that the environmental response of the nineteen kinds of near-isogenic dwarf lines showed a parallel relation with the character expression of the dwarf genes under the standard cultivation as a whole. However, in the internodes composing culm length, upper and lower internodes showed a compensative relation for their contribution to the increase of culm length.

Summary

Effects of the three environmental conditions were examined for the character expression of the nineteen kinds of near-isogenic dwarf lines and their recurrent parent, Shiokari.

There was a ignificant modification in the panicle and the culm lengths and the lengths of respective internodes. It is noted that most of the dwarf lines showed a prominent decrease in the panicle and the culm lengths, the lengths of the respective internodes, the number of spikelets and the panicle numbers under the non-fertilization condition. In most of the dwarf lines, the increased values of the culm length by the application of fertilizer negatively correlated with the increment of the upper internode elongation index showing a change toward the lower elongation type. However, the fluctuation of the characters was not pronounced in the environmental change from

the standard to the double-fertilized condition. The effects of dense planting were recognized in both the number of spikelets and the panicle number.

The authors classified the near-isogenic dwarf lines into the four groups depending on the relative elongation pattern of the upper and lower internodes and the exreme reduction of the second internode in the previous paper[6]. The extreme reduction of the second internode in d_1-, d_6-, d_{11}- and d_{18}^h-lines was hardly affected by the environmental conditions used in this study.

From the regression analysis using the data under the five environmental conditions such as the three different fertilizer levels, the planting density and the different year, it is recognized that the response of the most dwarf lines were parallel and smaller than those of Shiokari in the panicle and the culm lengths, the length of the second internode and the number of spikelets. In the panicle number, the five tillering dwarf lines showed a prominient response in comparison with those of the other lines. Further, the correlation existed between the degree of responses and the actual values of the characters in the standard cultivation.

From these observations, it is noted that the responses in the culm length and the second internode lengths showed a close correlation. It was implied that the fluctuation in the upper and lower internodes contribute to the increase of culm length by a compensative relation.

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