イネの少分げつ型の遺伝と形質発現

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Inheritance and Expression of Reduced Culm Number Character in Rice[1]

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A mutant with a reduced culm number was found in M_2 population of AC-3 (a strain regenerated from A-5 Akamuro by anther culture) after gamma-ray irradiation of dry seeds. In F_2 population of the crossing between the mutant line, N-133 and the original strain, A-5, it was demonstrated that a single recessive gene, *rcn* is responsible for the reduced culm number type. A pleiotropic effect showing dwarfness was expressed although the seed fertility was unaffected. In the linkage analysis, it was found that *rcn* was linked with the genes belonging to the first linkage group such as *wx* (glutinous endosperm) and *C* (Chromogen for anthocyanin) in the order of *wx-C-rcn*. In addition, *rcn* was epistatic to the dwarf genes, *d-2* (ebisu dwarf), *d-3*, *d-4*, *d-5* (triplicate genes for bunketsu waito) and *d-10* (toyohikari-bunwai). As for the relation with *d-6* (ebisumochi dwarf), a non-parental dwarf type with a reduced culm number and shorter lower (below the second) internodes occurred as a double recessive genotype. The character expression of the mutant gene, *rcn* was remarkably affected by the temperature conditions during the growth period. Plant height and culm number of the mutant recovered to nearly normal when grown in a plastic house with the application of nitrogen. Since the plant height and culm number were retarded by the treatment with cold water (15°C), it was demonstrated that the gene expression was conditioned by the low temperature.

KEY WORDS : Rice, mutant, reduced culm number, recessiveness, linkage, temperature-sensitive.

Introduction

A uni-culm character is used as a marker for both genetical and physiological studies in barley (SHANDS 1962, NONAKA 1973, 1974). Although a similar mutant, called reduced culm number type, was found in rice by FUTSUHARA and YAMAGUCHI (1963), this mutant line was lost because of high sterility. The authors recently obtained a similar mutant with high fertility by gamma-ray irradiation. In this study, the genetical and physi-

Table 1. List of strains used in the experiment

Strain No.	Name	Marker genes	Plant type
N-133	Mutant[1]	B^{Br}, *A*, *Pr*, *Rc*, *Rd*, $I\text{-}Bf^{+}$	reduced culm number
A- 5	Akamuro	C^{Br}, *A*, *Pr*, *Rc*, *Rd*, $I\text{-}Bf^{+}$	normal
A- 32	Furen-bozu	*Ur*-1	normal
A- 58	Kokushokuto-2	C^{B}, *A*, *Pr*, *Pn*, *Ph*, *wx*	normal
H- 85	Linkage tester	C^{+}, *d*-2, *Ur*-1	dwarf
H-126	Linkage tester	C^{Bp}, *A*, *Pl*, *d*-6, *Hg*	dwarf
N- 70	Toyohikari bunwai	*d*-10	tillering dwarf
N-140	Mutant[1]	C^{Br}, *A*, *Pr*, *Rc*, *Rd*, $I\text{-}Bf^{+}$	tillering dwarf

[1] Induced by gamma irradiation from A-5

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ological nature of the mutant character was investigated.

Materials and Methods

Strains used in the present experiments are shown in Table 1. A pure line, AC-3 which was regenerated from the anther culture of the strain, A-5 was used for the gamma-ray irradiations. Total exposure dose to the dry seeds was 20 kR. A mutant line having a uni-culm was named N-133. On the other hand, N-140 is another mutant strain having a tillering dwarf character which was induced by gamma irradiation of A-5. F_1 and F_2 plants of the crosses of N-133, were planted in the experimental paddy field. The recombination value was calculated following IMMER's productive ratio method. Several morphological characters were compared between the mutant line and the original strain, A-5 in the paddy field.

In order to examine environmental fluctuation in the expression of the character, the responses to fertilizer levels and different plant densities were investigated by using a split-plot design experiment in the paddy field. The three main-plot treatments were non-fertilization, standard fertilization (N: 7.2 kg, P_2O_5: 7.2 kg, K_2O: 4.5 kg per 10 a) and double quantities of fertilization. As for plant density, two conditions, namely narrow spacing at 7.5×30 cm and standard, 15×30 cm were used in each main plot. In all plots, four plants excluding the border plants were evaluated for ten morphological characters.

Plants in the plastic house were grown in pots of 3 *l* filled with soil. Nitrogen fertilizer was applied as a basal dressing in the levels of 0, 0.3, 0.6, 1.2 g per pot and 0.2 g of P_2O_5 and K_2O were added to all pots, respectively. Two plants were grown in each pot and eight plants were observed for the plant height and culm number in each treatment.

The influence of the cold water irrigation was examined both in the mutant and the original lines. Prior to the treatment, one plant was grown in each pot of 2 *l*, by soil culture in a plastic house. The treatments were initiated on June 22 and each pot was dipped in running water kept at 15°C in a big water bath located in the green house. After one month treatment, all materials were returned to the plastic house. The plant height and culm number were recorded at an interval of 10 days.

Results

1. Genetic analysis

F_1 plants of the cross between normal and the reduced culm number type indicated a

Table 2. F_2 segregations of reducad culm number type in the N-133×normal testers

Cross combination	Phenotype / Genotype	Normal / +	Reduced culm no. / *rcn*	Total	Goodness of fit: χ^2 (3 : 1)	Goodness of fit: p
N-133×A-5	Obs.	58	20	78	0.02	0.9—0.8
N-133×A-32	Obs.	207	63	270	0.40	0.6—0.5
N-133×A-58	Obs.	135	33	168	2.57	0.2—0.1
Total	Obs.	400	116	516	1.75	0.2—0.1

Homogeneity : χ^2=1.34, d.f.=2, p=0.6—0.5

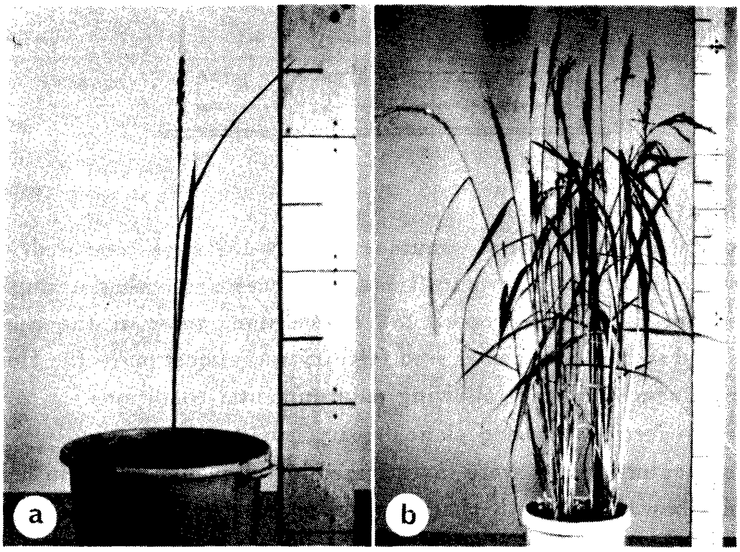


Fig. 1. Plant stature of the mutant, N-133 (One scale means 5 cm).
a. Reduced culm number type grown in paddy field.
b. Normally recovered type grown in plastic house (Two plants were grown in a plastic pot).

Table 3. Combined segregations between *rcn* and dwarf genes in F_2 populations

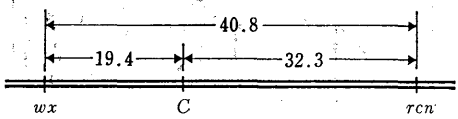
Cross combination	dwarf gene (*d*)	Genotype	+		*rcn*		Total	Goodness of fit		
			+	*d*	+	*d*		Ratio	χ^2	p
N-133×H- 85	*d*-2	Obs.	111	48	62		221	9 : 3 : 4	3. 29	0. 2—0. 1
N-133×H-126	*d*-6	Obs.	39	17	11	6	73	9 : 3 : 3 : 1	1. 89	0. 6—0. 5
N- 70×N-133	*d*-10	Obs.	129	40	49		218	9 : 3 : 4	0. 91	0. 7—0. 6
N-140×N-133	*d*-3, 4, 5[1)]	Obs.	70	21	21		112	9 : 3 : 4	2. 53	0. 3—0. 2

[1)] Triplicate recessive genes, *d*-3, *d*-4, *d*-5

normal type. In F_2 population, plants having one or two culms were discernible from the normal type (Table 2). In addition, the plant height was also reduced in the mutant type as shown in Fig. 1a. It is evident that a single recessive gene was responsible for the character. The authors adopted the gene symbol, *rcn*. Because the marker genes which was contained in A-5 did not segregate in the cross N-133 x A-5, it was assumed that the gene *rcn* was induced by the point mutation from the original stain, A-5.

Four kinds of dwarf strains were crossed with N-133 and the combined segregations between *rcn* and dwarf genes are shown in Table 3. In all crosses, the dwarf genes, *d-2*, *d-6*, *d-10* and the triplicate genes *d-3*, *d-4* and *d-5* showed an independent relation with *rcn*. The gene *rcn* indicated an epistasis to the dwarf genes used except *d-6*. However, the double recessive genotype, *rcn d-6* showing contraction of the lower internodes and greater expression of dwarfness was discernible in the F_2 population of the cross, N-133×H-126.

New linkage relations involving *rcn* were detected as shown in Table 4. Based on the recombination values among *C*, *wx* and *rcn*, three genes were located on the first linkage group in the following order:



2. Environmental fluctuation

The morphological characters of the mutant line, N-133 were compared with those of the original strain, A-5. As shown in Table 5, it was noted that a single culm type was expressed in the paddy field condition. In addition, most of the characters were prominently reduced in N-133, whereas seed fertility was almost perfect. However, these characters were influenced by the following environmental conditions.

(A) Response to fertilization and plant density levels

Plant height and culm number were investigated in the plants grown in field condition. Variance analysis showed that both characters were affected by strain, fertilization and plant density (Table 6). As to the effect of fertilization, plant height of N-133 and culm

Table 4. Linkage relationship between three genes, *rcn* (reduced culm number), *C* (Chromogen for anthocyanin) and *wx* (glutinous endosperm) in F_2 population of the cross, N-133×A-58

Gene pair		F_2 segregation				Total	R.C.V.[1] (%)	Goodness of fit		
		AB	*Ab*	*aB*	*ab*			Ratio	χ^2	p
C–rcn	O.	111	18	24	15	168		9 : 3 : 3 : 1	12.38	<0.01
(coup.)	C.	103.25	22.75	22.75	19.25	168.00	32.3		2.58	0.5—0.4
wx–rcn	O.	89	46	26	7	168		9 : 3 : 3 : 1	9.12	0.05—0.02
(rep.)	C.	90.99	35.01	35.01	6.99	168.00	40.8		5.81	0.2—0.1
C–wx	O.	78	51	37	2	168		9 : 3 : 3 : 1	22.75	<0.01
(rep.)	C.	85.58	40.42	40.42	1.58	168.00	19.4		3.84	0.3—0.2

1) Recombination value

Table 5. Comparison of some agronomic characters between A-5 and the mutant, N-133 (Paddy field, 1981)

Character		Strain		
		A-5	N-133	
Plant height	(cm)	86.4[1]	21.6[1]	(25.0)[2]
Culm number per plant		5.5	1.0	(18.2)
Panicle length	(cm)	19.6	5.7	(29.1)
Culm length	(cm)	65.6	15.9	(24.2)
1 st internode length	(cm)	31.6	9.5	(30.1)
2 nd internode length	(cm)	17.1	3.3	(19.3)
3 rd internode length	(cm)	13.4	2.7	(20.1)
4 th internode length	(cm)	4.3	0.6	(14.0)
Number of spikelets per panicle		104.4	6.5	(6.2)
Seed fertility	(%)	88.7	92.0	(103.7)

1) Mean value
2) Percentage to the normal strain, A-5

Table 6. Analysis of variance for plant height and culm number per plant (Paddy field)

Plant height

Source of variance	d. f.	Sum of square	Mean square	F value
Replication	1	2. 10	2. 10	<1
A : Strain	2	456. 69	228. 35	103. 33**
B : Fertilizer	1	25. 01	25. 01	11. 32*
A × B	2	9. 35	4. 68	2. 12
Error (1)	5	11. 09	2. 21	<1
C : Density of planting	1	19, 682. 55	19, 682. 55	1, 301. 76**
A × C	2	306. 20	153. 10	10. 13*
B × C	1	0. 46	0. 46	<1
A × B × C	2	2. 53	1. 27	<1
Error (2)	6	90. 73	15. 12	
Total	23	20, 586. 71		

Culm number

Source of variance	d. f.	Sum of square	Mean square	F value
Replication	1	0. 40	0. 40	4. 88
A : Strain	2	10. 33	5. 17	62. 99**
B : Fertilizer	1	1. 76	1. 76	21. 46**
A × B	2	2. 13	1. 07	12. 99**
Error (1)	5	0. 41	0. 08	<1
C : Density of planting	1	138. 72	138. 72	1, 109. 76**
A × C	2	7. 62	3. 81	30. 48**
B × C	1	1. 55	1. 55	12. 40*
A × B × C	2	1. 80	0. 90	7. 20*
Error (2)	6	0. 75	0. 13	
Total	23	165. 47		

*,** Singificant at the 5%, and 1% levels, respectively

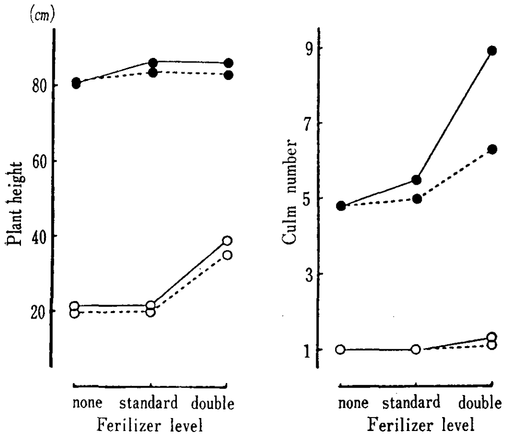


Fig. 2. Effects of fertilizer and plant density on plant height and culm number per plant (Paddy field).

Note : ● A-5 —— Standard planting

○ N-133 ······ Dense planting

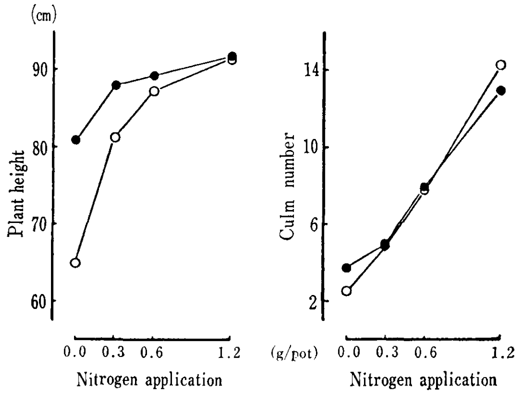


Fig. 3. Effects of nitrogen application on plant height and culm number per plant (Plastic house).

Note : ● A-5, ○ N-133

number of A-5 were conspicuously increased by the double quantities of fertilization (Fig. 2). It was noted that culm number of N-133 was rather stable for the change of both fertilization and plant density.

(B) Response to nitrogen fertilization

Plant height and culm number were measured in the plants grown in the plastic house. As shown in Figs. 1 b and 3, there was no difference in plant height and culm number between N-133 and A-5 in the treatment with nitrogen over 0. 6 g/pot. N-133 remarkably increased in plant height with increasing amount of nitrogen whereas the increment of A-5 was not so prominent. In culm number there was no difference between A-5 and N-133 in that both responded proportionally to the increase of nitrogen fertilization.

(C) Response to irrigation with cold water

As shown in Fig. 4, the growth of N-133 was retarded to some extent during the irrigation treatment with running water (15°C). The effect of the irrigation remained until the flowering stage both in plant height and culm number of N-133. The decrease of culm number of A-5 in the untreated plot is due to the shortage of nitrogen in the later part of the growth. Thus, it was demonstrated that the decrease of plant height and culm number of N-133 is dependent on the sensitivity to the low temperature during the growing stage.

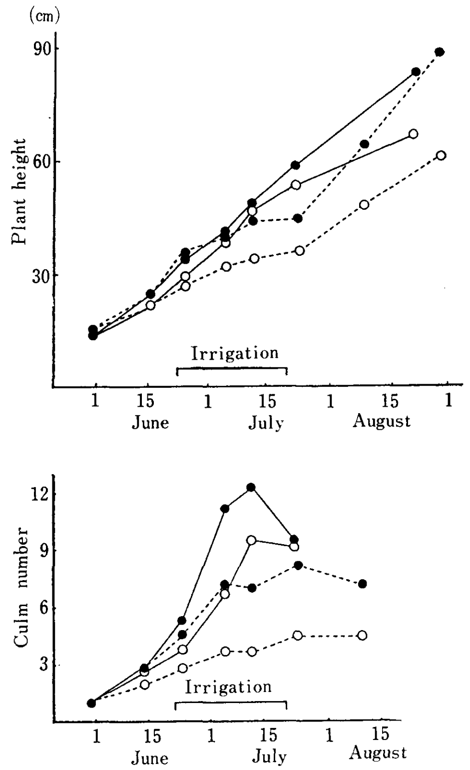


Fig. 4. Effects of irrigation with cold water (15°C) on plant height and culm number per plant.
Note : ● A-5 —— control
○ N-133 …… irrigated with cold water

Discussion

A mutant with the reduced culm number type caused by a single recessive gene was found in M_2 generation of the cultivar Fujiminori (FUTSUHARA and YAMAGUCHI 1963). Our material, N-133 was also induced by gamma irradiation and indicated reduced culm number and dwarfness with perfect seed fertility. Though genic identification was impossible because of extinction of the former mutant, the mutant character was responsible for the single recessive gene designated as *rcn*. In the linkage analysis, it was found that the gene, *rcn* is located on the first linkage group in the order of *wx-C-rcn*.

In the character expression of *rcn*, it was recognized that one or two culms develop under the condition of paddy field from year to year. However, the plant height of the mutants showed a considerable increase by the application of excessive fertilizer in some years. In the high temperature condition of plastic house, plant height and culm number of N-133 recovered to nearly the same as the original strain, A-5, in the application of nitrogen. It is evident that there is some difference between the temperature conditions in plastic house and outdoors and the heading date is accelerated at least ten days earlier in the former condtion. On the contrary, the irrigation treatment with cold water after the cultivation in a plastic house until June 22, inhibited growth in plant height and culm number of N-133 to some extent. Thus, it is considered that the character expression of the mutant was conditioned by low temperature during the growing period.

As for the effect of temperature for the expression of dwarfness, it is known that the growth and development of the wheat dwarf 1 from the cross, Marquillo × Kenya Farmer were inhibited at 16°C in 10-day old seedlings (CANVIN and YAO 1967, MAHON and CANVIN 1972), while the high temperature condition (25°-30°C) is needed for the reduction of culm elongation in Fukei 71 dwarf of rice (KITANO and FUTSUHARA 1981, 1982). Further detailed surveys of the temperature conditions will be dealt with in future studies. This mutant might be useful as a material for genetical and physiological studies.

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イネの少分げつ型の遺伝と形質発現

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AC-3（A-5 赤室の葯培養による再生系統）の種子に 20 kR のガンマー線処理を行って M_2 代集団を水田条件で養成したところ 1～2 本の分げつより成る突然変異体が見出された．この後代の少分げつ型系統（N-133）は，水田条件において1ないし2本の分げつを有する矮性型であった．N-133 と A-5 の交雑組合せの F_1 は正常型となり，F_2 では正常型：少分げつ型を 3：1 の比に分離した．従って本形質には，単純劣性遺伝子（*rcn*）の関与していることが明らかになった．蓬原・山口（1963）のさきに見出した少分げつ型と比べるならば，今回の少分げつ変異体は不稔性を示さぬ点で異なっており，おそらく関与遺伝子を互いに異にすると考えられる．N-133 と各種の矮性型系統との交雑組合せの F_1 では正常型を示し，F_2 の分離においては *rcn* が各種の矮性遺伝子，*d*-2（夷），*d*-3，*d*-4，*d*-5（分げつ矮稲）および *d*-10（豊光分矮）に対してそれぞれ上位的に作用する独立分離を示した．しかし，*d*-6 に対しては *d*-6 *rcn* なる2重劣性遺伝子型が第2節間の短縮と顕著な矮性型を示し，*rcn* 型や *d*-6 型と明らかに識別できて，独立の場合の 9：3：3：1 の分離比によく適合した．

少分げつ型は，環境条件によってかなり形質表現の変動がみられた．すなわち水田条件では施肥量の増加に伴い，N-133 の草丈は顕著に増大したが，分げつ数には変動がみられなかった．一方，ビニールハウス内の高温条件下で育成した場合には，草丈および分げつ数が原系統の A-5 と同程度まで増大し，草姿も正常型となった．また，ビニールハウス内でも6月22日まで育成した後に分げつ期および節間伸長期にわたって 15℃ の冷水による掛流し処理を行ったところ，草丈と分げつの両方が顕著な抑制を受けた．このような実験結果から少分げつ型の発現にあたっては，低温条件の必要であることが明らかになった．本突然変異体は，遺伝子分析や植物生理学的研究の材料として用いられよう．