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Full Length Research Paper

Plant architecture and its responses to high planting density and low fertilizer of reduced culm number mutants in rice (*Oryza sativa* L.)

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Plant architecture is of major agronomic importance as it determines the potential grain yield depending on environmental conditions in rice (*Oryza sativa* L.). Here, we characterized plant architecture and its response to low fertilizer and high planting density in five rice "reduced culm number (rcn)" mutants; "*rcn1-2*, *rcn2*, *rcn4-2*, *rcn5* and *rcn6*", originating from rice cultivar 'Shiokari', with 'Shiokari' as a parental control. Under control condition, a positive correlation was observed between tiller number and plant height showing that each rcn controls both apical and axillary shoots elongation. High density and low fertilizer had the negative effects on tillering and main shoot development involving main culm length, leaf number, panicle length, spikelet number on main culm in 'Shiokari'. The degrees of negative effect on main shoot development by the present environmental stresses were depended on '*rcn*' genotype. Among them, '*rcn6*' constantly developed main shoot architecture under low fertilizer or high density planting.

Key words: Tillering, reduced culm number mutant, low fertilizer, high density, rice.

INTRODUCTION

Plant architecture, involving tillering and plant height, is a major agronomic importance as it determines the adaptability of a plant to cultivation, its harvest index and potential grain yield (Reinhardt and Kuhlemeier, 2002). Rice (*Oryza sativa* L.), one of the dominant grain crops, feeds more than half the world's population. In most developing countries, the demand for rice increases dramatically with population growth. To meet this challenge new elite varieties of rice, with plant architecture that can produce much higher grain yield, need to be developed (Yuan, 1977; Khush, 2001). With the introduction of the 'green revolution' semi-dwarf varieties of rice demonstrated the value of architecture control (Khush 2001). Semi-dwarf varieties were shorter and more resistant to damage by wind and rain (lodging), and also responded better to nitrogen fertilizers by increasing grain yield rather than straw biomass. As a result, semi-dwarf varieties contributed substantially to dramatic increases in rice yields (David and Otsuka, 1994). The design of the most recent high yielding rice varieties, new plant type in International Rice Research Institute and "super" hybrid rice in China, focused on the reduced tillering capacity, large panicle size and improved lodging resistance (Peng et al., 2008). Plant architecture is regulated at numerous levels, including genetic determination and hormone signaling pathways depending on environmental factors. Our knowledge of the underlying molecular basis of plant architecture in rice has accumulated mainly through the characterization of rice mutants.

Numerous mutants will facilitate the identification of related functional genes associated genetic network that controls the rice plant architecture. To date, a total of ten "reduced culm number (rcn) and few tillering (ft)" mutants have been reported (Takamure et al., 1989; Takamure and Kinoshita, 1993; Takamure, 1994; Tang et al., 2001; Jiang et al., 2006; Yasuno et al., 2007; Ariyaratne et al.,

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2009). Based on the allelism test, nine '*rcn*' are controlled by independent loci (Takamure et al., 1989; Takamure, 1994; Takamure and Kinoshita, 1993; Jiang et al., 2006). In addition to the reduction of tillering, 'rcn1~6' significantly reduced culm length under paddy field (Takamure and Kinoshita, 1985; Takamure et al., 1999) showing that each '*rcn*' affects meristem elongation activity of both apical and axillary shoots. While the effects of each '*rcn*' on meristem activity were varied under the plastic house condition, '*rcn2*' significantly reduced tillering. '*rcn6*' significantly reduced tillering and culm length. The negative effects of *rcn1-1* (formerly *rcn1*), *rcn3*, *rcn4-1* (formerly *rcn4*) and *rcn5* on tillering and culm length disappeared under plastic house conditions. Takamure and Kinoshita (1985) reported that the negative effect of '*rcn1-1*' on tillering was independent of high fertilizer involving nitrogen, phosphate and potassium in the paddy field experiment suggesting that '*rcn1-1*' lacks in response to nitrogen, phosphate and potassium in activation of shoot elongation.

Little is known about the effect of low fertilizer and high planting density on other 'rcn' actions. The objectives of the present study were to clarify the effect of high density and low fertilizer on plant architecture in a series of five 'reduced culm number' mutants, '*rcn1*, *rcn2*, *rcn4*, *rcn5* and *rcn6*' with identical genetic background of rice cultivar 'Shiokari' to screen which mutant will be the most beneficial for crop yield.

MATERIALS AND METHODS

Plant materials

Rice (*Oryza sativa* L. ssp. *japonica*) cultivar 'Shiokari' and five independent rice 'reduced culm number' (rcn) mutants originating from 'Shiokari', namely S-97-61 (*rcn1-2*), N-174 (*rcn2*), N-187 (*rcn4-2*), N-185 (*rcn5*) and N-186 (*rcn6*) (Takamure et al., 1989; Takamure and Kinoshita, 1993; Takamure, 1994; Yasuno et al., 2007; Ariyaratne et al., 2009) were used in the present study.

Growth conditions

Germinated seeds were grown in a 30 ml cell-tray, filled with soil. Four weeks old seedlings were transferred to 3L pots filled with 2 kg of soil including 0.60 g of each N, P_2O_5 and K_2O per pot as control, and 0.15 g of each N, P_2O_5 and K_2O per pot (low fertilizer condition; 1F) on July 2009. In both fertilizer levels, plant density was arranged as single plant/pot (1P). For planting density response experiment, 0.60 g of each N, P_2O_5 and K_2O (4F) was added per pot and the density was arranged as 2 plants/pot (2P), 4 plants/pot (4P) and 8 plants/pot (8P). 6 plants in 1P experiment (control and 1F), 8 plants in 2P experiment, 12 plants in 4P experiment, 24 plants in 8P were grown under natural conditions at Obihiro University of Agriculture and Veterinary Medicine from July to October in 2009. Genotypes were randomly arranged every week to avoid positional effects. Active tiller number and plant height was measured weekly until the flag leaf emergence. Emergence of top of panicle was considered as flowering date, data was collected every day.

110 days after transplanting, panicle number, panicle length, number of spikelet/panicle, culm length (plant height), and dry-matter production, were measured. Statistical analysis was performed between 'Shiokari' and 'rcn', and control and each treatment using the t-test at 5, 1 and 0.1%, respectively. Correlation coefficient between tiller number and plant height was calculated under control condition.

RESULTS

Tillering and plant height

In 'Shiokari', tillering started at two weeks after planting, and took off between 6 and 7 weeks after planting. At eight weeks after planting, tillering stopped in 'Shiokari' (Figure 1A). Five '*rcn*' mutants lacked the period of drastic increase as observed in 'Shiokari'. '*rcn*' resulted in reduced tillers at variable level depending on genotype. Among them, '*rcn1-2*' was the most severe reduction in tiller number and developed a single tiller or less. The negative effect of '*rcn2*' on tillering was weak. Remaining three '*rcn*' reduced tiller moderately at the level between '*rcn1-2* and *rcn2*'. Increase pattern of plant height was classified into three groups: 'Shiokari' and '*rcn2*' increased plant height rapidly and were the highest group (Figure 1B). '*rcn4-2*, *rcn5* and *rcn6*' increased slightly. '*rcn1-2*' severely reduced the rate of increase of plant height and was the shortest shoot. As a result, the present study demonstrated that there is a positive correlation between the negative effects of 'rcn' on tiller number and plant height ($r = 0.83$, $p < 0.05$) showing that plants with few tillers were also shorter.

Plant architecture of rcn under control condition

Morphological characters at 110 days after planting under control (1P4F) are shown in Table 1. The results show that there were no appreciable differences in number of leaves developed by 'Shiokari' and all the five '*rcn*' mutants at flowering. However, flowering occurred 5 days earlier in '*rcn4-2* and *rcn6*' and 7 days later in '*rcn5*' compared to Shiokari. Panicle number was significantly reduced in all the mutants, with the highest reduction (93%) in '*rcn1-2*' compared to Shiokari. Similarly, both culm and panicle lengths were mostly reduced (58 and 42% respectively) in '*rcn1-2*', while the two parameters increased by 3 and 17% respectively in '*rcn2*' in comparision with Shiokari. Spikelet numbers in '*rcn1-2*, *rcn5* and *rcn6*' were significantly lower than in 'Shiokari', while the parameter was increased by 33% in '*rcn2*'. Dry weights of shoot and root were significantly reduced in all the '*rcn*' at variable levels.

Response to high density and low fertilizer

Morphological characters at 110 days after planting under

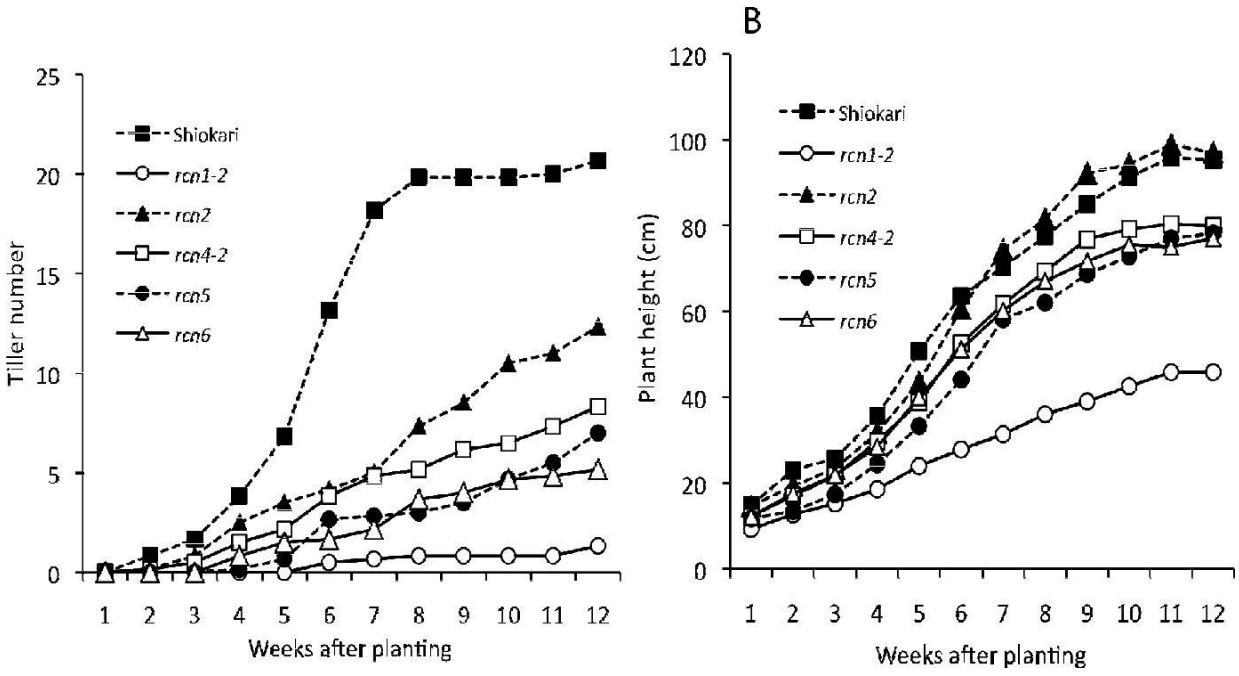

Figure 1. Kinetics of tiller number (A) and plant height (B) in rice (*Oryza sativa* L.) cultivar 'Shiokari' and independent five *rcn* mutants, *rcn1-2*, *rcn2*, *rcn4-2*, *rcn5* and *rcn6* originating from 'Shiokari' under control (1P4F) condition. Each value is mean of six plants.

each condition are shown in Table 2. In 'Shiokari', final leaf number was decreased significantly by increasing planting density and low fertilizer by a single leaf without changing flowering time. In five '*rcn*', no evident effect of planting density and low fertilizer on leaf number was observed. Under low fertilizer condition, flag leaf was opened without emergence of panicle from leaf sheath at 110 days after planting in '*rcn1-2*'. Panicle number was reduced to 78% and one third at high density and low fertilizer from control condition in 'Shiokari', respectively (Table 2). '*rcn1-2*' showed remarkable reduction of panicle number, developing a single or less tiller or culm across all conditions. The highest panicle number of '*rcn2*, *rcn4-2*, *rcn5* and *rcn6*', was obtained under control. In these genotypes, the panicle numbers of each genotype were significantly reduced by planting density. Under the highest planting density of 8P, 40, 49, 69 and 42% decrease from control were observed in '*rcn2*, *rcn4-2*, *rcn5* and *rcn6*', respectively. Under low fertilizer condition, 48, 63, 66 and 88% decreases from control were observed in '*rcn2*, *rcn4-2*, *rcn5* and *rcn6*', respectively. These data demonstrate that '*rcn1-2*' developed a single panicle under any planting density and fertilizer level. On the other hand, the panicle number of the other four '*rcn*' mutants was decreased by higher density and lower fertilizer, as similar with the response of wild type 'Shiokari'.

In 'Shiokari', increasing planting density from 1 to 8 plants per plastic pot significantly decreased culm length. Under low fertilizer condition, culm length decreased to 79%. In '*rcn1-2*', culm length was almost similar and between 23.5 and 30.5 cm across four densities. In '*rcn2*', a significant reduction was observed only under the highest density. Culm lengths of '*rcn4-2*, *rcn5* and *rcn6*' were not significantly affected by planting density. Even though the culm length of '*rcn5*' was not reduced by density, significant reduction was shown under low fertilizer condition. These data demonstrate that the response of culm length to planting density and low fertilizer was reduced in '*rcn1-2*, *rcn2* and *rcn5*', and disappeared in '*rcn4-2*' and '*rcn6*'. In 'Shiokari', maximum panicle length of 16.1 cm was obtained under control. Higher planting density significantly decreased panicle length in 'Shiokari' to 85% under higher planting density conditions. Low fertilizer also reduced panicle length to 81% in 'Shiokari'. '*rcn1-2*' developed constantly short panicle across four plant densities. High density and low fertilizer significantly reduced panicle length in '*rcn2*' and '*rcn5*'. No significant effect of higher planting density and low fertilizer on panicle length was observed in '*rcn4-2*' and '*rcn6*'. These data demonstrate that the response of panicle length to planting density and fertilizer level disappeared in '*rcn4-2*' and '*rcn6*'. An increasing density and low fertilizer significantly decreased spikelet number in 'Shiokari'. '*rcn1-2*' reduced spikelet number constantly across four densities. In '*rcn2*', similar response to high density and low fertilizer was observed as 'Shiokari'. In '*rcn4-2*', significant reduction was observed under higher density. In '*rcn5*' and '*rcn6*', dense planting and low fertilizer did not reduce spikelet number significantly.

Table 1. Days to flowering (FD), and panicle number (PN), leaf number (LN), culm length (CL), panicle length (PL), spikelet number (SPN), shoot dry weight (SDW) and root dry weight (RDW) under control condition at 110 days after planting (mean ± SD). LN, CL, PL and SPN were collected for main culm. Numbers in parentheses indicate the percentage change from 'Shiokari'.

Line	FD	LN	PN	CL (cm)	PL (cm)	SPN	SDW (g)	RDW (g)
Shiokari	66.0 ± 4.1 (100)	13.0 ± 0.0 (100)	17.0 ± 2.8 (100)	60.7 ± 5.8 (100)	16.1 ± 1.5 (100)	66.2 ± 10.2 (100)	11.6 ± 0.9 (100)	11.6 ± 0.9 (100)
rcn1-2	71.3 ± 2.1 (108)	11.8 ± 0.8** (91)	1.2 ± 0.4*** (7)	25.5 ± 4.7*** (42)	9.4 ± 1.3*** (58)	23.8 ± 6.0*** (36)	0.8± 0.3*** (3)	0.6 ± 0.2*** (5)
rcn2	63.6 ± 4.0 (96)	13.3 ± 0.5 (102)	8.2 ± 1.5*** (48)	62.5 ± 4.7 (103)	18.9 ± 1.3** (117)	88.3 ± 21.1* (133)	17.2± 2.6*** (64)	5.0 ± 1.6*** (43)
rcn4-2	60.5 ± 2.7* (92)	11.7 ± 0.5*** (90)	6.3 ± 2.4*** (37)	57.3 ± 5.5 (94)	14.0 ± 1.0* (87)	58.5 ± 4.6 (88)	8.7 ± 2.7*** (32)	2.9 ±1.2*** (25)
rcn5	73.0 ± 6.2* (111)	11.8 ± 0.4** (91)	4.2 ± 0.4*** (25)	50.6 ± 4.2** (83)	15.1 ± 1.1 (94)	48.2 ± 10.3* (73)	7.8 ± 1.4*** (29)	3.5 ± 0.8*** (30)
rcn6	61.0 ± 1.5 (92)	12.2 ± 0.4 (94)	5.2 ± 1.8 (31)	47.6 ± 2.9 (78)	13.8 ± 1.4 (86)	48.8 ± 8.8 (74)	4.5 ± 0.8 (17)	1.1 ± 0.2 (9)

*, **, ***; significant differences from 'Shiokari' at the 5, 1 and 0.1% levels, respectively.

Table 2. Days to flowering (FD), and panicle number (PN), leaf number (LN), culm length (CL), panicle length (PL), spikelet number (SPN), shoot dry weight (SDW) and root dry weight (RDW) at 110 days after planting (mean ± SD) under four planting density and low fertilizer. Numbers in parentheses indicate the percentage change from control (1P4F) condition of each line.

Traits	Treatment	Shiokari	*rcn1-2*	*rcn2*	*rcn4-2*	*rcn5*	*rcn6*
FD	1P4F	66.0±4.1 (100)	71.3±2.1(100)	63.6±4.0 (100)	60.5±2.7(100)	73.0±6.2(100)	61.0±1.5 (100)
	2P4F	67.3±4.4 (101)	67.6±4.4 (95)	63.4±1.4 (99)	60.9±3.8(101)	72.3±0.5 (99)	62.0±4.5 (102)
	4P4F	72.2±6.0 (109)*	69.4±2.4 (97)	64.0±3.7 (101)	61.4±4.1(101)	72.6±4.9 (99)	61.3±2.7 (101)
	8P4F	63.5±3.4(96)	64.7±0.5 (90)***	64.4±3.3 (101)	61.2±2.6(101)	72.0±9.9 (98)	60.6±3.7 (99)
	1P1F	66.0±1.9 (100)	> 110	63.0±3.6 (99)	58.8±1.8 (97)	74.2±6.9(102)	58.2±1.1 (95)*
LN	1P4F	13.0±0.0 (100)	11.8±0.8 (100)	13.3±0.5 (100)	11.7±0.5 (100)	11.8±0.4 (100)	12.2±0.4 (100)
	2P4F	12.6±0.5 (96)	11.9±0.6 (100)	13.0±0.5 (98)	11.6±0.5 (99)	12.8±0.7(108)	12.3±0.5 (101)
	4P4F	12.2±0.6 (93)**	11.8±0.6 (100)	12.2±0.7 (92)**	11.5±0.7 (98)	12.2±0.4(103)	12.2±0.6 (100)
	8P4F	11.9±0.7 (92)**	12.1±0.7(103)	12.6±0.9 (94)	13.0±0.0 (111)	11.5±0.7 (97)	11.9±0.4 (97)*
	1P1F	12.2±0.8 (93)*	11.5±0.5 (97)	12.5±0.8 (94)	11.5±0.5 (98)	11.7±0.5 (99)	12.0±0.7 (98)
PN	1P4F	17.0±2.8 (100)	1.2±0.4 (100)	8.2±1.5 (100)	6.3±2.4 (100)	4.2±0.4 (100)	5.2±1.8 (100)
	2P4F	9.5±1.7 (55)***	1.6±0.9 (133)	5.0±1.9 (61)**	5.1±2.1(81)	2.5±1.2 (59)*	3.6±1.4 (69)
	4P4F	5.4±1.9 (32)***	1.0±0.0(83)	3.8±0.8 (46)***	3.5±1.4 (55)**	3.4±0.9(81)	3.5±1.1 (67)*
	8P4F	3.8±1.5 (22)***	1.1±0.3(91)	3.3±0.8 (40)***	3.1±0.9 (49)**	2.9±0.4 (69)***	2.2±0.6 (42)***
	1P1F	5.8±1.0 (34)***	1.0±0.0A	4.0±0.0 (48)***	4.0±0.9(63)	2.8±0.8 (66)**	4.6±1.1 (88)
CL (cm)	1P4F	60.7±5.8 (100)	25.5±4.7(100)	62.5±4.7 (100)	57.3±5.5(100)	50.6±4.2(100)	47.6±2.9 (100)
	2P4F	54.5±6.4 (90)	30.5±3.4 (119)*	59.1±6.4 (95)	55.7±3.5 (97)	42.9±8.9 (85)	43.5±6.3 (91)
	4P4F	49.5±6.5 (82)**	24.0±3.2 (94)	60.4±3.7 (97)	51.3±8.9 (90)	48.0±8.7 (96)	43.0±4.9 (90)

Table 2. Contd.

	8P4F	53.3±5.4 (87)*	23.5±5.0 (92)	53.8±4.2 (86) ***	50.3±7.9 (88)	50.1±2.8 (99)	44.3±4.6 (93)
	1P1F	47.8±6.5 (79)**	13.3±6.0[B]	55.8±5.0 (89)	56.9±2.9 (99)	44.9±3.4 (89)*	45.4±2.7 (95)
	1P4F	16.1±1.5 (100)	9.4±1.3 (100)	18.9±1.3 (100)	14.0±1.0 (100)	15.1±1.1 (100)	13.8±1.4(100)
	2P4F	14.7±1.1 (91)	10.6±0.7 (112)	17.0±2.5 (90)	13.0±1.4 (93)	12.8±1.4 (85)*	14.0±1.0(101)
PL (cm)	4P4F	13.7±0.6 (85) ***	9.5±1.0 (101)	17.7±0.6 (94)*	13.5±1.3 (96)	12.9±3.7 (85)	13.3±1.2 (96)
	8P4F	13.7±1.8 (85)*	8.9±1.3 (94)	14.7±1.2 (78)***	13.2±1.9 (94)	14.0±0.9 (92)	13.6±1.3 (98)
	1P1F	13.1±0.6 (81)**	ND	16.0±2.3 (85)*	13.8±1.0 (98)	13.8±0.7 (91)*	13.9±1.1(101)
	1P4F	66.2±10.2 (100)	23.8±6.0 (100)	88.3±21.1 (100)	58.5±4.6 (100)	48.2±10.3 (100)	48.8±8.8(100)
	2P4F	52.4±4.5 (79)**	33.3±6.0 (140)*	76.9±16.5 (87)	53.7±11.9 (92)	47.5±16.3 (98)	45.5±3.3 (93)
SPN	4P4F	48.7±9.9 (74)**	25.3±7.6 (106)	72.1±10.5 (82)*	47.5±11.6 (81)*	44.8±7.6 (93)	40.3±7.6 (83)
	8P4F	50.8±7.2 (77)**	17.7±8.4 (74)	56.7±10.9 (64)***	45.3±8.8 (77)**	48.0±10.2 (99)	39.9±8.8 (82)
	1P1F	43.7±8.2 (66)**	ND	64.8±14.9 (73)	57.2±10.0 (97)	44.7±8.3 (92)	42.2±9.8 (86)
	1P4F	26.8±2.9 (100)	0.8±0.3 (100)	17.2±2.6 (100)	8.7±2.7 (100)	7.8±1.4 (100)	4.5±0.8 (100)
	2P4F	15.5±4.7(58)***	1.4±0.5 (175)*	9.5±3.9 (55)**	6.7±2.3 (77)	4.2±1.8 (54)**	3.1±0.8 (69)**
SDW (g)	4P4F	8.3±2.8 (31)***	1.0±0.3 (125)	7.4±1.5 (43)***	5.0±1.6 (57)**	4.5±2.1 (58)***	4.3±1.1 (96)**
	8P4F	5.3±1.3 (20)***	0.8±0.3 (100)	4.4±1.3 (26)***	3.3±1.2 (38)***	3.3±0.5 (42)***	1.9±0.8 (42)***
	1P1F	8.5±0.8 (32)***	0.2±0.1 (25)**	7.2±1.0 (42)***	5.2±0.6 (60)*	3.1±0.4 (40)***	3.4±0.9 (75)*
	1P4F	11.6±0.9 (100)	0.6±0.2 (100)	5.0±1.6 (100)	2.9±1.2 (100)	3.5±0.8 (100)	1.1±0.2 (100)
	2P4F	2.4±0.9 (21)***	0.8±0.4 (133)	1.3±0.5 (26)***	0.9±0.5 (31)**	4.2±1.8 (120)***	0.5±0.2 (45)***
RDW (g)	4P4F	2.1±0.8 (18)***	0.7±0.3 (117)	1.0±0.4 (20)***	1.2±0.8 (41)***	0.5±0.2 (14)***	1.0±0.4 (91)*
	8P4F	1.2±0.6 (10)***	0.5±0.2 (83)	0.6±0.3 (12)***	0.8±0.6 (27)***	0.6±0.3 (17)***	0.6±0.2 (55)***
	1P1F	2.9±0.7 (25)***	0.1±0.1 (17)***	1.5±0.4 (30)***	1.3±0.3 (45)*	1.3±0.3 (37)***	1.0±0.6(91)

*, **, ***; significant differences from each 1P4F treatment at the 5, 1 and 0.1% levels, respectively. A) culm number; B) plant height (cm); ND; no panicle was observed at 110 days after planting.

These results demonstrate that the response of spikelet number to planting density and fertilizer level was reduced or disappeared in '*rcn5*' and '*rcn6*'.

High density and low fertilizer reduced shoot dry weight and root dry weight significantly in 'rcn' as shown in 'Shiokari'. Inspite that '*rcn1-2*' has no visible change of shoot architecture, a drastic reduction of shoot dry weight and root dry weight were observed under the low fertilizer condition.

DISCUSSION

Each '*rcn*' reduced tiller number and plant height under control condition as reported in the previous paddy field experiments (Takamure et al., 1989; Takamure and Kinoshita, 1993; Takamure, 1994; Yasuno et al., 2007; Ariyaratne et al., 2009). In addition to tillering and plant height, '*rcn5*' delayed flowering by 7 days with decreased leaf number under control (1P4F) condition (Table 1). Alternatively, '*rcn4-2*' and '*rcn6*' reduced a single leaf until flowering and promoted flowering by

5 days under control condition. Based on the calculation from the final leaf number and days to flowering, it needs about 5 days to emergence of each leaf, referred to as the phyllochron, in '*rcn4-2*' and '*rcn6*', which was identical with 'Shiokari'. These results demonstrated that '*rcn4-2*' and '*rcn6*' promoted flowering and resulted in leafreduction. To our knowledge, two rice genes having pleiotropic effects on shoot branching and flowering have been reported. Firstly, '*Ghd7*' encoding a CCT (CO, co-like and timing of CAB1) domain protein on rice chromosome 7 has large pleiotropic effects on array of traits, including flowering time, plant height and grain number (Xue et al., 2008). In addition to these traits, '*Ghd7*' has a significant effect on shoot branching depending on genetic background (Xue et al., 2008). Secondary, '*DTH8*' encoding the *OsHAP3* subunit of a CCAAT-box binding protein (HAP complex) on chromosome 8 has also large pleiotropic effects on flowering time, plant height and number of grains per panicle (Wei et al., 2010).

Yan et al. (2010) also characterized '*Ghd8*' encoding the identical protein of '*DTH8*'. '*Ghd8*' up-regulated '*MOC1*', a key gene controlling shoot branching increasing the tiller number (Yan et al., 2010). Molecular mapping study demonstrated that '*rcn4*' and '*rcn6*' are not allelic to '*Ghd7*' or '*DTH8/Ghd8*' (Ariyaratne et al., 2009). It remains to elucidate weather if '*rcn4*' and '*rcn6*' function with '*Ghd7*' or '*DTH8/Ghd8*' in shoot branching and flowering controls. Plant height and tillering stature of '*rcn1-2*' was similar across all conditions. This character expression is well consistent with earlier report of '*rcn1-1*' with the genetic background of rice cultivar 'Akamuro' (Takamure and Knoshita, 1985). At low fertilizer, however, two kinds of remarkable negative effects were observed here in '*rcn1-2*'. Firstly, panicle was not emerged from flag leaf at 110 days after planting in '*rcn1-2*'. Kinetics of leaf number demonstrated that leaf emergence, phyllochron, was similar across all conditions in '*rcn1-2*'. These observations demonstrated that '*rcn1-2*' delayed panicle development without the negative effect of leaf development under low fertilizer condition. Secondary, low fertilizer condition accelerated the negative effect of plant growth by '*rcn1-2*' as demonstrated in both shoot and root dry weights. Based on the present data, '*rcn1-2*' may reduce the uptake or transport of nutrient from the poor soil condition.

Dense planting and low fertilizer reduced the apical meristem activity as shown in the reductions of culm length, leaf number, panicle length and spikelet number on main stem in 'Shiokari'. In '*rcn6*', however, the negative effects of dense planting and low fertilizer on culm length, panicle length and spikelet number of main culm were not observed (Table 2). Remaining '*rcn*' reduced the shoot development in the present environmental stresses. As a result, '*rcn6*' could maintain the apical shoot development but not axillary shoot development under dense planting and low fertilizer conditions. We need to address the detailed yield performance of '*rcn6*' with variable genetic background in field experiments and to clarify whether 'rcn6' might be one of the key genes controlling the interaction between apical shoot development and axillary shoot development under dense planting and low fertilizer conditions.

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