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Two Distinct Growth Types for Number of Developed Leaves, Heading Time, Culm and Panicle Lengths, and Internode Length within Near-isogenic Lines of Rice

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Abstract

There are two growth types of plants for the number of developed leaves, heading time, and culm and panicle lengths within a population of a homozygous rice cultivar. However, this phenomenon has not been deeply investigated, because of lack of concrete data. Rice breeders and physiologists have paid little attention to it, regarding it as a genetically uncontrollable environmental variation. To study more details of the phenomenon, we grew two near-isogenic lines of rice with each one of the alleles for the *Se1* locus conferring photoperiod sensitivity on chromosome 6 under natural long and short day-length conditions. In the line ER homozygous for the earliness allele *Se1-e*, and the line LR with the lateness allele *Se1-u*, N-leaf plants headed several days earlier than N+1-leaf plants. The N-leaf plants had shorter culms and longer panicles and were the upper-internode elongation type, whereas the N+1-leaf plants had opposite values of these characters. The proportion of these two kinds of plants changed in lines, plots and experiments. We discuss the meanings of this phenomenon from the viewpoints of rice cultivation to attain the uniform growth of plants, breeding to select individual plants with environmental variation, and fixation test to evaluate the uniformity needed as a cultivar.

Discipline: Crop production
Additional key words: breeding, cultivation, uniformity

Introduction

A pure line of rice, when released as a cultivar with favorable characteristics, has small coefficients of within-line variation in such quantitative characters as heading date, culm length, panicle length and so on. Rice producers use possible cultivation techniques to minimize the environmental variation and attain the uniform growth of rice plants throughout the growing period from germination to maturity. However, most of rice breeders and physiologists have been unaware of a precise feature of the environmental variation within a cultivar population.

Previous studies revealed that within a population a rice cultivar has two growth types of plants which develop N number of leaves and N+1 leaves on main culms, and that the N-leaf plants head slightly earlier and have shorter culms and longer upper-internodes than the N+1-leaf plants[1–4]. However, they did not show any data of individual plants in their reports, though dealing with average values for characters. Hence the phenomenon has remained unsolved as an uncontrollable environmental variation without further studies. Presence of two distinct growth types in a cultivar population affects the efficiency of management techniques for controlling plant growth, the uniformity among plants within a cultivar, and the stability of rice production.

We have been studying the proportions of different growth types appearing in various cultivars under some environmental conditions. This paper reports definite data of two growth types for the number of developed leaves, heading time, culm and panicle lengths, and internode length in two near-isogenic lines with particular genotypes for a photoperiod sensitivity locus *Se1* on chromosome 6 in rice.

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Materials and methods

1. Plant materials

Two near-isogenic lines, ER and LR, were grown in a paddy field and a greenhouse of the Agriculture and Forestry Research Center, University of Tsukuba, at 36º 6′ north latitude. The two lines were derived from a cross between a Malaysian cultivar Morak Sepilai and a Japanese cultivar Fujisaka 5 followed by four backcrosses with Fujisaka 5 as the recurrent parent. The hybrid population showed a monogenic segregation for heading time which was controlled by a photoperiod sensitivity locus *Se1* on chromosome 6[5]. The heterozygosity at the *Se1* locus was maintained through four successive backcrosses and succeeding 13 selfing generations, and thereafter the homozygosity was kept for 10 more generations by the single-seed-descent method. ER has a photoperiod-insensitive and earliness allele *Se1-e*, while LR has a photoperiod-sensitive and lateness allele *Se1-u*. LR heads 30 days later than ER under long day-length conditions, but seven days earlier under short day-length conditions[6,7].

2. Cultivation and measurement

The two lines in the Bc_4F_{23} generation were grown in a paddy field under natural long day-length conditions in the summer of 2002. Seeds of the two lines were sown on April 17 on soil in nursery boxes in a vinyl house. Seedlings at 5.4- to 5.6-leaf stage were selected and transplanted on May 16 to a paddy field at a single plant per hill with spacing of 30 cm × 15 cm and five rows of 4.5 m each in two replicates. Fertilizers were applied as basal dressing at the rate of 5 g N, 12 g P_2O_5 and 12 g K_2O m^{-2}. The number of developed leaves and heading date were observed on main culms of 90 plants from the central three rows. Heading was identified when the tip of a panicle appeared from the sheath of a flag leaf.

Under natural short day-length conditions in the winter of 2003, the two lines of Bc_4F_{24} were grown in a greenhouse with the lowest temperature at 20ºC. Four germinated seeds were planted on soil containing 0.7 g each of N, P_2O_5 and K_2O in a plastic pot 19 cm in diameter on February 7. Heading date was observed on main culms of 20 plants from five pots of each line.

In the summer of 2003, the two lines were grown in a paddy field where cultivation management was almost the same as in 2002 except for transplanting date on May 20. The number of developed leaves and heading date were examined on main culms of 200 plants for each line. Panicle length and elongated internode lengths over 2 mm were measured on a main culm of each plant after harvested at maturity, and culm length was calculated

Table 1. Distributions of heading date in ER and LR grown in the summer of 2002 and the summer of 2003

Year	Line	Plot	No. of developed leaves	No. of plants heading on: July 14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	•	•	•	August 13	14	15	16	17	18	19	20	21	22	23	24	25	Total	Mean days from sowing
2002	ER	1	12		4	5	12	15	12	7	1																											56	91.9
			13						4	18	4																											26	94.0
	ER	2	12	1		10	32	16	21	1																												81	91.6
			13				1	1	2	1	2	3																										10	94.1
	LR	1	15																						4	10	15	12	10	4								55	120.5
			16																									1	6	7	6	1	1	5				27	123.8
	LR	2	15																							2	1	6	12	6								27	121.7
			16																										6	13	13	8	5	11	1			57	124.5
2003	ER		13									2	1		1																							4	97.8
			14									10	20	27	56	39	10	5	2	1	2																	172	100.0
			15										1	1	5	10	6	3	8	2																		36	101.9
	LR		17																													30	65	7				102	130.8
			18																													12	44	27	4	5	3	95	131.5
			19																														2	1	1			4	131.8

Seeds were sown on April 17, and seedlings were transplanted on May 16, 2002 and on May 20, 2003, respectively.

Table 2. Distributions of heading date in ER and LR grown in the winter of 2003

Line	No. of developed leaves	No. of plants heading on																Mean days from sowing
		April															Total	
		11	12	13	14	15	16	17	18	19	20	21	22	23	24	25		
ER	10						1		2	2	2						7	70.6
	11									2	3	1	1	4		1	12	73.5
LR	9	1															1	63.0
	10	1	4	4	4	1	4	1									19	65.8

Seeds were sown on February 7, 2003.

from the total internode lengths.

Results

The two lines, ER and LR, had two types for the number of developed leaves on main culms and heading date in two plots in the summer of 2002 (Table 1). Every plot of ER with an earliness allele *Se1-e* had more 12-leaf plants which headed two days earlier on the average than 13-leaf plants. LR with a lateness allele *Se1-u* headed about 30 days later than ER, and was composed of 15-leaf and 16-leaf plants, of which proportions changed in plots. The 15-leaf plants headed about three days earlier than the 16-leaf plants in this line.

In the summer of 2003, ER and LR had three types for the number of developed leaves (Table 1). Four, 172 and 36 plants had 13, 14 and 15 leaves, respectively, in ER. The majority of about 200 plants in LR had 17 or 18 leaves, but only four plants had 19 leaves. Because of low temperature through their growing period in that summer, the two lines developed two more leaves and headed eight days later than those in the previous year. The 14-leaf plants headed two days earlier than the 15-leaf ones in ER, and the17-leaf plants headed slightly earlier than the 18-leaf ones in LR.

In the winter of 2003, ER headed about eight days later than LR (Table 2). The 10-leaf plants headed three days earlier than the 11-leaf plants in ER. In LR, there was only a single plant with 9 leaves and the rest of the plants had 10 leaves.

Henceforth when two types mainly appearing in each line are the subjects for further discussions, those plants with fewer leaves are referred to as N-leaf plants and those with one more leaf as N+1-leaf plants. Throughout the experiments, each of the two lines had unstable proportions of N-leaf and N+1-leaf plants in its population of the different cultivation seasons, and the single-leaf increase resulted in heading delay of two to three days on the average.

In ER, 14-leaf plants had five elongated internodes on main culms, and most of 15-leaf plants had six. In LR, 17-leaf and 18-leaf plants had 8 and 9 elongated internodes, respectively. The N-leaf plants had longer panicles and shorter culms with the longer internodes of I and II and shorter internodes below III than the N+1-leaf plants (Table 3, Fig. 1). There were positive correlations between I and II, and between III to VIII internode lengths, but negative correlations between I or II and

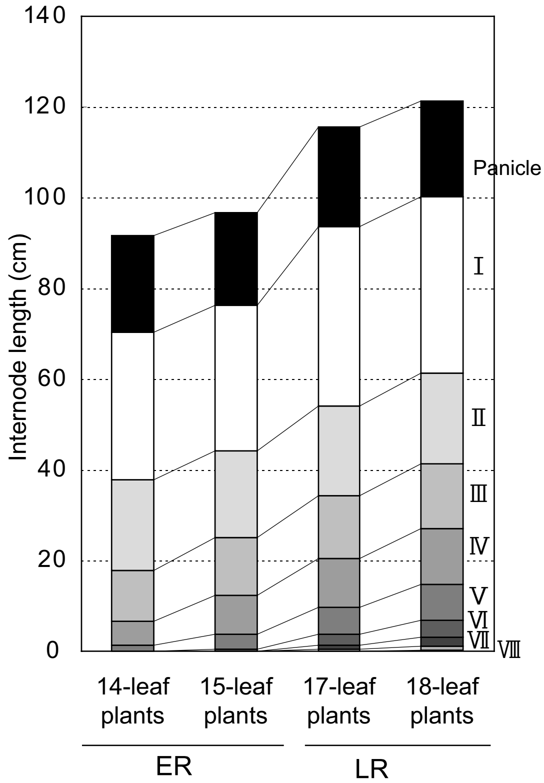

Fig. 1. Internode lengths in ER and LR grown in the summer of 2003

Table 3. Internode lengths of plants with the different number of leaves in ER and LR grown in the summer of 2003

Line	No. of developed leaves	No. of plants	Culm length (cm)	Panicle length (cm)	Internode length (cm)										
					I	II	III	IV	V	VI	VII	VIII	IX	I–II	III–IX
ER	14	172	70.4	21.3**	32.5	20.2**	11.0	5.4	1.3	0.0				52.7**	17.7
	15	36	76.2**	20.5	32.1	19.0	12.9**	8.5**	3.3**	0.4*				51.1	25.1**
LR	17	102	93.6	22.0**	39.5*	19.9	13.8	10.8	5.8	2.5	0.9	0.4	0.0	59.4	34.2
	18	95	100.3**	21.1	39.0	20.0	14.3**	12.3**	7.8**	3.9**	1.9**	0.8**	0.3	59.0	41.3*

* & **: Significant for a larger value at the 5% and 1% level by Student's t-test, respectively, when internode lengths were compared between 14-leaf and 15-leaf plants in ER, and 17-leaf and 18-leaf plants in LR.

Table 4. Correlation coefficients between internode lengths in ER (above the diagonal, n = 208) and LR (below the diagonal, n = 197) grown in the summer of 2003

Internode	Panicle	I	II	III	IV	V	VI	VII	VIII
Panicle		0.389**	0.615**	–0.252**	–0.433**	–0.356**	0.068		
I	0.609**		0.337**	–0.165*	–0.167*	–0.121	–0.129		
II	0.421**	0.470**		–0.229**	–0.399**	–0.348**	–0.055		
III	–0.226**	–0.167*	–0.176*		0.740**	0.631**	0.417**		
IV	–0.668**	–0.339**	–0.260**	0.398**		0.905**	0.614**		
V	–0.696**	–0.427**	–0.174*	0.380**	0.774**		0.667**		
VI	–0.525**	–0.378**	–0.210**	0.457**	0.702**	0.826**			
VII	–0.422**	–0.262**	–0.136	0.428**	0.651**	0.710**	0.813**		
VIII	–0.303**	–0.134	–0.064	0.305**	0.544**	0.631**	0.685**	0.847**	
IX	–0.059*	0.123	–0.078	0.025	0.251**	0.353**	0.407**	0.648**	0.920**

* & **: Significant at the 5% and 1% level, respectively.

those below III (Table 4). The N-leaf and N+1-leaf plants showed two distinguishable groups in their distribution for culm and panicle lengths, and for length of the upper internodes of I + II and the lower internodes below III (Fig. 2). In each of the two lines, the N-leaf plants headed early, had short culms and long panicles, and were the upper-internode elongation type, compared with the N+1-leaf plants.

Discussion

The two lines, ER and LR, with the particular genotypes for a photoperiod sensitivity locus *Se1* on chromosome 6 showed two growth types of N-leaf and N+1-leaf plants in each population. Irrespective of reverse change in earliness and lateness under the long and short daylength conditions in ER and LR[6,7], N-leaf plants always headed one to three days earlier on the average than N+1-leaf plants (Table 1 & 2). Physiological mechanisms causing these two growth types within a pure-line population have been obscure, though previous researches[1–3] reported without any data that N+1-leaf plants seemed to grow faster than N-leaf plants from the early seedling stage. More studies are needed to clarify the processes of leaf development and panicle differentiation bringing about a variation for heading.

Cultivation techniques are well operated in rice production to minimize growth variation among plants within a cultivar, but an incontrollable variation is known to have some ranges for quantitative characters such as heading time, and culm and panicle lengths. The present study revealed that N-leaf and N+1-leaf plants widened the ranges of variation for those characters in a given population, and the proportion of these two kinds of plants changed in lines, plots and experiments. If some cultivars show a fixed proportion of N-leaf and N+1-leaf plants in a wide range of environments or in particular environments, and if the proportion can be controlled by cultivation practices, yield and grain quality of rice can be improved by appropriate growth management according to that proportion. If any cultivar has only N-leaf plants in its population, growth management will be simplified due to their uniform growth with a smaller variation for characters, though all the plants become vulnerable to meteorological and biological hazards at the same time.

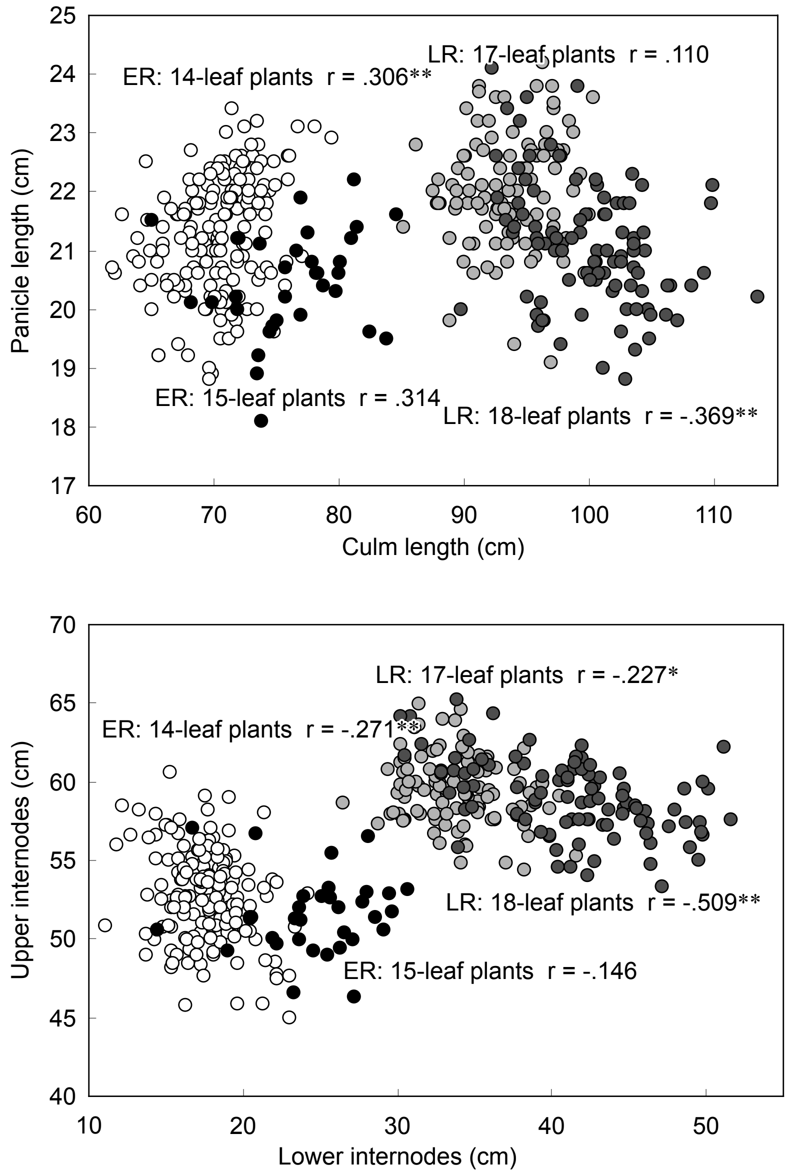

Fig. 2. Relationships between culm and panicle lengths, and between upper internodes of I + II and lower internodes below III in ER and LR grown in the summer of 2003

○&●: 14- and 15-leaf plants of ER, respectively.
◍&◍: 17- and 18-leaf plants of LR, respectively.
*&** : Significant at the 5% and 1% level, respectively.

The particular proportion of N-leaf and N+1-leaf plants, if any, will have an influence on the effectiveness of plant selection in rice breeding, since heading time, and culm and panicle lengths are primary characters for selection. There were the maximum differences of 10 days in heading date, 20% in culm length and 15% in panicle length between N-leaf and N+1-leaf plants (Table 1, Fig. 2). Even if plants with earlier heading, a shorter culm but a longer panicle, or those with the opposite characters, are selected from a population genetically homozygous for these characters, their progeny lines will show no genetic advance. Breeders often deal with these kinds of large environmental variation unconsciously as selection objectives, without noticing that there is no correlation between individual values of selected plants and averages of progeny lines for a combination of these characters.

Developed lines should be certified before release as cultivars that have nearly zero heritability for any character. The level of fixation is usually shown by the distribution of individuals, averages and coefficients of variation for heading date, culm length and panicle length in 30 to 50 plants from 5 to 10 sister lines each. These values may change with the proportion of N-leaf and N+1-leaf plants like in the present study, but a line with only N-leaf plants will have the smallest value for expression of fixation. The number of plants tested and the range of variation for each character should be decided to express the level of fixation in homozygous fixed lines. However, we have little information on the proportions of N-leaf and N+1-leaf plants for cultivars or genotypes, environments and growth-controlling techniques.

Effectiveness of plant selection and accuracy of fixation evaluation depends on whether there exist any cultivars or genotypes having a proper proportion of plants with different numbers of developed leaves. Though two types for the number of developed leaves on main culms existed mainly in the present study, three to four types also appeared in some cultivars under some cultivation conditions (Table 2, Otani et al. 1950, our unpublished data). From these above-mentioned viewpoints of cultivation and breeding, proportions of plants with different numbers of developed leaves and other related characters should be studied more for cultivars or genotypes under various environmental conditions.

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