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Relationship between the Size of the Apical Dome at the Panicle Initiation and the Panicle Components in Rice

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Abstract : Breeding for high-yielding rice has been directed toward those types that have a larger number of spikelets per panicle. The objective of this study was to examine the relationship within a cultivar between the size of the apical dome (AD) and the morphological characters of the panicle components such as the number of primary rachis-branches (PBs), secondary rachis-branches (SBs), and spikelets per panicle. Rice plants (cv. Akenohoshi) were subjected to four short-day (10h photoperiod) treatments at various developmental stages to change the duration of the vegetative stage and the AD size at panicle initiation (PI). Shoot apices having ADs were sampled at two-day intervals from the late vegetative stage to the early reproductive stage. The sections of the shoot apices were embedded in paraffin and stained with toluidine blue O. The base diameter and height of the ADs were measured with an ocular micrometer, and at heading, the numbers of PBs, SBs, and spikelets were counted. A delay in the start of the short-day treatment increased the total number of leaves on the main culm, extending the vegetative stage. Extension of the vegetative stage increased the AD diameter at PI. However, the effect of the short-day treatments on the AD height was unclear. Enlargement of ADs was accompanied by the increase in the number of differentiated PBs, but not always by that in the number of SBs and spikelets. The results suggested that spikelet number is influenced by plant nutritional conditions as well as by the AD size at PI.

Key words : Apical dome, Photoperiodism, Primary rachis-branch, Reproductive stage, Rice, Spikelet number, Vegetative stage.

Spikelet number per unit area determines the sink size of rice because the variability of single grain weight is small within a genotype. Spikelet number per unit area is the product of panicle number per unit area and spikelet number per panicle. A negative correlation is generally observed between these two numbers. Recent efforts for breeding high-yielding rice genotypes have been directed to those types having a larger number of spikelets per panicle, such as the new plant type (NPT) of the International Rice Research Institute (Khush, 1996). High-yielding varieties recently bred have a larger number of spikelets per panicle than previous modern japonica varieties (Ishikawa et al., 1999; Kusutani et al., 1999). Because some of these heavy panicle types have thicker culms (Ookawa and Ishihara, 1992) and a positive correlation generally exists between the spikelet number per panicle and the thickness of the neck nodes or the first elongated internodes (Matsushima, 1957), it is expected that heavy panicle types may have a larger apical dome (AD) at panicle initiation (PI). Fukushima (1999) indicated that the varietal difference in spikelet number per panicle was related to the diameter of a young panicle primordium and the ratio of the diameter of a primary rachis-branch (PB) primordium to that of a young panicle primordium. The former, the diameter, is related to the number of differentiated PBs, and the latter, the ratio, to the number of higher-order branches. High-yielding cultivars (Yamagishi et al., 1992) and the NPT (Fukushima, 1999) had a larger AD in diameter at PI and produced more spikelets per panicle. These previous studies suggest that the diameter of the AD at PI is the primary factor that determines the difference among cultivars in spikelet number per panicle.

The diameter of the AD during the vegetative stage increases with increasing plant age in leaf number, and the diameter at the time of the differentiation of a leaf primordium positively correlated with the width of the corresponding fully-expanded leaf blade (Yamazaki, 1963a). Rice plants under sparse planting conditions or sufficient nitrogen conditions had a large vegetative AD (Yamazaki, 1963b), and a larger number of spikelets per panicle. These previous studies may imply that a shorter duration of vegetative growth results in the formation of smaller ADs, and smaller panicles with fewer spikelets.

The objective of this study is to examine the relationship between spikelet number and AD size in the early reproductive stage. We cultivated rice cultivar 'Akenohoshi' under a long-day condition and gave short-day treatments at various developmental stages to obtain rice plants with various AD diameters at the stage of PI. This paper describes the effect of the photoperiod treatment on the size of AD at the various developmental stages of

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Abbreviations : AD, apical dome; NPT, new plant type; PB, primary rachis-branch; PI, panicle initiation; SB, secondary rachis-branch.

panicles, as well as the relationships in AD size with the numbers of PBs, secondary rachis-branches (SBs), and spikelets which determine the final panicle size.

Materials and Methods

1. Plant material and treatments

A pot experiment was conducted outdoors at the Experimental Farm of Kyoto University, Kyoto, Japan. Rice cultivar 'Akenohoshi' was used because it has a large number of spikelets per panicle and moderate photoperiodic sensitivity. Surface-sterilized seeds were germinated at 32°C for 24 h. Seeds selected for uniformity were sown on May 23, 1998. Germinated seeds were planted in Wagner pots (1/5000a) containing upland field soil, equivalent to 3.0 kg in oven-dried weight from the Experimental Farm (alluvial, loam sand), twenty germinated seeds per pot, using the circular dense-culture method (Satake, 1972). Tillers were removed every week. The pots were watered at field capacity level for nine days after sowing, and thereafter kept flooded with 2 to 3 cm of water. Liquid fertilizer, containing 0.15g nitrogen as ammonium sulfate, 0.15 g P_2O_5 as sodium dihydrogenphosphate, and 0.15 g K_2O as potassium chloride, was applied weekly. All plants were grown under a natural day length for nine days, and then exposed to a long-day condition (16 h photoperiod) to prevent panicle differentiation until the start of the short-day treatments (Fig. 1). For the long-day treatment natural daylight was supplemented with artificial light from two 60W white incandescent lamps from 4 a.m. to 6 a.m. and from 6 p.m. to 8 p.m.

Rice plants grown under long days were subjected to a 10h photoperiod for 19 to 21 days from the time when the plant age reached 5.0, 6.7, 9.0, and 10.9, which are referred to as SD1, SD2, SD3, and SD4 groups, respectively (Fig. 1). The plants were given short days by shading from 5p.m. to 7a.m. with silver plastic sheets (Sekisui Chemical Co., Ltd., Japan). The air temperature during the dark treatment was not controlled. After the short-day treatments, the plants were exposed to natural day length.

2. Preparation of materials for microscopic observations

Five to ten plants per group were sampled at two-day intervals during the period from the late vegetative stage to the early stage of spikelet differentiation; the latter stage being identified by rapid internode elongation as described below. At each sampling, the plant age in leaf number was recorded, regarding the incomplete leaf preceded by coleoptile as the first leaf. The roots were removed, and the shoot (approximately 3 cm long) was cut from the base of the main culm. The shoot apices were fixed in formalin-acetic-alcohol (70% ethanol : acetic acid : formalin = 90 : 5 : 5), and then dehydrated in an alcohol series ranging from 40% n-butanol and 25% ethanol in water to absolute n-butanol. The sections

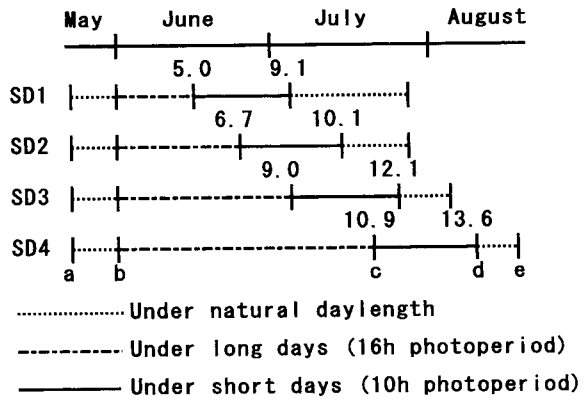


Fig. 1. Time courses of long- and short-day treatments given to Akenohoshi at various developmental stages.
a : sowing date, b : start of long-day treatment (16h), c : start of short-day treatment, d : end of short-day treatment (10h), e : heading.
The number in the figure indicates plant age in leaf number at the start and at the end of the short-day treatments.

were then embedded in paraffin. Serial longitudinal sections (10 μm thick) were cut. They were stained with 0.05% toluidine blue O and each of them was examined under a light microscope. These serial sections were then used for measurements of the diameter and height of AD as well as for the determination of the developmental stage of the panicle.

The growth of AD through successive plastochrons can be shown as a saw-toothed line (Yamazaki, 1963a; Lyndon, 1998). At the end of each plastochron, the formation of a new primordium results in an abrupt reduction in the size of the AD, from maximal to minimal. To measure AD size precisely, it is desirable to select the sections at the beginning of each plastochron, when the AD size is minimal. In this experiment, plant age in leaf number was measured for all plants and we collected samples uniform in plant age as much as possible. The synchrony between leaf emergence and the differentiation of a leaf primordium (Yamazaki, 1963a) was also used to obtain uniform samples. However, because of the restriction in the numbers of pots and plants, uniformity of the sections was not satisfactory to obtain sufficiently precise data to analyze the relationship between AD size and morphological characters of panicle components.

The stages of PI, the PB differentiation, and SB differentiation were identified using the method of Matsushima and Manaka (1956) with a small modification by Xu and Vergara (1986). The PI stage was defined as the stage of neck-node differentiation, when the first bract was observed. The stage of PB differentiation was defined as the period from the differentiation of the second bracts to that of the first basal SB, in which the bract-increasing stage was included (Xu and Vergara, 1986; Senanayake et al., 1991). The stage of SB differentiation was defined as the period from the differ-

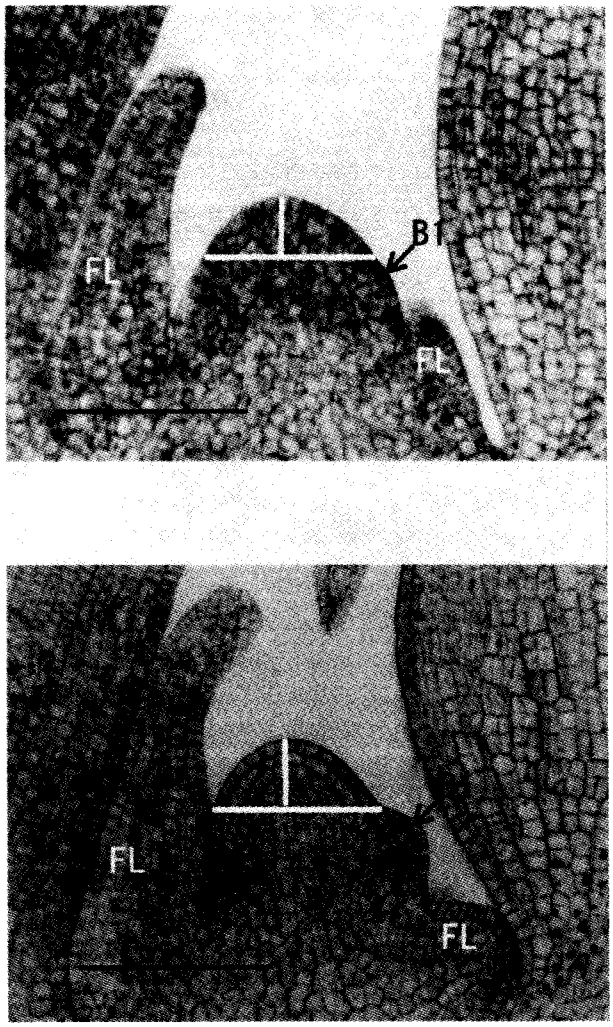


Fig. 2. Measurement of the diameter and the height of the apical dome in the vegetative stage and the neck-node differentiation stage.
The white, horizontal lines indicate the diameter of the apical dome. The white, vertical lines indicate the height of the apical dome. The black bars indicate 100 μm. B1 is the first bract at the neck node. FL is the primordium of a flag leaf.
The upper figure is just at the onset of a new primordium differentiation. The lower figure is when a new primordium is easily observed.

entiation of the first, basal SB to that of the first spikelet on the distal PB. At the spikelet differentiation stage, rapid internode elongation started, and we terminated panicle sampling for microscopy.

The identification of neck-node differentiation was difficult (Xu and Vergara, 1986), and we could only identify the second bract differentiation. We estimated the date of neck-node differentiation as two days before the second bract differentiation based on the observation that a new bract appears about two days after the first bract initiation (Matsushima and Manaka, 1956).

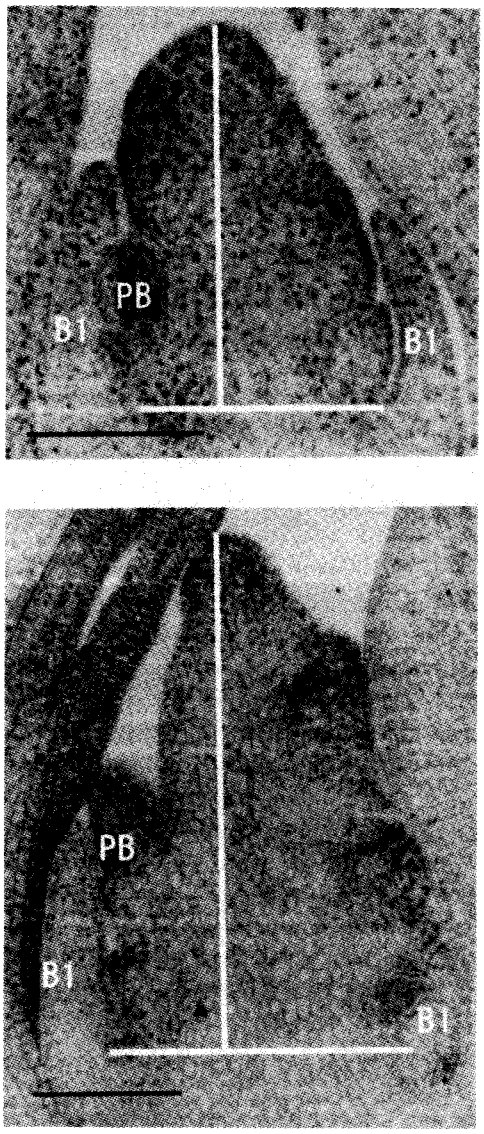
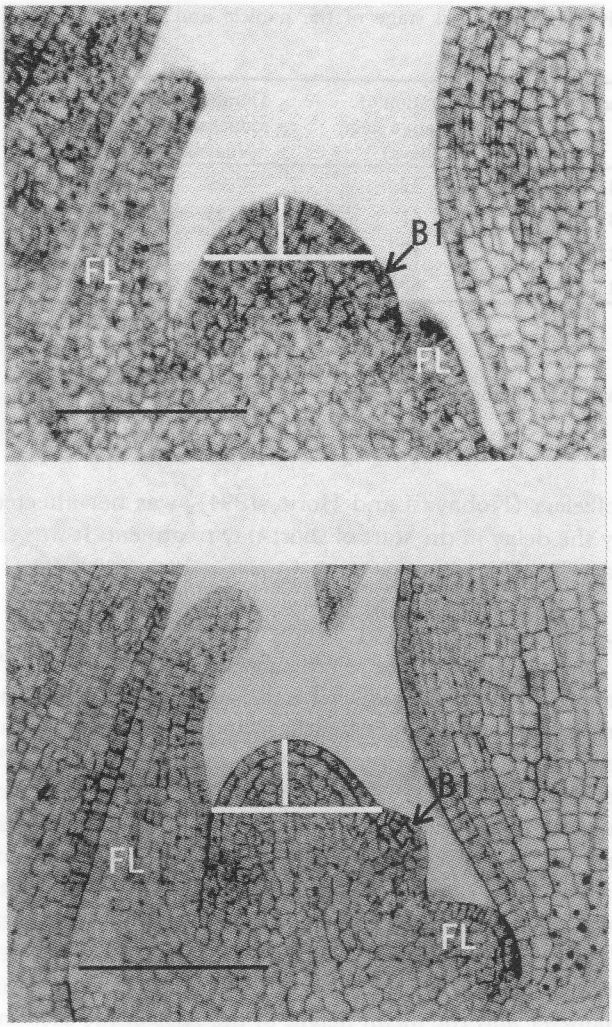


Fig. 3. Measurement of the diameter and the height of the apical dome after the differentiation of the second bract. The white, horizontal lines indicate the diameter of the apical dome. The white, vertical lines indicate the height of the apical dome. The black bars indicate 100 μm. B1 is the first bract at the neck node. PB is the primordium of a primary rachis-branch.
The upper figure shows an apical dome at the stage of primary rachis-branch differentiation. The lower figure shows an apical dome at the stage of secondary rachis-branch differentiation.

3. Measurement of AD size and morphological characters of panicle components

The base diameter and the height of ADs at the late vegetative stage and PI stage were measured according to the method of Yamazaki (1963a). The definitions of the diameter and the height of AD in this study are shown schematically in Fig. 2. The maximum diameter and the maximum height were determined after examining all the longitudinal sections of each AD using an ocular micrometer. After the second bract differentiation, the diameter and the height of AD inside the first bract



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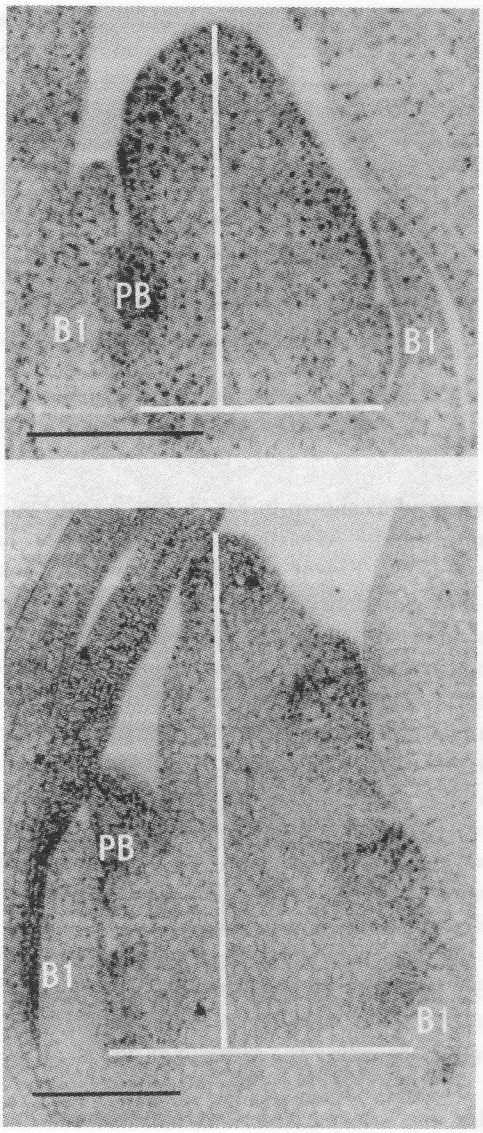

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Table 1. The dates on which rice attained the respective developmental stage of the panicle and the durations of vegetative and reproductive stages.

Group	PI**	ESP***	Heading	Duration of vegetative stage (days)	Duration of reproductive stage (days)
SD1*	June 29 (37)	July 5 (43)	July 28 (66)	37	29
SD2	July 3 (41)	July 9 (47)	July 28 (66)	41	25
SD3	July 11 (49)	July 17 (55)	August 5 (74)	49	25
SD4	July 27 (65)	August 2 (71)	August 18 (87)	65	22

Values in parentheses indicate days after sowing.
* See Fig. 1.
** The Panicle initiation stage when neck-node differentiation was detected.
*** The early stage of spikelet differentiation.

were measured as shown in Fig. 3. Fig. 2 and Fig. 3 show the sections of the ADs that had the maximal diameter and the maximal height among the serial sections. Most of the selected sections were the median longitudinal sections. However, the sections after PB differentiation were not always the median longitudinal sections because the growth of PBs disordered the symmetry of the young panicle and made its structure complex.

At heading, after measuring the blade length of flag leaf and the total number of leaves on the main culm, more than 50 panicles were sampled from each group to measure panicle length and the numbers of each panicle component (PBs, SBs, and spikelets). The panicle length was defined as the length from the neck node to the panicle tip. The numbers of final and degenerated spikelets, PBs, and SBs were counted according to Matsushima (1957). The number of degenerated organs was measured by counting the vestiges of degenerated organs on the panicles either with the naked eye or with a binocular microscope. The number of differentiated spikelets was defined as the sum of the numbers of the final spikelets and the degenerated spikelets. Similarly, the numbers of differentiated PBs and SBs were obtained.

Results

1. Effect of short days on panicle development

The earlier the short-day treatment started, the shorter the duration of the vegetative stage in rice cultivar 'Akenohoshi' (Table 1). The plants exposed to short days from the earliest date (SD1) differentiated neck nodes on June 29 on the average, and thus the length of the vegetative stage in SD1 was 37 days. In the plants exposed to short days from the latest date (SD4), plants differentiated neck nodes on July 27, making the length of the vegetative stage 65 days.

The later the start of the short-day treatment, the shorter the duration of the reproductive stage and the period from the early stage of spikelet differentiation to heading. However, the duration from PI to the early stage of spikelet differentiation, which is the most critical duration in determining the number of differentiated spikelets (Kobayasi and Horie, 1994), was not affected by the delay in the start of short-day treatment. It was six days in all groups.

2. The size of apical domes

The date when the plants attained the stage of PI varied by about ten days with the individual in the same group. For example, the earliest and latest dates of the second bract differentiation were June 23 and July 3, respectively in SD1. After PI, the AD size rapidly increased. To compare AD size among the experimental groups SD1, SD2, SD3, and SD4, we classified the paraffin sections into four developmental stages: the late vegetative stage (seven days preceding PI), the stage of PI (neck-node differentiation), the stage of PB differentiation, and the stage of SB differentiation. The mean diameter and the mean height of the ADs in the sections at the same stage are shown in Table 2. At any developmental stage, AD diameter was decreased by the shortening of the duration of the vegetative stage. The diameter of AD at the late vegetative stage (seven days preceding PI) was 71.5 μm in SD1, and 35% larger than that, 96.6 μm, in SD4. At the stage of PI, the ratio of the diameter in SD4 to that in SD1 was 1.33. These results suggest that the AD diameter at around the PI stage was in proportion to that at the late vegetative stage. After PI, the diameter of AD in SD4 increased more rapidly than the others, and the ratio of the diameter at the stage of PB differentiation in SD4 to that in SD1 became 1.88. After SB differentiation, the ratio of the AD diameter in SD4 to that in SD1 decreased to 1.30.

We could not find any clear relationship between the duration of the vegetative stage and the height of the ADs at either the late vegetative stage or PI stage. After PI, AD height rapidly increased, and the ADs of the plants with longer durations of vegetative growth were larger in height. The AD height in SD4 was larger than that in SD1 by 111% at the stage of PB differentiation and by 19% at the stage of SB differentiation.

Table 2. The effects of short-day treatments on the dimensions of apical dome (AD) at four developmental stages.

Measurements	Treatment	VGS*	PI**	PB***	SB****
Diameter (μm)	SD1	71.5± 2.6 a	79.5± 4.0 a	97.8±11.4 a	183.9±23.3 a
	SD2	87.4± 0.0 b	82.2± 5.1 a, b	130.1±16.8 a, b	221.1±24.4 a
	SD3	79.7 #	No data	144.8±18.7 a, b	192.2 #
	SD4	96.6± 3.1 b	106.0± 5.7 b	183.8±12.3 b	238.7± 9.3 a
Height (μm)	SD1	47.5± 7.0 a	64.1± 6.7 a	114.1±20.0 a	338.9± 9.0 a
	SD2	43.7± 2.6 a	66.8±18.0 a	159.0±30.2 a, b	396.8±28.4 a
	SD3	51.4 #	No data	170.1±38.4 a, b	359.6 #
	SD4	40.1± 3.3 a	50.8± 8.6 a	240.4±26.8 b	403.0±31.0 a

* This stage spans seven days preceding neck-node differentiation.
** This stage is the neck-node differentiation stage (panicle initiation stage).
*** This stage includes both the bract-increasing stage and the primary rachis-branch differentiation stage.
**** This stage spans the beginning of basal secondary rachis-branch differentiation and just before spikelet differentiation on a distal primary rachis-branch.
# Data number was one and was excluded from statistical analysis.
Each value shows mean±standard error.
Means within a column followed by the same letter are not significantly different at 5% level among the treatments with Tukey HSD test.

Table 3. The effects of short-day treatments on morphological characters at heading.

Treatment	Total leaf number of the main culm	Panicle length (cm)	Flag leaf blade length (cm)
SD1	11.4±0.1 a	18.7±0.4 a	25.0±0.9 a
SD2	11.8±0.0 b	17.6±0.1 b	21.4±0.4 b
SD3	12.9±0.0 c	16.7±0.1 c	21.4±0.4 b
SD4	14.4±0.1 d	19.4±0.1 a	28.8±0.6 c

Each value shows mean±standard error.
Means within a column followed by the same letter are not significantly different at 5% level among the treatments with Tukey HSD test.

Table 4. The effects of short-day treatments on the numbers of differentiated spikelets, primary rachis-branches, and secondary rachis-branches.

Treatment	Differentiated spikelets	Differentiated PBs	Differentiated SBs
SD1	111.9±3.9 a	7.1±0.1 a	21.1±0.7 a
SD2	97.3±2.2 b	7.4±0.1 a	17.7±0.5 b
SD3	93.3±1.4 b	8.5±0.1 b	15.5±0.3 c
SD4	122.6±2.7 c	10.0±0.1 c	21.9±0.5 a

Each value shows mean±standard error.
PBs : Primary rachis-branches, SBs : Secondary rachis-branches.
Means within a column followed by the same letter are not significantly different at 5% level among the treatments with Tukey HSD test.

3. Effect of short days on the morphological characters of the panicle components

The shorter the duration of the vegetative stage, the lower the total number of leaves on a main culm (Table 3). The total leaf number in SD1 (11.4) was lower than that in SD4 (14.4) by three leaves. At the beginning of the short-day treatments, the difference in the number of leaves between SD1 and SD4 was 5.9 (Fig. 1). The photoperiodic sensitivity of very young rice plants is generally weak, and so the plants in SD1 might have needed more days to induce reproductive growth than those in the other groups. The duration of the vegetative stage had no relationship with the length of panicle or flag leaf blade. However, there was a positive correlation between the length of panicle and flag leaf blade (Table 3, $r=0.932$).

The number of differentiated PBs decreased with reducing the duration of the vegetative stage. The number of differentiated PBs in SD4 was 10.0, which was 41% higher than that in SD1 (Table 4). This finding indicates that plants having larger AD diameters at the stage of PI due to extended duration of the vegetative stage differentiated a larger number of PBs on the main culm. There was no clear correlation between the duration of the vegetative stage and the number of differentiated spikelets or SBs, though the plants in SD4 differentiated the largest numbers of spikelets and SBs. The plants in SD2 and SD3 differentiated a larger number of PBs (7.4 and 8.5, respectively) than those in SD1, but differentiated a smaller number of spikelets and SBs. The number of differentiated spikelets was more closely correlated with the number of differentiated SBs than with that of differentiated PBs.

Discussion

This study indicated that extension of the duration of the vegetative stage by delaying the start of short-day (10h) treatment caused enlargement of AD diameter at the stage of PI. The study also showed that the panicles

that differentiated from larger ADs differentiated a larger number of PBs. Several studies have indicated that the final size of or the number of aboveground organs in rice correlated with the size of AD at the time of their differentiation (Yamazaki, 1963a; Fukushima, 1999). Yamazaki (1963a) showed that the final size of rice leaves on a culm was larger, the higher the node position, and found that the final size of the leaf was proportional to the AD size at the time of its differentiation. This finding could explain the fact that later-differentiated leaves generally have a larger leaf size. In the present study, however, the difference in the final length of flag leaves could not be explained by the difference in the AD size at the PI stage. The final size of a leaf is affected not only by the AD size, but also by the environments under which it develops (Yamazaki, 1963c).

The present result that the number of differentiated PBs on a panicle increased with the increase in the AD diameter at the PI stage, agrees with the results in the previous studies on varietal difference in spikelet number per panicle (Yamagishi et al., 1992; Fukushima, 1999). However, Yamagishi et al. (1996) and Kobayasi and Horie (1999) could not fully explain the cultivar difference in spikelet number on the basis of the difference in the AD size at the PI stage. The potential sink size (the product of the number of differentiated spikelets and single grain weight) showed a high positive correlation with the growth duration of rice (Wada and Sta. Cruz, 1989, 1990). Matsuba (1991) suggested that the AD size at the PI stage determines the number of differentiated PBs and the potential number of spikelets. Although a shorter growth duration decreases nitrogen absorption (Wada and Sta. Cruz, 1989, 1990), it is possible that the lower yield potential of early cultivars is partially due to the smaller ADs associated with the shorter duration of the vegetative stage.

Apical dome size at the PI stage may be one of the factors that affect the morphological character of the panicle components, particularly the number of differentiated PBs per panicle. However, nitrogen, non-structural carbohydrate, and plant growth regulators may also affect the morphological character of the panicle components (Matsuba, 1991; Kobayasi and Horie, 1994). In this experiment, measurement of AD size was not accurate enough to analyze the relationship between AD size and morphological character of panicle components, although we selected samples for uniformity as much as possible. To analyze the combined effect of AD size, nitrogen, non-structural carbohydrates, and plant growth regulators on the morphological character of the panicle components, it is necessary to obtain more precise data of AD size. For example, Mu et al. (2000) used only the sections of ADs that have 1-5 layers in the new primordium to measure AD size.

In this study, no clear relationship was observed between the number of differentiated spikelets per panicle and the AD size at the PI stage. On the other hand, evidence has been accumulated to show that the number of differentiated spikelets is related to plant nitrogen conditions during the early reproductive stage (Kobayasi and Horie, 1994; Hasegawa et al., 1994). Kobayasi and Horie (1994) showed that the increase in the plant nitrogen concentration during the period from the stage of PI to that of the spikelet differentiation caused the increase in spikelet number by increasing the number of differentiated SBs on PB. These previous studies, along with the results of the present study, suggest that, although the AD size at the PI stage affects the number of differentiated PBs in a rice panicle and may have the potential to determine the spikelet number per panicle, the number of spikelets is also influenced by the plant nutritional conditions, especially nitrogen conditions, during panicle development.

References

Fukushima, A. 1999. Differentiation and development of the branching of panicle with reference to the number of spikelets in rice. Jpn. J. Crop Sci. 68 : 77-82**.

Hasegawa, T., Koroda, Y., Seligman, N.G. and Horie, T. 1994. Response of spikelet number to plant nitrogen concentration and dry weight in paddy rice. Agron. J. 86 : 673-676.

Ishikawa, T., Fujimoto, H., Kabaki, N., Maruyama, S. and Akita, S. 1999. Dry matter production before heading and determination of number of spikelets of rice cultivar "Takanari". Jpn. J. Crop Sci. 68 : 63-70**.

Khush, G.S. 1996. Prospects of and approaches to increasing the genetic yield potential of rice. In R.E. Evenson et al. eds., Rice Research in Asia : Progress and Priorities. CAB International, Wallingford. 59-71.

Kobayasi, K. and Horie, T. 1994. The effect of plant nitrogen condition during reproductive stage on the differentiation of spikelets and rachis-branches in rice. Jpn. J. Crop Sci. 63 : 193-199**.

Kobayasi, K. and Horie, T. 1999. The relationship between apical meristem size and the number of differentiated spikelets per panicle for different rice cultivars. Jpn. J. Crop Sci. 68 (Extra issue 2) : 190-191*.

Kusutani, A., Ueda, K. Asanuma, K. and Toyota, M. 1999. Studies on varietal difference in yielding ability in rice — Relationship between source-sink ratio and yield—. Jpn. J. Crop Sci. 68 : 21-28**.

Lyndon, R.F. 1998. The Shoot Apical Meristem : Its Growth and Development. Cambridge University Press, Cambridge. 174-177.

Matsuba, K. 1991. The morphogenetic mechanism of formation of the panicle branching system in rice plants (*Oryza sativa L.*). Bull. Chugoku Natl. Agric. Exp. Stn. 9 : 11-58***.

Matsushima, S. and Manaka, T. 1956. Developmental Process of the Young Panicle of Rice and its Identification -Developmental Process of the Young panicle with Concerning All Shoots and its Criterion and the Characteristics of Developmental Stages-. Nogyo Gijutsu Kyokai, Tokyo. 1-57*.

Matsushima, S. 1957. Analysis of developmental factors determining yield and yield prediction in lowland rice. Bull. Natl. Inst. Agric. Sci. A5 : 1-271***.

Mu, C., Yamagishi, J., Nemoto, K. and You, Z. 2000. The size of

shoot apex during flag leaf and floral initiation stage in relation to panicle characteristics in rice varieties. Jpn. J. Crop Sci. 69 (Extra issue 2) : 228-229*.

Ookawa, T. and Ishihara, K. 1992. Varietal difference of physical characteristics of the culm related to lodging resistance in paddy rice. Jpn. J. Crop Sci. 61 : 419-425**.

Satake, T. 1972. Circular dense-culture of rice plants in pots, the purpose of obtaining many uniform panicles of main stems. Proc. Crop Sci. Soc. Jpn. 41 : 361-362*.

Senanayake, N., De Datta, S.K., Naylor, R.E.L. and Thompson, W.J. 1991. Lowland rice apical development : Stages and cultivar differences detected by electron microscopy. Agron. J. 83 : 1013-1023.

Wada, G. and Sta. Cruz, P.C. 1989. Varietal difference in nitrogen response of rice plants with special reference to growth duration. Jpn. J. Crop Sci. 58 : 732-739.

Wada, G. and Sta. Cruz, P.C. 1990. Nitrogen response of rice varieties with reference to nitrogen absorption at early growth stage. Jpn. J. Crop Sci. 59 : 540-547.

Xu, X.B. and Vergara, B.S. 1986. Morphological changes in rice panicle development. A review of literature. IRRI Res. Pap. Ser. No.117 : 1-13.

Yamagishi, J., Nemoto, K. and You, Z. 1996. Growth of shoot apex during floral initiation in two rice varieties, Nipponbare and Akenohoshi. Jpn. J. Crop Sci. 65 (Extra issue 2) : 49-50*.

Yamagishi, J., Yajima, T., Etoh, K., Suzuki, H. and Inanaga, S. 1992. Relation of number of spikelets per panicle to the characteristics of shoot and the size around growing point at panicle initiation stage in rice varieties. Jpn. J. Crop Sci. 61 : 568-575**.

Yamazaki, K. 1963a. Studies on leaf formation in rice plants. II. The development of leaves in relation to their position on a stem. Proc. Crop Sci. Soc. Jpn. 32 : 81-88***.

Yamazaki, K. 1963b. Studies on leaf formation in rice plants. III. Effects of some environmental conditions on leaf development. Proc. Crop Sci. Soc. Jpn. 32 : 145-151***.

Yamazaki, K. 1963c. Studies on leaf formation in rice plants. IV. Some experiments revealing the role of processes in leaf formation. Proc. Crop Sci. Soc. Jpn. 32 : 237-242***.

*In Japanese.

**In Japanese with English abstract.

***In Japanese with English summary.