

Cultivar Difference in the Response of Root System to Nitrogen Application in Rice Plant*

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Abstract : This study was conducted to examine whether the root system development in rice plant under different nitrogen (N) application regimes is related to adaptability for heavy manuring (AHM) of the cultivar. Four rice cultivars that differ in AHM were grown in plastic pots (25 cm in diameter, 30 cm in depth), under three N levels, which were equivalent to 5 kg-N/1000 m² (5 N plot), 10 kg-N/1000m² (10 N plot) and 30 kg-N/1000 m² (30 N plot). The plants were harvested 33 days after sowing and at heading stage. In the 33-day-old plants, growth of root system was inhibited with increasing N application, apart from the production of the nodal roots, which was promoted. Although the root responses differed with the cultivars, the differences were not related to those of AHM. On the other hand, in the heading-stage plants, the total number and length of nodal root axes per plant increased. But again, notable differences among the cultivars were not recognized. In contrast, different responses to N application according to AHM of the cultivars was found in lateral root development. The cultivars with AHM showed a substantial increase in total lateral root length per plant at 30 N plot as compared with those in 5 N and 10 N plots, whereas the lateral root growth of the cultivars with high AHM remained relatively unchanged under the different N levels.

Key words : Adaptability, Heavy manuring, Nitrogen application, Rice, Root system.

イネ根系の窒素施用に対する反応の品種間差異 : 田中実秋・山内 章・河野恭廣 (名古屋大学)

要 旨 : 耐肥性程度の異なる水稻 4 品種を用い, 異なる窒素施用量が根系発達に及ぼす影響を, 根系構成要素別に比較検討した。窒素施用量の違いにより 3 処理区をもうけ, 各品種 3 反復で実験を行った。処理区は 5 N 区 (5 kg-N/1000 m²), 10 N 区 (10 kg-N/1000 m²), 30 N 区 (30 kg-N/1000 m²) とし, 施肥量を 2 分して基肥と追肥 (播種後 35 日) で与えた。サンプリングは播種後 33 日と出穂期に行なった。播種後 33 日目の個体では, 全品種で窒素増肥に伴い節根数は 10 N 区と 30 N 区で増加したが, 総節根長, 総根長の窒素増肥に対する反応は, 5 N 区に対し, 30 N 区で減少する品種と, 全処理区で同等の値を示す品種に別れた。出穂期の個体では, 全ての品種において 33 日目の個体と比較して, 窒素施用量の増加に伴う節根軸長の抑制程度が小さく, 節根数の増加とあいまって総節根長は増加した。一方, 側根の発達程度には品種間差異が認められ, 品種の耐肥性程度の大小によって明確に異なる反応を示した。耐肥性程度の小さな品種は, 窒素増肥に伴って側根を発達させ, 30 N 区においても側根長を増加させたが, 耐肥性の大きな品種は, 30 N 区において側根長を増加させず 10 N 区と同様の値を示した。

キーワード : イネ, 根系, 耐肥性, 窒素施肥。

Increase of rice yield has been achieved by the development of cultivars with improved adaptability for heavy manuring (AHM), especially nitrogen (N) dressing, which has been coupled with the improvement of cultivation technologies suitable for these cultivars. The concept of AHM implies various growth responses of a whole plant, such as tolerance to rice blast, lodging resistance and morphological and physiological characteristics under heavy manuring conditions. Cultivars with high AHM sharply respond to heavy manuring, which leads to increased yield. Cultivars with low AHM in turn respond to

heavy N application in such ways that they tend to be susceptible to lodging, rice blast and so on, and decrease grain-straw ratio, which results in the reduction of yield.

For many years, a number of investigations on this adaptability have been carried out, but most of them focused on the growth responses of above-ground organs. In contrast, only a few studies were conducted on root growth responses to the different amount of N application. Kawata *et al.*⁸⁾ reported that a large amount of application of chemical N fertilizer in paddy field inhibited the root growth of a rice cultivar, especially the elongation of roots, which resulted in the formation of a small-sized root system. In relation to the AHM of rice cultivars, the reports of Doi⁴⁾ and

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Tsunoda¹⁵⁾ indicated that when plants were grown under low N conditions in culture solution, nodal root axis elongation for the cultivars with low AHM was superior than in those with high AHM, while the difference tended to become smaller as the N concentration increased. Our previous investigation¹³⁾ showed that inhibition of rice seminal root elongation by low ammonium-N concentration (4 mg L^{-1}) in culture solution was generally greater in the cultivars with low AHM than in those with high AHM.

Besides, the researchers have been little interested in the growth responses of lateral roots, which are the major components of a root system, to different N applications. In this area, Kawata *et al.*⁹⁾ reported that the growth of lateral roots on the superficial axile roots were increased by the top-dressing of N fertilizer between tillering and heading stages.

This study, therefore, aims to examine the response of a whole root system, which includes axile and lateral roots, to the different amount of N application. The responses were compared among four rice cultivars with different AHM at two growth stages, *i.e.*, just before the application of N top-dressing, and at heading stage.

Materials and Methods

The following four rice cultivars that differ in AHM were selected as test plants; Gin-nen (indica type, very low AHM¹¹⁾), Tamanishiki (japonica type, low AHM¹¹⁾), Habataki (indica-japonica hybrid cultivar, developed at Hokuriku National Agricultural Experiment Station as a high yielding cultivar in 1989, thus expected to have high AHM), Norin 25 (japonica type, high AHM¹¹⁾). Kawashima⁶⁾ examined the effects of container size on the root growth of rice under submerged conditions, and concluded that the three different container sizes, which were 14 cm in depth and 25 cm in diameter, 28 cm depth and 25 cm diameter, and 58 cm depth and 70 liters in volume, did not affect the nodal root elongation of rice plants. Thus we used the plastic pot 25 cm in diameter and 30 cm in depth in this study. Rice plants were grown in the plastic pots filled with loamy sand soil (Koh-nan city, Aichi) under submerged and outdoor conditions.

Three levels of N application were made as

follows; Compound fertilizer (12% N; 16% P_2O_5 ; 14% K_2O) was applied at the rate of 2.1 g per pot for all the plots, 1.18 g of ammonium sulphate was added for 10 N-plot and 5.90 g of ammonium sulphate was added for 30 N-plot, so that the N level of 5 N, 10 N and 30 N-plot was equivalent to 5 kg-N/1000 m², 10 kg-N/1000 m², and 30 kg-N/1000 m², respectively, based on the soil surface area of the pot. Half of the fertilizers were applied as basal dressing, and the rest were applied 35 days after sowing as top dressing.

Six pots were prepared for one plot of each cultivar. Three pregerminated seeds of each cultivar were sown in center position of each pot on July 7, 1990 and thinned to one plant per pot seven days after sowing. At 33 days after sowing and heading stage, three plants of each cultivar were sampled from every plot.

Heading dates of Tamanishiki, Habataki and Norin 25 were between the 7th and 9th of September and those of Gin-nen were between the 14th and 16th of September. Thus, the sampling at heading stage was done on Sept. 10 for Tamanishiki, Habataki and Norin 25 and Sept. 17 for Gin-nen, respectively.

At each sampling, root systems were carefully washed out from the soil, then separated from shoots. Plant age in leaf number, plant height and number of tillers was recorded, and then the shoots were oven-dried at 80°C for 2 days and weighed. Root systems were preserved in 10% formalin for further study.

Separating all nodal roots from the node base, their number per plant was counted, and the each root axis length was measured with a ruler. The length of an entire root system was measured with the root length scanner (Common Wealth Aircraft Co. LTD) after cutting each nodal root into 2 to 3 cm segments. During this process, some lateral root segments detached from nodal root axes were collected from two plants for each cultivar in every plot. And their length was determined with root length scanner and the dry weight obtained to estimate specific root length. Total lateral root length was estimated by subtracting total length of the nodal root axes from that of the whole root system. Collecting all the nodal root segments of each plant, root dry weight was determined as ash-free organic root matter^{2,14)}.

Table 1. Effect of different amount of nitrogen application on shoot growth of four rice cultivars (33-day-old plant).

Cultivar	N-level (kg/10a)	Plant age in leaf number	Plant height (cm)	Number of tillers	Shoot dry weight (g)
Gin-nen	5	10.1 a	72.7 a	14.3 a	6.82 a
	10	10.1 a	79.7 b	23.0 b	10.71 b
	30	11.3 a	88.4 c	33.7 c	15.06 c
Tamanishiki	5	10.4 a	62.7 a	11.3 a	3.91 a
	10	10.9 a	63.9 a	17.0 b	5.74 b
	30	11.1 a	71.9 b	25.0 c	8.07 c
Habataki	5	9.8 a	63.8 a	13.0 a	6.25 a
	10	10.2 b	67.5 b	18.0 b	9.04 b
	30	10.3 b	76.0 c	24.7 c	10.22 b
Norin 25	5	10.2 a	59.1 a	11.3 a	3.88 a
	10	10.9 a	61.1 ab	18.3 b	5.95 b
	30	10.8 a	65.4 b	22.7 c	7.43 c

Data are means of 3 plants. Data followed by the same letter in each column are not significantly different by Duncan's multiple range test ($P=0.05$).

Table 2. Effect of different amount of nitrogen application on number of nodal roots per plant, length of single nodal root axis and root dry weight per plant of four rice cultivars (33-day-old plant).

Cultiver	N-level (kg/10a)	Number of nodal roots	Length of single nodal root axis (cm)	Root dry weight (g)
Gin-nen	5	318.0 a	23.8 a	2.17 a
	10	414.7 b	22.2 a	2.43 a
	30	447.7 b	16.6 b	1.97 a
Tamanishiki	5	242.3 a	21.7 a	1.14 a
	10	294.0 b	18.1 b	1.10 a
	30	360.0 c	15.0 c	1.08 a
Habataki	5	321.3 a	22.5 a	1.67 a
	10	405.0 b	19.8 b	1.89 a
	30	384.3 b	14.6 c	1.09 b
Norin 25	5	273.0 a	21.1 a	1.12 a
	10	353.0 b	17.2 b	1.19 a
	30	379.3 b	15.2 c	1.14 a

Data are means of 3 plants. Data followed by the same letter in each column are not significantly different by Duncan's multiple range test ($P=0.05$).

Results

1. Growth responses of the 33-day-old plants

Table 1 shows the shoot growth parameters for the plants sampled 33 days after sowing. Almost all the parameters of shoot growth

increased significantly with increasing N application in all the cultivars. Table 2 shows the number of nodal roots per plant, length of single nodal root axis, and root dry weight per plant. The number of nodal roots was significantly greater in 10 N and 30 N plots than in 5 N plot for all the cultivars, while length of

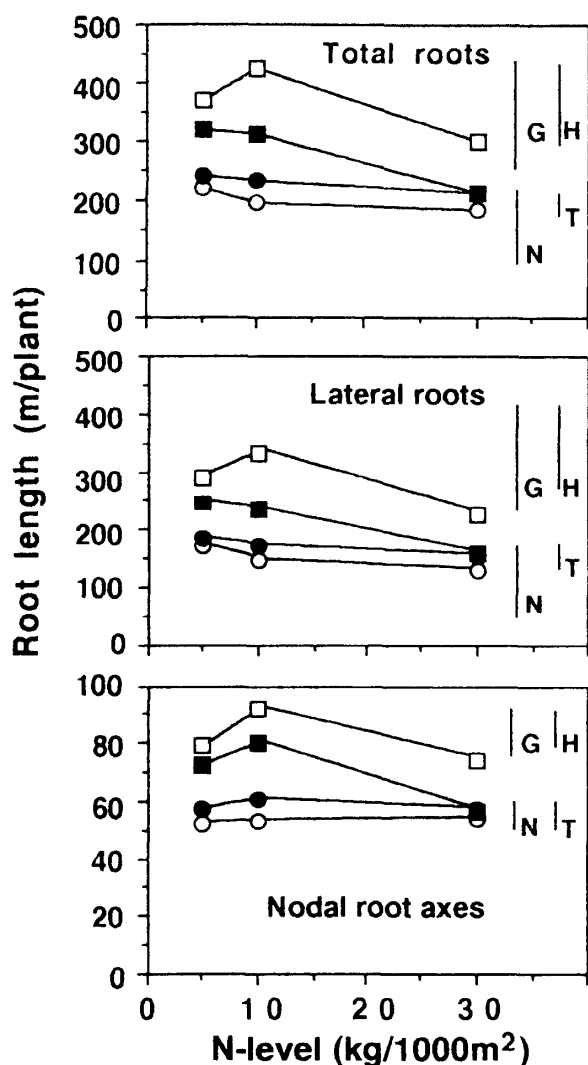


Fig. 1. Changes in total root length, total lateral root length and total nodal root axes length of Gin-nen (\square), Tamanishiki (\circ), Habataki (\blacksquare) and Norin 25 (\bullet) as affected by different N levels (33-day-old plant). Vertical bars with letter in the figure indicate LSD ($P=0.05$) of each cultivars; G, Gin-nen; T, Tamanishiki; H, Habataki; N, Norin 25.

single nodal root axis in 30 N plot was the shortest among the three plots in all the cultivars. In contrast, no difference was found in the effect of N application amount on root dry weight for all the cultivars except that of Habataki in 30 N plot, which was smaller than those in the other two plots. Table 3 shows the S/R ratios of the 33-day-old and heading stage plants. The ratio increased with increasing N application in 33-day-old plants in all the cultivars.

Fig. 1 shows the total root length, total

lateral root length and total nodal root axis length of the 33-day-old plants grown under different N application regimes. In changing pattern of the three root length parameters with increasing N application, the four cultivars could be divided into two groups; one group included Tamanishiki and Norin 25, whose parameters were scarcely affected by the N application regimes, and the other included Gin-nen and Habataki, whose parameters slightly increased in 10 N plot, but substantially decreased in 30 N plot as compared with those in 5 N plot.

2. Growth responses of heading-stage plants

Table 4 shows the shoot growth parameters for heading-stage plants. Plant age in leaf number and plant height of all the cultivars increased with increasing N application, although in Tamanishiki and Habataki, the difference in plant height between 10 N and 30 N plots was not very clear. In all the cultivars, both number of tillers and productive tillers, and shoot dry weight tended to increase as the amount of applied N increased and was the greatest in 30 N plot.

Table 5 shows the number of nodal roots per plant, length of single nodal root axis and root dry weight per plant for the heading-stage plants. Number of nodal roots of all the cultivars increased significantly with increasing N application and the greatest values were obtained in 30 N plot. Length of single nodal root axis showed a tendency to slightly decrease in 30 N plot in all the cultivars. Though root dry weight showed a similar trend with the number of nodal roots, their responses to different N levels were different among the cultivars. Gin-nen and Tamanishiki (cultivars with low AHM) showed a greater increment of root dry weight in 30 N plots than Habataki and Norin 25 (cultivars with high AHM). The S/R ratios of heading-stage plants increased with increasing N application (Table 3), but the extent of increase was relatively small as compared with those of the 33-day-old plants in all the cultivars.

Fig. 2 shows the total root length, total lateral root length and total nodal axis length of the heading-stage plants. In striking contrast to the 33-day-old plants, total nodal root axis length of all the cultivars substantially increased with increasing N application. This

Table 3. Effect of different amount of nitrogen application on S/R ratio of four rice cultivars.

Cultivar	N-level (kg/10a)	Growth stage	
		33-day-old	Heading-stage
Gin-nen	5	3.12 a	7.19 a
	10	4.41(1.41) b	9.02(1.25) a
	30	7.76(2.49) c	12.39(1.72) b
Tamanishiki	5	3.43 a	9.16 a
	10	5.21(1.52) a	10.22(1.12) b
	30	7.65(2.23) b	13.19(1.44) c
Habataki	5	3.72 a	8.05 a
	10	4.81(1.29) a	8.78(1.09) a
	30	9.42(2.53) b	11.56(1.44) b
Norin 25	5	3.45 a	7.69 a
	10	5.02(1.46) b	10.06(1.31) b
	30	6.57(1.90) c	13.29(1.73) c

Data are means of 3 plants. Numerals in parentheses are the ratio to 5N plot. Data followed by the same letter in each column are not significantly different by Duncan's multiple range test ($P=0.05$).

Table 4. Effect of different amount of nitrogen application on shoot growth of four rice cultivars (heading-stage plant).

Cultivar	N-level (kg/10a)	Flag leaf position	Plant height (cm)	Number of tillers	Number of productive tillers	Shoot dry weight (g)
Gin-nen	5	14.0 a	120.9 a	14.3 a	14.3 a	43.1 a
	10	14.7 a	138.7 b	25.7 b	25.3 b	76.0 b
	30	14.7 a	151.1 c	42.3 c	35.3 c	134.6 c
Tamanishiki	5	15.0 a	96.7 a	12.7 a	11.7 a	30.3 a
	10	15.0 a	109.9 b	16.7 b	14.7 a	40.7 b
	30	16.0 b	114.5 b	34.3 c	27.0 b	80.6 c
Habataki	5	13.3 a	90.0 a	13.0 a	12.3 a	35.3 a
	10	13.0 a	100.9 b	16.7 a	14.0 a	43.6 b
	30	14.3 b	101.9 b	34.3 b	25.0 b	67.8 c
Norin 25	5	14.7 a	96.4 a	14.3 a	10.7 a	26.7 a
	10	14.3 a	104.2 b	22.7 b	16.0 b	41.8 b
	30	15.0 a	113.1 c	32.3 c	28.3 c	63.7 c

Data are means of 3 plants. Data followed by the same letter in each column are not significantly different by Duncan's multiple range test ($P=0.05$).

increment was caused by that of nodal root number, judging from less inhibition of the length of single nodal root axis seen with increasing N application, as shown in Table 5. An obvious difference among cultivars was observed in the growth responses of lateral

roots with increasing N application. This difference was found to correspond to that in the AHM of cultivars, namely, Gin-nen and Tamanishiki, which are reputed for their low AHM. They sharply responded to N application and their total lateral root length substan-

Table 5. Effect of different amount of nitrogen application on number of nodal roots per plant, length of single nodal root axis and root dry weight per plant of four rice cultivars (heading-stage plant).

Cultivar	N-level (kg/10a)	Number of nodal roots	Length of single nodal root axis (cm)	Root dry weight (g)
Gin-nen	5	527.5 a	31.4 a	6.00 a
	10	814.0 b	30.2 a	8.39 b
	30	1093.3 c	27.3 a	10.86 c
Tamanishiki	5	479.3 a	28.4 a	3.39 a
	10	611.7 a	28.1 a	3.97 a
	30	1101.3 b	24.4 b	6.12 b
Habataki	5	660.7 a	23.0 a	4.38 a
	10	725.7 a	23.1 a	4.99 a
	30	935.7 a	23.4 a	5.87 b
Norin 25	5	560.0 a	26.0 a	3.48 a
	10	723.7 b	26.1 a	4.16 ab
	30	1085.3 c	22.7 b	4.81 b

Data are means of 3 plants. Data followed by the same letter in each column are not significantly different by Duncan's multiple range test ($P=0.05$).

tially increased as the amount of applied N increased. In contrast, the lateral root growth of Habataki and Norin 25, which are reputed for their high AHM, scarcely responded to increased N applications except that of Habataki which in 10 N and 30 N plots tended to increase as compared with 5 N plot though the difference was not significant. Accordingly, the total root length of all the cultivars showed the same trend with the total lateral root length since the main portion of the total root length in a root system was accounted for by the lateral roots¹⁶⁾. Table 6 shows the specific root length⁵⁾, which is also termed as root fineness¹⁷⁾, of lateral roots in heading-stage plants. Although the reliability of data may be limited because of the limited replications as well as the method used as mentioned earlier, a tendency can be seen that the specific root length of lateral roots of Gin-nen and Tamanishiki readily increased, but those of Habataki and Norin 25 decreased or remained relatively unchanged with increasing N application.

Discussion

In this series of studies, we have paid special attention to the differences among root system components in responses to differentiated N

application regimes instead of dealing with an entire root system as a mass or investigating only part of root system to represent a whole root system response.

In our previous paper¹³⁾, we reported that the seminal root axis elongation in seedling stage was more severely inhibited by N in culture solution for the cultivars with low AHM as compared with those with high AHM. The difference started to become clear even at a very low (0.4 mg L^{-1}) N concentration. In this study, which examined the later growth stages, and thus whole root system including nodal roots, it was found that the responses of nodal root axis elongation and their concomitant lateral root development were also different among cultivars.

The elongation response of nodal root axis can be evaluated by the length of a single nodal root axis and the total nodal root axis length of a whole root system. For 33-day-old plants, the total nodal root axis length of Tamanishiki and Norin 25, which are japonica type, scarcely changed with increasing N application (Fig. 1) due to the fact that increased number of nodal root axes per plant was cancelled by the decrease of single nodal root axis length (Table 2).

In contrast, Gin-nen (indica type) and

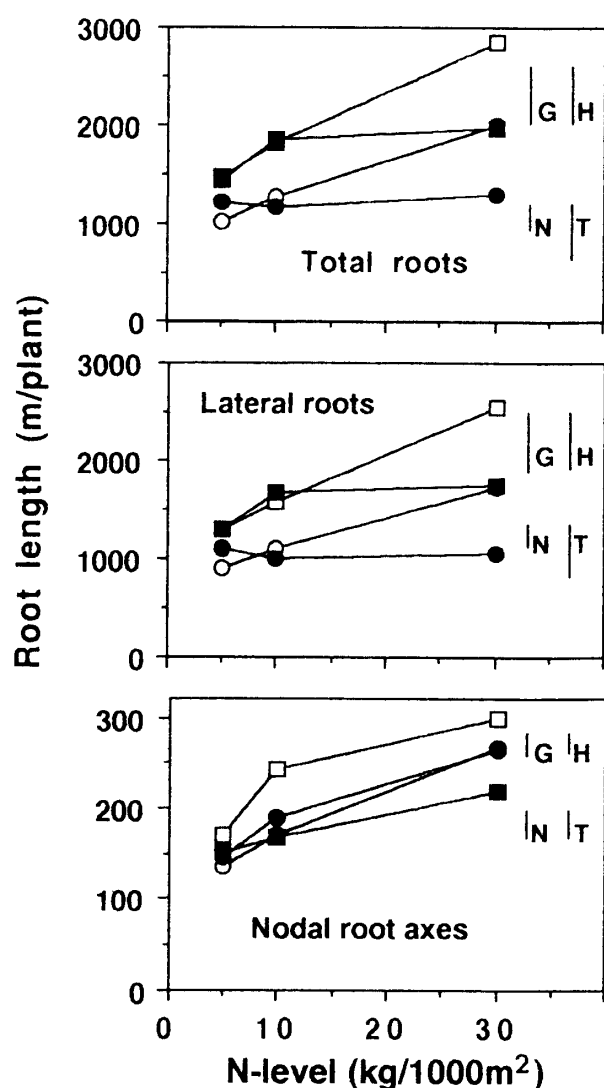


Fig. 2. Changes in total root length, total lateral root length and total nodal root axes length of four cultivars as affected by different N levels (heading-stage plant). Vertical bars with letter and symbols are the same with those in Fig. 1.

Habataki (indica-japonica hybrid cultivar) did not decrease the single nodal root axis length as much as the two japonica cultivars, and the number of nodal roots significantly increased from 5 N to 10 N plots (Table 2). As a result, the total nodal root axis length of Gin-nen and Habataki slightly increased up to 10 N plot (Fig. 1), and then turned to decrease significantly at 30 N plot (Fig. 1). These differences between japonica and indica cultivars seem to concur with the findings by Tanaka¹²⁾ that indica type cultivars were more susceptible than japonica to heavy N application in terms of inhibition of nodal root

axis elongation. He evaluated the inhibitory effects of N based only on the length of the longest nodal root axis in a root system, however.

On the contrary, for the heading-stage plants, the inhibitory effects of N application increment on the length of single nodal root axis were much less recognized (Table 5). In addition to that, the plants produced more nodal root axes as the amount of applied N increased (Table 5). Consequently, the total nodal root axis length per plant increased for all the cultivars (Fig. 2). However, no clear difference in this respect was noted at this growth stage.

In our previous paper¹³⁾, the response of the seminal root axis elongation to the different N treatments was clearly different among the cultivars according to their AHM, but the response of nodal root elongation was not as clear as in the seminal root. This may possibly be attribute to the difference in the habit and timing of rooting for nodal roots among the cultivars. In this study, although substantial differences among the four cultivars were observed in terms of nodal root elongation responses to different N application regimes, the differences were not related to those in AHM of the cultivars, but rather in ecotype, *i. e.*, japonica and indica type.

In contrast, we found very interesting and contrasting differences in lateral root development between the cultivars with low and high AHM. And this difference was not found for the 33-day-old plants (Fig. 1), but was very pronounced for the heading-stage plants (Fig. 2), which had received the top dressing. Namely, lateral root growth in terms of total lateral root length of Gin-nen and Tamanishiki (low AHM cultivars) markedly increased at 30 N plot as compared with those in 5 N and 10 N plots. By contrast, the lateral root growth of Habataki and Norin 25 (high AHM cultivars) was scarcely affected by the three N levels.

Nitrogen application is known to alter the dry matter distribution between shoot and root^{3,10)}. In both stage, the S/R ratios increased with increasing N application (Table 3). But no consistent tendency related to the AHM of cultivars was found.

This fact implies that the differences in lateral root development mentioned above

Table 6. Effect of different amount of nitrogen application on specific root length of lateral roots of four rice cultivars (heading-stage plant).

Cultivar	N-level (kg/10a)	Specific root length (m/g)
Gin-nen	5	411.1
	10	422.2
	30	531.6
Tamanishiki	5	550.4
	10	664.0
	30	698.8
Habataki	5	671.5
	10	870.9
	30	645.8
Norin 25	5	776.0
	10	637.0
	30	627.0

Data are means of 2 plants.

can not be explained simply by the increased dry matter allotment to the root system, but we also need to examine how the allocated dry matter was utilized for the development of lateral roots.

In this aspect, the specific root length of lateral roots in heading-stage plants was estimated (Table 6). The specific root length of lateral roots of Gin-nen and Tamanishiki readily increased, but those of Habataki and Norin 25 decreased or remained relatively unchanged with increasing N application.

Increased specific root length indicates two possibilities. One is that the production of thinner roots was promoted, and the other that the specific gravity and/or diameter of roots was decreased. Since the authors do not know any experimental evidence that supports the latter possibility, it seems likely that the increment of total lateral root length was caused mainly by the enhanced production of thinner roots. These thin lateral roots roughly correspond to S-type first order (non-branching lateral root) and the second or higher order lateral roots.

Summarizing the responses of the whole root system, the cultivars with low AHM (Gin-nen and Tamanishiki) formed a longer root system by producing more nodal roots, whose

elongation only slightly inhibited, associated with the promoted production of lateral roots, especially thin roots, as the amount of N application increased. On the other hand, the root system development of the cultivars with high AHM (Habataki and Norin 25) remained relatively unchanged under the N application regimes, except for the nodal root production, which was enhanced.

In this experiment, the total lateral root length was estimated by subtracting the total nodal root axis length from the length of an entire root system, which was measured by using the root length scanner. Morita *et al.*¹¹⁾ pointed out that the accuracy of measurement by using the root length scanner depended on root thickness and showed that the length of root with a diameter less than 100 μm would be underestimated. This may explain the substantial difference in the total length of a whole root system between ours and that estimated by direct measurement⁷⁾.

In this respect, during the measurement, we observed that the lateral root diameter of Gin-nen and Habataki were distinguishably greater when compared with those of Tamanishiki and Norin 25. Thus, the difference in the estimated lateral root length among the cultivars was independent of the difference in lateral root diameter. Furthermore, if the root length could have been correctly measured including the thin lateral roots, the difference found between low and high AHM cultivars would become even more distinct, which will strengthen our conclusion.

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* In Japanese with English Summary.

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