### Contribution of Nitrogen Absorbed during Ripening Period to Grain Filling in a High-Yielding Rice Variety, Takanari

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Abstract : High-yielding rice varieties require a large accumulation of N in panicles. The objectives of this study were to clarify the change in N allocation during the ripening period (Exp. 1) and to quantify the contribution of N absorbed during the ripening period to panicle N at maturity (Exp. 2) in the high-yielding variety Takanari in comparison with that in Nipponbare as a control. In Exp. 1, <sup>15</sup>N-labeled N (<sup>15</sup>N) was applied at heading to investigate the distribution of newly absorbed N as well as the allocation of plant N. In Exp. 2, split <sup>15</sup>N application was performed during the filling period to estimate the above contribution. In Exp. 1, the allocation of plant N and absorbed <sup>15</sup>N to the panicles was larger and that to the leaves was smaller in Takanari than in Nipponbare during the ripening period, although Takanari accumulated more N at maturity. The difference in N allocation suggested that the difference in N demand in panicles would be larger than that in N uptake. In Exp. 2, the varietal difference in the grain filling duration was observed: Nipponbare accumulated little N in the panicles after 28 d after heading (DAH), while Takanari accumulated about a quarter of its panicle N during that time. An estimate showed that in Takanari, 13.5% of the panicle N was derived from N absorbed after 28 DAH. These results suggest that the utilization of newly absorbed N until a later period after heading is important for the achievement of high yields.

Key words : Grain filling, High-yielding variety, Nitrogen partitioning, Rice, Ripening period.

Nitrogen (N) is one of the most important nutrients for rice production in paddy fields. Correlations between N accumulation and yields have been shown in many studies (Cassman et al., 1993; Tirol-Padre et al., 1996; Singh et al., 1998; Witt et al., 1999; Yao et al., 2000; Ju et al., 2006). In general, 70 to 100% of N accumulated in plants at harvest is absorbed before heading (Higuchi and Yoshino, 1986; Miyama and Okabe, 1986; Ying et al., 1998). During the ripening period, the developing panicles become the major N sink and a large amount of N is remobilized from leaf blades (leaves) and sheaths+culms (stems) to panicles (Wada et al., 1986; Sheehy et al., 1998). As a result, 30 to 77% of N in plants is allocated to the grains in the panicles at harvest (Witt et al., 1999).

Dry-matter production during the ripening period is important for the yield. Sixty to 100% of the carbohydrates accumulated in panicles at harvest are derived from photosynthates produced during the ripening period (Yoshida, 1981). Since N content is closely correlated with the photosynthetic rate in individual leaves (Yoshida and Coronel, 1976; Uchida et al., 1982; Makino et al., 1988; Peng et al., 1995; Ladha et al., 1998), leaf N plays a significant role in dry-matter production. Frequently, it is stated that delayed efflux of N from leaves (i.e., delayed senescence) is important for enhancing dry-matter production and improving grain filling. In a highyielding variety, Akenohoshi, a larger amount of leaf N is maintained during the ripening period than in a standard variety (Ookawa et al., 2003). However, leaf N has another role as a major source for the panicle N (Mae and Ohira, 1981). In the study of Wada and Wada (1991), a correlation between the sink size and the amount of N remobilized from the leaves to the panicles was observed. Moreover, the grain yield was positively correlated with N remobilization from vegetative organs to panicles (Samonte et al., 2006; Zhang et al., 2007). Therefore, it is difficult to emphasize the importance of N partitioning to either leaves or panicles for achieving a high yield. Characteristics of plant N allocation during the ripening period in high-yielding varieties must be investigated further.

High-yielding varieties have a large number of spikelets per unit area and a relatively high percentage of filled grains (Yamamoto et al., 1991; Xu et al., 1997). The number of spikelets, which mostly determine the yield under favorable conditions, is generally proportional to the amount of plant N at the

Received 16 July 2008. Accepted 27 November 2008. Corresponding author: M. Ida (aida@mail.ecc.u-tokyo.ac.jp, fax+81-3-5841-8048). **Abbreviations** : DAH, days after heading; N, nitrogen; <sup>15</sup>N, <sup>15</sup>N-labeled nitrogen; NUEDP, nitrogen use efficiency for dry-matter production; NUEPY, nitrogen use efficiency for panicle yield; SPE, spikelet production efficiency per unit plant N.

panicle formation stage (Murayama, 1967; Wada, 1969; Hasegawa et al., 1994; Kobayasi and Horie, 1994). In addition to the large accumulation of N at this stage, high-yielding varieties have a large number of spikelets due to high efficiency of spikelet production per unit plant N (SPE, spikelet production efficiency) (Yamamoto et al., 1991; Yoshida et al., 2006). Having large reserves of N in vegetative tissues at heading is important to meet the large demand for N in panicles (Sheehy et al., 1998), but a high SPE means limited storage of N per spikelet in plants at the heading stage. Therefore, N absorption after heading is expected to be more important for high-yielding varieties than for standard varieties. To investigate the distribution and remobilization of N absorbed at different growth stages to the plant organs, we need to use  ${}^{15}$ N-labeled N ( ${}^{15}$ N) (Kichey et al., 2007). It has been shown that a large fraction of <sup>15</sup>N applied at heading is distributed to panicles at harvest (Wada et al., 1973; Arai and Kono, 1980; Oritani, 1984; Sheehy et al., 2004). However, the differences in the partitioning of N absorbed during the ripening period between high-yielding varieties and standard varieties have not been investigated. Consequently, although some studies have reported high-yielding varieties to absorb a large amount of N after heading (Higuchi and Yoshino, 1986; Ookawa et al., 2003), the contribution of N absorbed after heading to meeting the large N demand in panicles of high-yielding varieties is not well known.

The objectives of this study were to clarify the change in N allocation during the ripening period (Exp. 1) and to quantify the contribution of N absorbed during the ripening period to panicle N at maturity (Exp. 2) in a high-yielding variety. We used Takanari, a high-yielding variety, and Nipponbare as a standard. Takanari has high SPE (Yoshida et al., 2006; Saitoh and Danno, 2007) and relatively high grain-filling ability (Xu et al., 1997). In Exp. 1, <sup>15</sup>N was applied at heading to investigate the varietal difference in the distribution and remobilization during the ripening period of newly absorbed N as well as the allocation of plant N. In Exp. 2, split <sup>15</sup>N application was performed during the filling period to estimate the contribution of N absorbed during the ripening period to the panicle N In the discussion, major determinants of N allocation during the ripening period, such as N uptake and N remobilization, and the possible importance of N absorbed during the ripening period for meeting the large demand for N in panicles of Takanari are evaluated in comparison with Nipponbare.

#### **Materials and Methods**

Experiments were conducted in 2001 (Exp. 1) and 2002 (Exp. 2) in the paddy field of Field Production Science Center (Nishitokyo, Japan) of Graduate School of Agricultural and Life Sciences, The University of Tokyo. The varieties used were Takanari, a high-yielding variety, and Nipponbare as a standard. Seeds were sown on April 27 and the seedlings were transplanted on May 25 in 2001, and on April 20 and May 21 in 2002. Compound fertilizer was incorporated into soil at the rates of 6, 8 and 9 g m<sup>-2</sup> of N, P<sub>2</sub>O<sub>5</sub> and K<sub>2</sub>O, respectively, just before transplanting. Hill spacing was 0.3 by 0.15 m, with one seedling per hill in both years. Ammonium sulfate was top-dressed at the rate of 2 g m<sup>-2</sup> of N on July 12 in 2001 and on July 19 in 2002.

### 1. <sup>15</sup>N feeding and sampling

#### (1) Experiment 1

<sup>15</sup>N feeding was conducted at heading. Fifty plastic pipes with an inner diameter of 10 cm and length of 15 cm were inserted into soil to the depth of 1–2 cm. Each pipe was centered on a hill having an average number of tillers, selected from a 6 m×6 m plot. The solution of <sup>15</sup>N-labeled ammonium sulfate (10.3% atom <sup>15</sup>N excess) was applied inside the pipes at the rate of 0.135 g of N per hill, which is equivalent to 3 g m<sup>2</sup> of N. To the plants without <sup>15</sup>N-application, ammonium sulfate was also top-dressed at the rate of 3 g m<sup>2</sup> of N.

Tops of nine plants having average numbers of panicles were harvested at heading. Five plants having average fresh weights were selected and used for determining N content of each organ. To determine the distribution of N and <sup>15</sup>N during the ripening period, we harvested five <sup>15</sup>N-applied plants at 3, 6, 10, 15, 20, 30 and 50 d after heading (DAH), and used them for determining the contents of N and <sup>15</sup>N in each organ.

### (2) Experiment 2

<sup>15</sup>N feeding was conducted at –11, 0, 14 and 28 DAH. Fifteen plastic pipes, the same as those used in Exp.1, were used in each feeding. Each pipe was centered on a hill having an average number of tillers, selected from an 8 m×6 m plot. Each time the pipes were set, a solution of <sup>15</sup>N-labeled ammonium sulfate (70.6% atom <sup>15</sup>N excess) was applied inside the pipes at the rate of 0.023 g of N per hill, which is equivalent to 0.5 g m<sup>-2</sup> of N. Plants without <sup>15</sup>N application were not top-dressed during the filling period.

To determine the change in N content of each organ during the ripening period, we used plants without <sup>15</sup>N application. Tops of twelve plants having average numbers of panicles were harvested at –11, 0, 14, 28 and 42 DAH. Six plants having average fresh weights were selected in each sampling and used for determining N content. To determine the distribution and reallocation of N absorbed during the ripening period, we harvested five <sup>15</sup>N-applied plants 10 d after each <sup>15</sup>N application and at maturity and determined the <sup>15</sup>N content in each organ. The days of sampling were decided based on the results of <sup>15</sup>N accumulation and distribution in Exp.1.

	Variety	Number of spikelets (1)	Number of panicles	Number of spikelets per panicle	N in tops at heading (2)	$\mathrm{SPE}^\dagger$ (1)/(2)
		$(\times 10^3 \text{ hill}^{-1})$	$(hill^{-1})$	-	$(\text{mg hill}^{-1})$	$(mg^{-1})$
Exp. 1	Takanari	$1.78 \pm 0.07$	$8.8 \pm 0.3$	$203\pm6$	$417 \pm 16$	4.28
	Nipponbare	$1.30\pm0.07$	$13.5\pm0.4$	$96\pm3$	$340\pm14$	3.83
		**	**	**	**	
Exp. 2	Takanari	$2.25 \pm 0.02$	$9.8\pm0.2$	$230\pm2$	$441\pm5$	5.09
	Nipponbare	$1.48 \pm 0.01$	$14.9\!\pm\!0.3$	$100 \pm 1$	$392\pm12$	3.78
		**	**	**	**	

Table 1. Number of spikelets, number of panicles, number of spikelets per panicle, amounts of N in tops at heading and SPE in rice varieties Takanari and Nipponbare in Exp. 1 (2001) and Exp. 2 (2002).

Values are means  $\pm$  SE (n=6 for the number of spikelets, the number of panicles, and the number of spikelets per panicle; n=5 for the amount of N in tops at heading in Exp. 1, n=6 in Exp. 2).

<sup>†</sup>, SPE, spikelet production efficiency, was calculated as the average number of spikelets divided by the average amount of N in tops at heading.

\*\* indicates significant difference at 1% (t-test).

### 2. Measurements of dry weight and contents of N and ${\rm ^{15}N}$

Immediately after each sampling, the plants were separated into panicles, leaves and stems. The dry weight of each part was measured after drying at 80°C for at least two days. N concentration was determined with an auto analyzer (AACS-III, Bran+Luebbe Inc., Norderstedt, Germany) after the Kjeldahl digestion. The nitrogen content of each sample was calculated as the product of the dry weight and the N concentration. <sup>15</sup>N percentage excess was determined by the optical emission spectroscopic method (Kumazawa, 1970) with a <sup>15</sup>N analyzer (N-150, JASCO Corp., Tokyo, Japan). The <sup>15</sup>N content of each sample was calculated as shown below (Mae and Ohira, 1981).

<sup>15</sup>N content=

<sup>15</sup>N atm % excess of each sample

 $^{15}N$  atm % excess of  $(^{15}NH_4)_2$  SO4 fed to the plants  $\times N$  content

### 3. Calculation of NUEPY and NUEDP

Nitrogen use efficiencies for panicle yield (NUEPY) and for dry-matter production (NUEDP) were calculated as the ratios of panicle dry weight and top dry weight to the amount of N in tops at maturity. For the calculation, five plants harvested at 50 DAH in Exp. 1 and six plants harvested at 42 DAH in Exp. 2 were used.

### 4. Determination of the number of spikelets and spikelet production efficiency (SPE)

At plant maturity, 30 plants having average numbers of panicles were harvested. Six plants having average weights of panicles were selected and used to determine the number of spikelets, the number of panicles, the number of spikelet per panicle and SPE. SPE was calculated as the average number of spikelets divided by the average amount of N in tops at heading.

## 5. Estimation of the origin of panicle N at maturity by partitioning the growth period

In Exp. 2, the amount of N absorbed in the interval i and then distributed to panicles at maturity,  $N_{panicle}^{*}(i)$ , was estimated using the following equation:

 $N_{\text{panicle}}^{*}(i) = \Delta N_{\text{uptake}}(i) f_{\text{panicle}}(i)$ 

The interval covers from -11 DAH to maturity.  $\Delta N_{uptake}(i)$  is the amount of N which was accumulated in tops in the interval *i*, and  $f_{panicle}(i)$  is the ratio of N accumulated in the interval *i* and then distributed to panicles at maturity to the amount of N which was accumulated in the interval *i*. The average of the distribution ratios of <sup>15</sup>N applied at the beginning and end of the interval *i* was used as  $f_{panicle}(i)$ , except for the interval from 28 DAH to maturity, where the distribution ratio of <sup>15</sup>N applied at the beginning of the interval *i* was substituted for  $f_{panicle}(i)$ . The amount of N which was absorbed before -11 DAH and then distributed to panicles at maturity was calculated by subtracting the sum of  $N_{panicle}^*(i)$  from the amount of N in panicles at maturity.

### Results

### 1. N accumulation, spikelet production and plant growth

The total solar radiation from transplanting to harvest was 1639 MJ m<sup>-2</sup> in 2001 and 1809 MJ m<sup>-2</sup> in 2002. The average temperature was 24.6°C in 2001 and 24.0°C in 2002. The heading dates of the varieties, at which about a half of the panicles had emerged, were August 14 and 21 in 2001 and August 13 and 14 in 2002 in Takanari and Nipponbare, respectively.

Takanari had a smaller number of panicles but a

	Variety	Panicle dry weight (1)	Top dry weight (2)	N in tops at maturity (3)	$\frac{\text{NUEPY}^{\dagger}}{(1)/(3)}$	NUEDP <sup>‡</sup> (2)/(3)
		$(g hill^{-1})$	$(g hill^{-1})$	$(\text{mg hill}^{-1})$	$(g g^{-1})$	$(g g^{-1})$
Exp. 1	Takanari	$36.3\pm1.4$	$68.7 \pm 1.6$	$714\pm17$	$51\pm1$	$96 \pm 1$
	Nipponbare	$26.5 \pm 1.6$	$67.3 \pm 2.3$	$585\!\pm\!22$	$45\pm1$	$115\pm1$
		**	ns	**	**	**
Exp. 2	Takanari	$42.7 \pm 1.2$	$71.4 \pm 2.5$	$610\pm25$	$70\pm2$	$117\pm2$
	Nipponbare	$29.8 \pm 1.1$	$64.6\!\pm\!2.1$	$503\pm16$	$59\pm2$	$128\pm2$
		**	ns	**	**	**

Table 2. Panicle dry weight, top dry weight, amount of N in tops, NUEPY and NUEDP at maturity in rice varieties Takanari and Nipponbare in Exp. 1 (2001) and Exp. 2 (2002).

Values are means  $\pm$  SE (n = 5 in Exp.1; n = 6 in Exp. 2).

<sup>†</sup>, NUEPY, nitrogen use efficiency for panicle yield (panicle dry weight).

<sup>‡</sup>, NUEDP, nitrogen use efficiency for dry-matter production (top dry weight).

\*\* and ns indicate significant difference at 1 % and no significant difference at 5 % (t-test).



Fig. 1. Changes in the amounts of N in tops (a), panicles (b), leaves (c) and stems (d); and changes in the distribution of N to each organ (e) during the ripening period in rice varieties Takanari (○) and Nipponbare (▲) in Exp. 1 (2001). Bars indicate standard errors (n=5).

larger number of spikelets per hill than Nipponbare due to a much larger number of spikelets per panicle (Table 1). Takanari showed higher SPE as well as larger N accumulation in tops at heading than Nipponbare (Table 1).

Panicle dry weight at maturity was larger in Takanari than in Nipponbare (Table 2). Top dry weight at maturity tended to be heavier in Takanari than in Nipponbare but the difference was not significant (Table 2). NUEPY was higher but NUEDP was lower in Takanari than in Nipponbare (Table 2). This inverse relation for NUEPY and NUEDP in Takanari and Nipponbare was seen in both Exp. 1 and Exp. 2, although the values were larger in Exp. 2 than in Exp.1 (Table 2).

# 2. Changes in amounts and partitioning of N and <sup>15</sup>N during the ripening period after the application of <sup>15</sup>N-labeled N at heading (Exp. 1)

The amount of N in tops increased rapidly at first and the rate of the increase gradually decreased with the progress of ripening (Fig. 1a). Takanari had larger amounts of N in tops than Nipponbare throughout the measurement period (0–50 DAH) (Fig. 1a). The amount of N in panicles increased rapidly until 20 DAH in Nipponbare and until 30 DAH in Takanari



Fig. 2. Changes in the amounts of <sup>15</sup>N-labeled N in tops (a), panicles (b), leaves (c) and stems (d); and changes in the distribution of <sup>15</sup>N-labeled N to each organ (e) during the ripening period in rice varieties Takanari (○) and Nipponbare (▲) in Exp. 1 (2001). <sup>15</sup>N-labeled ammonium sulfate was top-dressed at heading. Bars indicate standard errors (n=5).

and the difference between Takanari and Nipponbare became larger after 20DAH (Fig. 1b). The amount of N in the leaves increased at first, reached the maximum at 6 DAH in Takanari and at 10 DAH in Nipponbare, then decreased rapidly until 20 DAH and decreased slowly thereafter until 50 DAH (Fig. 1c). The net decrease in the amount of N in leaves during the measurement period was greater in Takanari than in Nipponbare (Fig. 1c). The change in the amount of N in stems was similar to that in leaves until 20 DAH, but differed thereafter; while the amount of N in leaves consistently decreased, the amount of N in stems reversed its trend from decreasing to increasing at 20 DAH in Nipponbare and at 30 DAH in Takanari (Fig. 1c, d). The allocation of plant N to panicles was larger and that to leaves was smaller in Takanari than in Nipponbare, and the percentage of N distributed to panicles at 50 DAH was 68.1% in Takanari and 54.1% in Nipponbare (Fig. 1e).

The accumulation of <sup>15</sup>N in tops was larger in Takanari than in Nipponbare (Fig. 2a) and the recovery of <sup>15</sup>N at 50 DAH was 26.6 and 19.0% in Takanari and Nipponbare, respectively. The amount of <sup>15</sup>N in panicles increased rapidly at first and gradually until about 30 DAH (Fig. 2b). The amount of <sup>15</sup>N in leaves increased at first, reached a maximum at 10 DAH, followed by a rapid decrease until 20 DAH and gradual decrease until 50 DAH (Fig. 2c). The amount of <sup>15</sup>N in stems showed the same downward trend as in leaves until 20 DAH and increased slightly again thereafter (Fig. 2d). The distribution of <sup>15</sup>N to each organ differed with the variety; Takanari distributed <sup>15</sup>N more to panicles and less to leaves than Nipponbare throughout the measurement period; the difference in distribution to panicles was about 8% and that to leaves was about 5% on average (Fig. 2e).

## 3. Contribution of N absorbed during the ripening period to panicle N (Exp. 2)

Fig. 3 shows the distribution of <sup>15</sup>N applied at -11, 0, 14 and 28 DAH to panicles, leaves and stems, measured at 10 days after <sup>15</sup>N application (a) and at maturity (b) in 2002. Measurement at 10 days after each <sup>15</sup>N application was used to evaluate the initial <sup>15</sup>N partitioning, since the uptake of <sup>15</sup>N applied at heading was almost finished within 10 days and the <sup>15</sup>N accumulation in leaves and stems was near the maximum at that time in Exp. 1 (Fig. 2).

When the <sup>15</sup>N was applied at -11 DAH, little difference was observed between Takanari and Nipponbare in the distribution of <sup>15</sup>N at 10 days after the application, but Takanari distributed more <sup>15</sup>N to panicles and less to leaves than Nipponbare at maturity (Fig. 3). In both varieties, the distribution of <sup>15</sup>N to vegetative organs was decreased and that to panicles increased with the delay in application of <sup>15</sup>N from -11 DAH to 14 DAH. In Nipponbare, however, the distribution to panicles was decreased and that to stems was increased with the delay in application of <sup>15</sup>N from 14 DAH to 28 DAH, while in Takanari the distribution of <sup>15</sup>N at these days was almost the same (Fig. 3).



Fig. 3. Distribution of <sup>15</sup>N to panicles, leaves and stems in rice varieties Takanari and Nipponbare, measured at 10 days after <sup>15</sup>N application (a) and at maturity (b), after the application of <sup>15</sup>N-labeled ammonium sulfate at –11, 0, 14 and 28 DAH in Exp. 2 (2002).



Fig. 4. Percent contribution to panicle N of N accumulated at different growth stages (a) and that of N absorbed at different stages (b) in rice varieties Takanari and Nipponbare in Exp. 2 (2002).

Fig. 4 shows the percent contribution to panicle N of the N accumulated at different growth stages and that of N absorbed at different stages (i.e.  $N_{panicle}^*(i)$ ). The amount of panicle N at maturity was larger in Takanari than in Nipponbare, mostly due to the difference in the accumulation of N after 28 DAH; Takanari accumulated about a quarter of its panicle N after 28 DAH, while Nipponbare accumulated little N during that time (Fig. 4a). The proportions of panicle N originating from N absorbed before and after heading to the panicle N at maturity were about 70% and 30%, respectively, in both Takanari and Nipponbare (Fig. 4b). In Takanari, however, 13.5% of the panicle N at maturity was derived from N absorbed after 28 DAH (Fig. 4b).

### Discussion

The allocation of plant N to panicles during the ripening period was larger and that to leaves was smaller in Takanari than in Nipponbare during the ripening period in Exp.1 (Fig. 1e). A similar result was also obtained in Exp. 2 (data not shown). This tendency in N allocation agrees with the results that the rates of distribution to panicles of <sup>15</sup>N applied at heading (Exp. 1) and at various times during the filling period (Exp. 2) were higher and those to leaves were lower in Takanari than in Nipponbare (Figs. 2e, 3). In general, high-yielding varieties accumulate larger amounts of N in their tops than standard

varieties (Higuchi and Yoshino, 1986; Hiraoka et al., 1992; Ookawa et al., 2003). Our study also showed that N accumulation in tops at maturity was larger in Takanari than in Nipponbare (Table 2); the amounts were equivalent to those in previous studies conducted in Japan (Hiraoka et al., 1992; Katsura et al., 2008). On the other hand, large N accumulation in panicles is generally required for the achievement of high yields. In the present study, Takanari accumulated more N in the panicles than Nipponbare (Figs. 1b, 4a). Since N is remobilized from leaves to panicles to meet the difference between the N demand in panicles and its supply through the roots during grain filling (Wada and Wada, 1991; Sheehy et al., 2004), N partitioning is mostly determined by the balance between the N demand in panicles and the N uptake by plants. Therefore, the difference in N allocation between Takanari and Nipponbare in this study suggests that the difference in N demand in panicles would be larger than that in N uptake.

While Takanari has better light intercepting characteristics (Xu et al., 1997; Saitoh et al., 2002) and produces greater biomass at harvest (Saitoh et al., 2000), its smaller N partitioning to leaves after heading is not advantageous for the photosynthetic activity, resulting in lower NUEDP in comparison with that of Nipponbare in this study (Table 2). In the study of Ookawa et al. (2003), however, Akenohoshi, another high-yielding variety, distributed a larger proportion of N to leaves, which contributed to the maintenance of a higher rate of photosynthesis during the ripening period compared with Nipponbare. Accordingly, the N distribution pattern during the ripening period differs even among high-yielding varieties, which could affect dry-matter production during this period. Yield in Takanari is larger than that in Akenohoshi (Kobata et al., 2006), and thus Takanari is supposed to require more N in panicles than Akenohoshi. The greater demand for N in panicles compared to N uptake in Takanari might be the source of this difference in the N distribution pattern.

The fraction of panicle N at maturity originating from N absorbed after heading was about 30% in both Takanari and Nipponbare (Fig. 4b). N accumulated in panicles has been reported to be composed of N absorbed at all growth stages (Oritani and Yoshida, 1984; Oritani, 1984; Mae, 1986; Sheehy et al., 2004), and the percentage shown here is similar to those obtained in previous studies (Mae, 1986; Sheehy et al., 2004). However, the details of the progress of N accumulation in panicles and the origin of panicle N for Takanari were different from those for Nipponbare (Figs. 1b, 4). In Exp. 2, Takanari accumulated about a quarter of the panicle N after 28 DAH while Nipponbare accumulated little N during that time (Fig. 4a) and about half of the panicle N accumulated after 28 DAH in Takanari was derived from N absorbed in

this period (Fig. 4b). The accumulation of panicle N in Takanari was also larger than that in Nipponbare after 20 DAH in Exp.1 (Fig. 1b). At the heading stage, Takanari had a smaller reserve of N relative to its sink size, as indicated by larger SPE (Table 1). Nevertheless, Takanari showed larger remobilization of N from leaves to panicles in Exp. 1 (Fig. 1). As a result, the amount of N in leaves was at a low level during the late ripening period in Takanari (Fig. 1c). This tendency was also observed in Exp. 2 (data not shown). Since drawing N from leaves raises the risk of losing the photosynthetic capacity to meet the carbohydrate demand in panicles, especially when the N reserves at heading are small, the newly absorbed N and the extended panicle sink activity in Takanari are important for meeting the large N demand in panicles.

As panicles developed, the partitioning of <sup>15</sup>N to panicles increased and that to vegetative organs decreased in both Takanari and Nipponbare (Fig. 3). By delaying <sup>15</sup>N application from 14 DAH to 28 DAH, however, the distribution of <sup>15</sup>N to panicles decreased and that to stems increased in Nipponbare, although it was almost maintained in Takanari (Fig. 3). Since Oryza sativa generally has perennial capability (Sakagami et al., 1999a; 1999b), the increase in the <sup>15</sup>N fraction in stems is probably for the growth of ratoons. In the short term, newly absorbed N is distributed among plant organs depending on their N demand (Sheehy et al., 2004). The difference in the change in <sup>15</sup>N distribution at 10 days after its application suggested that the decrease in the N sink activity of panicles and the increase in that of stems began earlier in Nipponbare than in Takanari. This tendency was consistent with the result of Exp. 1, in which N reaccumulation in stems was observed after 20 DAH in Nipponbare and after 30 DAH in Takanari (Fig. 1d). Although the varietal difference in the amount of N reaccumulation and its determinant are not clear because of limited information, the delay of N reaccumulation in stems should be associated with the extension of the sink activity in panicles, and these traits are important for the utilization of more N resources absorbed by plants.

The factors causing the difference in the duration of N accumulation in panicles are not well understood. In general, N content increases in parallel with dry weight in each spikelet and there is a difference in the time of growth depending on the position of the spikelets on a panicle (Iwasaki et al., 1992). The growth of superior spikelets, which are located on the primary rachis-branches at the upper part of a panicle, precedes that of inferior spikelets, which are located on the secondary rachis-branches at the lower part of the panicle (Nagato, 1941; Arai and Kono, 1979; Iwasaki et al., 1992). Takanari has a large number of spikelets per panicle with a large number of secondary rachis-branches (Hiraoka et al., 1992; Xu et al., 1997; Ishikawa et al., 1999). Thus, there is a possibility that the number of spikelets that grow later would be greater in large panicles and this might allow Takanari to extend the duration of the sink activity in panicles. Besides, in the study of Shinano et al. (2006), N uptake was inhibited by panicle removal, suggesting the control of N uptake by N demand in panicles. In Takanari, therefore, the extended duration of sink activity in panicles might enhance N uptake after heading, although in the present study, the increase of N accumulation was not as large as that of N demand in panicles. Further investigation of the physiological factors causing longer grain filling and their relationship with N uptake is important for better understanding of grain filling.

In summary, although Takanari accumulated a larger amount of N in its tops, N remobilization from leaves to panicles appeared to be larger and the amount of N left in leaves became smaller during the late filling period in Takanari than in Nipponbare. As a result, N partitioning to panicles during the ripening period was larger and that to leaves was smaller in Takanari than in Nipponbare, suggesting that the varietal difference in N demand in panicles would be larger than that in N uptake. An estimate of the origin of panicle N showed that N absorbed for a long period after heading contributed to meeting the greater demand for N in panicles in Takanari. The utilization of newly absorbed N until a later period after heading, and the extension of sink activity of panicles were suggested to be important for the achievement of high yield in Takanari.

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<sup>\*</sup> In Japanese.

<sup>\*\*</sup> In Japanese with English abstract.

<sup>\*\*\*</sup> In Japanese with English summary.