Performance of a High-Yielding Modern Rice Cultivar Takanari and Several Old and New Cultivars Grown with and without Chemical Fertilizer in a Submerged Paddy Field

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Abstract: A high nitrogen-uptake capacity and effective use of absorbed nitrogen for dry matter and grain production are required to improve the production cost and environmental pollution. We characterized grain yield, dry matter production and nitrogen accumulation in six rice cultivars: Sekitori (released in 1848) and Aikoku (1882), referred to as SA cultivars hereafter; Koshihikari (1956); Nipponbare (1963) and Asanohikari (1987), referred to as NA cultivars hereafter; and Takanari (in 1990) as a high-yielding modern cultivar. The plants were grown with and without chemical fertilizer in a submerged paddy field. When plants were supplied with manure and chemical fertilizer, Takanari consistently produced the heaviest grain and dry matter, followed by the NA cultivars, and the SA cultivars the lightest. Dry matter production before heading was greater in Takanari and the NA cultivars due to the longer duration of vegetative growth. Dry matter production after heading was greatest in Takanari, with a larger crop growth rate (CGR), and smallest in the SA cultivars with a shorter ripening time. Greater dry matter production during ripening was accompanied by the greater accumulation of nitrogen by Takanari and NA cultivars. These plants developed a larger amount of roots. The smaller light extinction coefficient of the canopy was also attributed to the higher CGR in Takanari. When plants were grown without chemical fertilizer, Takanari also produced heavier grain and dry matter, which resulted from the greater dry matter production before heading, which was due to the longer period of vegetative growth. The greater dry matter production and nitrogen accumulation by Takanari and NA cultivars were evident when plants were grown with chemical fertilizer. Koshihikari was characterized by a higher CGR and greater nitrogen accumulation during ripening in the absence of chemical fertilizer which should be noted in efforts to decrease rates of nitrogen application.

Key words: Dry matter production, Grain yield, Light extinction coefficient, Nitrogen accumulation, Old and new cultivars, Rice, Root length density.

Efficient agricultural production that conserves resources and preserves environmental quality is vital in order to meet the basic food demands of the rapidly increasing world population (Alva et al., 2005). Appropriate culture of high-yielding rice cultivars is very important in this context, and the use of fertilizers is a critical factor in achieving the maximum potential yield of rice crops. Nitrogen is the most important component of fertilizers in rice production, and the major input in rice paddies (Ntamatungiro et al., 1999). Nitrogen is involved in all metabolic processes in plants and 75% of leaf N is associated with chloroplasts, which are essential for dry matter production through photosynthesis (Arima, 1995; Mae, 1995). In rice, nitrogen increases leaf area and the rate of photosynthesis and it increases dry matter production and grain yield if no lodging occurs and pests can be controlled effectively.

In the past, nitrogen fertilizer has been applied in large amounts in rice production systems and the methods of application were modified in efforts to improve yield (Matsushima, 1976, 1980). However, negative effects on the environment resulted from so-called heavy-input agriculture, as a consequence of the widespread use of nitrogen fertilizers (National Research Council, 1989; Hirel and Lemaire, 2005). Even in paddy rice cultivation, nitrogen fertilizer affects the quality of water at the land preparation and air (Hasegawa, 2003). Heavy nitrogen application also increases the cost of rice production. We need to develop rice cultivation methods that would increase the absorption of nitrogen at each growth stage of rice plants (Wada et al., 1986), maintaining high and reliable dry matter production and grain yield.

Application of nitrogen as controlled-release fertilizer at transplanting might be an effective method for minimizing loss of nitrogen from fertilizers. An improvement in the nitrogen-uptake capacity of rice plants and an effective use of absorbed nitrogen for dry matter and grain production (refer to as nitrogen use efficiency), as well as improvement of application methods, might permit the establishment of...
our efforts in improving nitrogen-uptake capacity and nitrogen use efficiency in rice, we characterized the ecophysiological and varietal characteristics, in terms of grain and dry matter production, as well as nitrogen accumulation, with and without the application of nitrogen-containing chemical fertilizer, of several old and new rice cultivars as well as Takanari as one of the elite modern cultivars in Japan that were grown in a submerged paddy field.

Materials and Methods

1. Plant materials and cultivation of rice plants

(1) Plant materials

On the basis of the results of a preliminary experiment, we selected five cultivars as representatives of old and new cultivars from among more than 10 representative cultivars of rice (*Oryza sativa* L.) that have been grown in the Kanto region of Japan over the past 100 yr, as listed in Table 1. In addition, we included Takanari, released in 1990, as a high-yielding modern cultivar. During selection, we considered the heading time of cultivars that fell within a two-week window.

(2) Cultivation

Plants were grown in the paddy field of the University Farm (latitude, 35°41′N; longitude, 139°29′E), in alluvial (clay loam) soil from Tama River, in 2002, 2005 and 2006. In 2002, the experimental plants were laid out in a split-plot arrangement where with and without chemical fertilizer was the main plot and rice cultivars as sub-plots. In 2005 and 2006 where only plants applied chemical fertilizer were grown, the experiment was laid out in a randomized complete block design with three replicates each year. The size of each plot was approximately 10 m$^2$ per replicate. Plants were grown with chemical fertilizer according to conventional practices (referred to as plants with chemical fertilizer hereafter) and without chemical fertilizer (referred to as plants without chemical fertilizer hereafter) in the paddy field after manure was applied.

For plants grown with chemical fertilizer in 2002,
rice seedlings at the fourth-leaf expansion stage were transplanted on 22 May at a density of 22.2 (30 × 15 cm) hills m⁻² with three plants per hill. Barnyard manure was applied at a rate of approximately 2 kg m⁻² each year in the field for more than 20 yr. Barnyard manure in recent 10 yr contains approximately 0.76% total nitrogen (wet basis, approximately 47% moisture content). Chemical fertilizer was applied at rates of 5.0, 5.0 and 5.0 g m⁻² of N, P₂O₅, and K₂O, respectively, as basal fertilizer and 3.0 and 3.0 g m⁻² of N and K₂O, respectively, as top-dressing to Koshihikari, Sekitori, Aikoku and Takanari plants on 22 July and to Asanohikari and Nipponbare plants on 29 July, respectively. In 2005 and 2006, we used basically the same cultivation and plant establishment methods. Barnyard manure at a rate of approximately 2 kg m⁻² and chemical fertilizer at rates of 5.0, 5.0 and 5.0 g m⁻² of N, P₂O₅, and K₂O, respectively, as basal fertilizer and at rates of 1.0 and 1.0 g m⁻² of N and K₂O, respectively, as top-dressing were applied at the panicle-formation stage, respectively. Heading time (50% heading) and harvest time are shown in Table 2. Harvest time was determined when the color of all of the first rachis branches turned to yellow. Lodging occurred in Sekitori and Koshihikari at the late ripening stage in each of the three years of the experiment. Plants were held erect by binding plants on four hills together when lodging occurred.

For the plants without chemical fertilizer in 2002, the same cultivation and plant establishment methods were used as in the case of the plants with chemical fertilizer, except that only barnyard manure was applied at 2 kg m⁻² as basal fertilizer and no basal chemical fertilizer and no top-dressing was applied. No lodging was observed in any of the cultivars.

2. Measurements of dry weight and leaf area

The number of stems was counted for a total of 25 to 40 hills for each replicate and then five hills with an average number of stems were selected at heading and at harvest for measurements of dry weight. In 2005, sampling was also done at 27 d after heading stage. Plants were separated into leaves, leaf sheaths plus stems, and panicles. Leaf area was measured with the automatic area meter (AAM-8; Hayashi Denko Co., Tokyo, Japan) immediately after separation of leaves, and leaves were then dried in a ventilated oven at 80°C for more than four days or to constant weight. Preliminary sampling was also done at transplanting as a reference to calculate the increment of dry weight and leaf area. The crop growth rate (CGR), net assimilation rate (NAR), and the mean leaf area index (mean LAI) were calculated according to Beadle (1993).

3. Measurements of grain yield and yield components

The plants in an area of approximately 2.0 m² for each replicate were harvested for determinations of yield per unit area. Yield was determined for brown rice. Fully ripened grains were selected by sieving through 1.8-mm mesh and adjusted to a moisture content of 14.5%. The harvest indices were calculated as the total grain weight with 14.5% moisture divided by total dry weight. Yield components for each replicate were determined for five hills with an average number of panicles.

4. Determination of nitrogen content

Five hills with an average number of panicles per replicate were selected and one hill was used for the determination of mean nitrogen concentration of a single plant. Each plant was separated into leaves, stems plus leaf sheaths, and panicles and dried in an oven for more than 4 d. After weighing, the total nitrogen concentration of the plant was determined with a CN analyzer (MT-600; Yanako Inc., Kyoto, Japan) and total nitrogen content was expressed as the product of total above-ground dry weight and the nitrogen concentration.

5. Measurement of light extinction coefficients

The relative light intensities above the canopy and within the canopy at different heights at 10-cm intervals from the soil surface were measured simultaneously with two silicon-photodiode light sensors (320 to 730 nm; S-1133; Hamamatsu Photonics Co., Hamamatsu, Japan), under diffused light condition at 17 or 18 d after heading in 2006. The responses of the sensors to light intensity were confirmed to be identical prior to measurements. Four neighboring hills with average numbers of panicles were selected from each replicate for determinations of canopy structure. The plant material within each 10-cm layer was collected and separated into leaf blades, leaf sheaths plus stems, and panicles. Leaf area was measured with the automatic area meter, as described above. The light extinction coefficient was calculated from the cumulative leaf area index and the relative light intensity inside the canopy (Monsi and Saeki, 1953).

6. Measurement of root length density

We selected a total of three pairs of hills with average numbers of panicles from each replicate for measurements of root length density (cm cm⁻³). Three soil cores of 50 mm in diameter and 750 mm in length were taken between hills (15 cm space between hills) at the early ripening stage with a cylindrical tube (FV-493-1MB; Fujiwara Factory, Tokyo, Japan) in 2006. The roots were carefully washed and fixed with 70% ethanol until measurements of root length. Root length (cm) and density (cm cm⁻³) were determined with an image analysis system (WinRHIZO; Regent Instruments Inc., Quebec, Canada).
7. Statistical analysis

The analysis of variance was performed to detect the difference among treatments by ANOVA. The significance of mean values was analyzed using Tukey’s test (0.05) except for that of the light extinction coefficient and root sample which was analyzed using LSD (0.05) in 2006.

Results

1. Weather conditions

The weather conditions changed, fundamentally, as in an average year during each of the three years of the experiment (Fig. 1), but some differences were noted as follows. The daily mean temperature was higher in July and the monthly duration of sunshine was greater in July, August and October in 2002 than in 2005, 2006 and an average year (data for an average year were obtained as an averages for the 30 yr from 1971 to 2000). The monthly sunshine duration was longer in September and monthly precipitation was greater in May, July and August in 2005 than in 2002, 2006 and an average year. The monthly sunshine duration was shorter in June and July in 2006 than in 2002, 2005 and an average year.

2. Analysis of variance between chemical fertilizer application and cultivars and between year and cultivars

Preliminary analysis of variance showed significant interaction between chemical fertilizer and rice cultivars in 2002 growing season with and without fertilizer (Table 3). There was also significant interaction between year and cultivars grown with fertilizer in 2002, 2005 and 2006 (Table 4).

3. Plants with chemical fertilizer

(1) Comparisons of dry matter accumulation, grain yields, harvest indices and yield components

Among the cultivars examined in this study, in all three years, the newly released high-yielding cultivar Takanari consistently produced a significantly higher grain yield than the other cultivars, when grown with chemical fertilizer (Figs. 2A1, 2B1, 2C1). It was followed, in this ranking, by Asanohikari and Nipponbare (referred to as NA cultivars hereafter). The oldest cultivars, released more than 100 years ago, Sekitori and Aikoku (referred to as SA cultivars hereafter), had the lowest grain yield. Koshihikari was intermediate, in terms of grain yield, between the NA and SA cultivars. For the three years of the study, Takanari produced a

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Table 3. Analysis of variance of the effect of chemical fertilizer application on grain yield, dry weight and nitrogen accumulation in rice cultivars in 2002.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>GY (g m⁻²)</th>
<th>Dry weight (g m⁻²)</th>
<th>Accumulated N (g m⁻²)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Harvest</td>
<td>Heading increase</td>
<td>Harvest increase</td>
</tr>
<tr>
<td>Fertilizer (N)</td>
<td>**</td>
<td>**</td>
<td>**</td>
</tr>
<tr>
<td>Rice cultivar (C)</td>
<td>**</td>
<td>**</td>
<td>**</td>
</tr>
<tr>
<td>N × C</td>
<td>**</td>
<td>**</td>
<td>ns</td>
</tr>
</tbody>
</table>

* Increase in dry weight after heading to harvest; ** Increase in accumulated N after heading to harvest; ns, Not significant; * Significant at 0.05 probability level; ** Significant at 0.01 probability level.
significantly larger amount of dry matter than the other cultivars, followed by the NA cultivars, while the SA cultivars produced the least (Figs. 2A2, 2B2, 2C2). Koshihikari was intermediate, in terms of dry weight production, between the NA and SA cultivars. The harvest index was also consistently highest in Takanari in each of the three years (Figs. 2A3, 2B3, 2C3). Except in the case of Takanari, no large differences were observed among the cultivars in each of the three yr although the harvest index of Asanohikari in 2002 and that of Koshihikari in 2005 tended to be higher than those of the other cultivars.

With respect to yield components, the number of panicles per square meter was significantly larger in Asanohikari and Sekitori followed by Koshihikari, Nipponbare and Aikoku, in that order, while Takanari had the lowest number (Table 5). However, the number of spikelets per panicle was significantly higher in Takanari, a panicle weight-type cultivar, and resulted in a significantly higher number of spikelets per square meter than in other cultivars. Takanari was followed by Sekitori, and Nipponbare, Asanohikari and Aikoku with respect to the spikelet number per panicle, and Koshihikari had the lowest numbers. The percentage of filled grains was significantly higher in Asanohikari than in the other cultivars except in Nipponbare. In spite of the large number of spikelets in Takanari, the percentage of filled grains was not significantly lower than in all the other cultivars with the exception of Asanohikari. The 1,000-kernel weight was, however, heavier in Nipponbare and Asanohikari than in all the other cultivars. In this ranking, these cultivars were followed by Koshihikari, Aikoku, and Takanari, and Sekitori had the lightest 1,000-kernel weight.

**Table 4. Analysis of variance of the influence of year on grain yield, dry weight and harvest index in rice cultivars grown with chemical fertilizer in 2002, 2005 and 2006.**

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Grain yield (g m⁻²)</th>
<th>Dry weight (g m⁻²)</th>
<th>Harvest index (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Year (Y)</td>
<td>**</td>
<td>**</td>
<td>**</td>
</tr>
<tr>
<td>Rice cultivar (C)</td>
<td>**</td>
<td>**</td>
<td>**</td>
</tr>
<tr>
<td>Y × C</td>
<td>**</td>
<td>**</td>
<td>**</td>
</tr>
</tbody>
</table>

** Significant at 0.01 probability level.

**Fig. 2.** Grain yield at 14.5% moisture content (A1, B1 and C1), dry matter weight at harvest (A2, B2 and C2), and harvest index (A3, B3 and C3) in rice plants grown with chemical fertilizer in 2002 (A), 2005 (B) and 2006 (C). Columns with the same letters are not significantly different at the 5% level, as determined by Tukey’s test (n=5).
Table 5. Yield components in rice plants grown with chemical fertilizer in 2002.

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Panicle no. (m²⁻¹)</th>
<th>Spikelet no. (per panicle)</th>
<th>Total spikelets (×10³ m⁻²)</th>
<th>% filled grains</th>
<th>1,000-kernel weight (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Takanari</td>
<td>290.5 c</td>
<td>164.0 a</td>
<td>47.7 a</td>
<td>75.8 bc</td>
<td>21.3 b</td>
</tr>
<tr>
<td>Asanohikari</td>
<td>377.4 a</td>
<td>88.9 c</td>
<td>32.7 c</td>
<td>86.5 a</td>
<td>22.3 a</td>
</tr>
<tr>
<td>Nipponbare</td>
<td>362.6 ab</td>
<td>96.6 bc</td>
<td>34.2 c</td>
<td>81.2 ab</td>
<td>22.7 a</td>
</tr>
<tr>
<td>Koshihikari</td>
<td>368.2 a</td>
<td>85.6 c</td>
<td>32.0 c</td>
<td>70.7 cd</td>
<td>21.6 b</td>
</tr>
<tr>
<td>Aikoku</td>
<td>334.9 b</td>
<td>88.9 c</td>
<td>30.3 c</td>
<td>71.6 cd</td>
<td>21.6 b</td>
</tr>
<tr>
<td>Sekitori</td>
<td>377.4 a</td>
<td>108.1 b</td>
<td>40.5 b</td>
<td>67.0 d</td>
<td>19.2 c</td>
</tr>
</tbody>
</table>

Means with the same letters in a given column are not significantly different, as determined at the 5% level by Tukey’s test (n = 3).

Fig. 3. Dry weight (A1, B1, C1) at heading, time from transplanting to heading (A2, B2, C2), crop growth rate (A3, B3, C3), mean LAI (A4, B4, C4), and net assimilation rate (A5, B5, C5) from transplanting to heading in rice plants grown with chemical fertilizer in 2002 (A), 2005 (B), 2006 (C). Columns with the same letters are not significantly different at the 5% level, as determined by Tukey’s test (n=3). Heading time was determined when 50% of the plants started heading by visual observation. The difference in heading time among replication was not significant.
(2) Analysis of differences in dry matter accumulation

Dry weight at heading was heavier in Takanari and the NA cultivars than in Koshihikari and the SA cultivars. Nipponbare, whose heading date was latest, had the heaviest dry weight at heading (Figs. 3A1, 3B1, 3C1). The increase in dry weight from heading to harvest was significantly higher in Takanari than in the SA cultivars and tended to be higher than in the NA cultivars and in Koshihikari (Figs. 4A1, 4B1, 4C1). The increase in dry weight after heading was larger in Koshihikari than in the SA cultivars in 2005 and 2006, resulting in the greater dry matter accumulation in Koshihikari at harvest.

(3) Comparison of crop growth rates (CGRs) and analysis of CGRs among cultivars

To identify the factors responsible for differences in dry matter accumulation, we compared crop growth rates (CGRs) and the duration of growth before heading, as well as after heading, among cultivars. The time from transplanting to heading was longer in Nipponbare and shorter in Koshihikari (Figs. 3A2, 3B2, 3C2). The CGRs of
Takanari and the NA cultivars tended to be higher than those of Koshihikari and the SA cultivars (Figs. 3A3, 3B3, 3C3). Since we found no consistent differences, in terms of the net assimilation rate, among cultivars, the relatively higher mean leaf area index (LAI) might contribute to the higher CGRs in Takanari and the NA cultivars (Fig. 3).

The duration of ripening tended to be longer in the NA cultivars than in the SA cultivars although the difference was small in 2006. However, it was not longer in Takanari and Koshihikari than in the other cultivars. The CGR after heading was consistently higher in Takanari than in the other cultivars in each of the three yr (Figs. 4A3, 4B3, 4C3). Koshihikari had the next highest CGR. We failed to observe any consistent differences in CGR after heading between the NA and SA cultivars.

We compared dry matter production among cultivars at the late ripening stage, from 27 d after heading to harvest, in 2005. The increase in dry weight was larger in Takanari and in the NA cultivars, followed by Koshihikari. The CGR from 27 d after heading to harvest was significantly higher in Takanari than in the other cultivars (Fig. 5B) and resulted in the significantly larger increase in dry weight (Fig. 5A). The higher CGR in Takanari was mainly attributable to the significantly higher net assimilation rate (Fig. 5D). The CGR of Koshihikari was the second-highest due to the higher NAR.

(4) Canopy structure and the light extinction coefficient
We analyzed canopy structures and the light-intercepting characteristics of the canopy at the early ripening stage to clarify the factors responsible for the greater dry matter accumulation in three specific cultivars. The
stratified distributions of each organ of the three selected cultivars are shown in Fig. 6. The relative positions of leaves and panicles differed among the cultivars. The height of panicles was almost the same as that of the highest leaves of the canopy in Aikoku. By contrast, panicles were located below the tops of canopy leaves and were completely embedded within the canopy in Takanari and Nipponbare. The relative positions of panicles were lower in Takanari than in Nipponbare. The average light extinction coefficient of the canopy, as indicated by the slope of the regression line during the early ripening period, tended to be smaller in Takanari than in Nipponbare, and it was significantly smaller than in Aikoku (Fig. 7).

(5) Nitrogen accumulation

The newly released cultivar Takanari consistently accumulated the largest amount of nitrogen, as determined at harvest in 2002 and 2005 (Figs. 8A1, 8B1). The amount of accumulated nitrogen in Koshihikari and the NA cultivars tended to be larger than in the SA cultivars although that in Nipponbare tended to be smaller in 2002. We found no clear differences, in terms of accumulated nitrogen at heading, between the old and the new cultivars in both years examined (Figs. 8A2, 8B2). However, the amount of nitrogen accumulated from heading to harvest was significantly larger in Takanari in both 2002 and 2005 (Figs. 8A3, 8B3). Although the increase from heading to harvest in Nipponbare tended to be smaller in 2002, that in the SA cultivars tended to be the smallest in both 2002 and 2005. Moreover, the amount of nitrogen accumulated at the late ripening stage, from 27 d after heading to harvest, was significantly larger in Takanari followed, in this ranking, by Koshihikari and the NA cultivars (Fig. 9). The SA cultivars accumulated the smallest amounts of nitrogen during this period.

Fig. 7. Light extinction coefficients at the early ripening stage for three selected rice cultivars grown with chemical fertilizer in 2006. Measurements were made at 17 or 18 d after heading. Columns with the same letters are not significantly different at the 5% level, as indicated by LSD.

Fig. 8. Accumulated nitrogen (N) at harvest (A1, B1), at heading (A2, B2), and from heading to harvest (A3, B3) in rice plants grown with chemical fertilizer in 2002 (A), 2005 (B), respectively. Columns with the same letters are not significantly different at the 5% level, as determined by Tukey’s test (n=3).
(6) Root length density
We compared the root length density (cm cm⁻³) in each 12.5 cm layer of soil, as well as the total root length from the surface to a depth of 75 cm, among cultivars. Takanari had a significantly higher root length density in the 0 to 12.5 cm layer and from 12.5 to 25 cm in the upper soil layer than Nipponbare and Aikoku (Table 6). Takanari also had a significantly longer total root length, followed by Nipponbare, with Aikoku having the lowest.

4. Plants grown without application of chemical fertilizer
(1) Comparisons of dry matter accumulation, grain yields, harvest indices and yield components among cultivars
In the absence of chemical fertilizer in 2002, Takanari had a significantly higher grain yield than the NA cultivars and Koshihikari although significant interaction between chemical fertilizer and rice cultivars was observed. The SA cultivars had the lowest yield (Fig. 10A). However, higher dry weights at harvest were recorded for Nipponbare and Takanari, followed by Asanohikari and Koshihikari, while the oldest SA cultivars gave the lowest values (Fig. 10B). Moreover, we found no clear differences, in terms of harvest index, among cultivars even though Nipponbare tended to have the lowest index (Fig. 10C).

Fig. 9. Accumulated nitrogen (N) from 27 d after heading to harvest in rice plants grown with chemical fertilizer in 2005. Columns with the same letters are not significantly different at the 5% level, as determined by Tukey’s test (n=3).

Fig. 10. Grain yield at 14.5% moisture content (A), dry matter weight at harvest (B), and harvest index (C) for rice plants grown without chemical fertilizer in 2002. Columns with the same letters are not significantly different at the 5% level, as determined by Tukey’s test (n=3).

Table 6. Root length densities (cm cm⁻³) in each 12.5-cm layer of soil and total root lengths at the ripening stage in the rice plants with chemical fertilizer in 2006.

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Depth (cm)</th>
<th>Total root length (cm cm⁻³)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0–12.5</td>
<td>12.5–25</td>
</tr>
<tr>
<td>Takanari</td>
<td>10.9 a</td>
<td>4.8 a</td>
</tr>
<tr>
<td></td>
<td>(0.8)</td>
<td>(0.5)</td>
</tr>
<tr>
<td>Nipponbare</td>
<td>8.0 b</td>
<td>3.0 b</td>
</tr>
<tr>
<td></td>
<td>(0.6)</td>
<td>(0.3)</td>
</tr>
<tr>
<td>Aikoku</td>
<td>7.0 b</td>
<td>2.9 b</td>
</tr>
<tr>
<td></td>
<td>(0.5)</td>
<td>(0.8)</td>
</tr>
</tbody>
</table>

Means in each layer of soil with the same letters are not significantly different at the 5% level, as indicated by Least Significant Difference (LSD). Standard deviations are given in parenthesis (n = 3).
Takanari and resulted in the highest total number of spikelets per square meter. Unlike in the case with chemical fertilizer application, the percentage of filled grains was significantly lower in Takanari than in other cultivars. The 1,000-kernel weight was highest in Koshihikari and lowest in Takanari and Sekitori.

(2) Analysis of differences in dry matter accumulation
We analyzed the differences in dry matter accumulation by comparing dry weights at heading, as well as increases in dry weight from heading to harvest, among cultivars. At heading, the Takanari and NA cultivars had above-ground parts with the highest dry weights while Koshihikari and SA cultivars had the lowest (Fig. 11A1). By contrast, we found no consistent differences, in terms of the increase in dry weight from heading to harvest, among cultivars although Koshihikari had the largest and Aikoku had the smallest values (Fig. 11B1). Takanari did not produce the heaviest dry matter when grown without chemical fertilizer.

(3) Comparison of crop growth rates (CGRs) and analysis of CGRs
To identify the factors responsible for the differences in dry matter accumulation, we compared the CGRs, NARs and mean LAIs before heading, as well as after heading, among cultivars. The time from transplanting to heading was longer in the NA cultivars and Takanari than in the SA cultivars and Koshihikari (Fig. 11A2). The CGR before heading tended to be highest in Takanari, followed by the NA cultivars and Koshihikari. The SA cultivars had the lowest CGRs (Fig. 11A3).

After heading, the time from heading to harvest tended to be longer for the NA cultivars and Takanari than for Koshihikari and the SA cultivars (Fig. 11B2). Koshihikari had the highest CGR (Fig. 11B3) by keeping relatively large mean LAI (Fig. 11B4) and NAR (Fig. 11B5). The CGR in Takanari seemed comparable with the other cultivars except in Koshihikari although Takanari tended to maintained relatively high mean LAI and NAR.

(4) Nitrogen accumulation
Takanari tended to accumulate a larger amount of nitrogen, as measured at harvest, even without chemical fertilizer (Fig. 12A). Koshihikari and the NA cultivars followed in this ranking, while the SA cultivars came last. The amount of accumulated nitrogen at heading followed almost the same trend except in Koshihikari (Fig. 12B). However, the amount of nitrogen accumulated from heading to harvest tended to be larger in Koshihikari than in the other cultivars (Fig. 12C).

Discussion
In recent decades the grain yield of rice has increased markedly due, for example, to improvement of cultivars designed for higher yields and improvements in crop management for specific cultivars. In the present study, we compared grain yields and dry matter production among some old and some relatively new cultivars, which are representative of the early-to medium-maturity cultivars in the Kanto region of Japan, and a modern high-yielding cultivar, Takanari. Either with or without the application of chemical fertilizer, Takanari consistently produced the heaviest grain, followed by the NA cultivars (Figs. 2, 10). The SA cultivars produced the lightest grain. These results indicate that grain yield has improved with time as a result of plant breeding, irrespective of the application or absence of chemical fertilizer. High-yielding cultivars can still outperform older or traditional cultivars, even without nitrogen fertilizer or with reduced application of nitrogen fertilizer (Hasegawa, 2003). We attributed the differences in grain yield in the present study to differences in dry matter production although a higher harvest index also contributed to the highest grain yield in Takanari when grown with the chemical fertilizer (Fig. 2). An increase in harvest index results in an increase in grain yield in improved rice cultivars that produce heavier grain (Evans et al., 1984; Romyen et al., 1998; Kiniry et al., 2001). This observation was also reported for rice cultivars from the Kanto region of Japan (Ito, 1973).

However, in the cultivars used in the present study, we only found this observation to hold for Takanari when it was grown with chemical fertilizer. Previous studies demonstrated that the new cultivars had a greater capacity for dry matter production than the old ones (Tanaka et al., 1968; Hayami, 1982; Takeda et al., 1983). However, the reasons for this difference were not investigated in detail, in particular, with respect to the accumulation and efficiency of use of nitrogen. In the present study, we can conclude that dry matter production was greater in a cultivar that was released recently. We attempted to characterize the cultivars that we used in our research in terms of dry matter production and nitrogen accumulation. With respect to yield components, our results are consistent with those in a previous report in which Yang et al. (2002) showed that a higher number of spikelets per panicle do not necessarily result in poor grain filling in the recently released cultivar (Table 5).

The timing of achievement of maturity by a cultivar is determined by the time from sowing to heading. Heading times differed by about two weeks among the cultivars we selected for this study (Table 2). The timing affects the amount dry matter that is accumulated. Therefore, we compared dry matter production before and after heading for plants grown with and without the chemical fertilizer.

1. Plants grown with chemical fertilizer
We observed larger dry matter production before heading in Takanari and the NA cultivars (Figs. 3A1, 3B1, 3C1). The time from transplanting to heading was longer in Takanari and the NA cultivars than in the other cultivars. The difference in dry matter production...
Table 7. Yield components of rice plants grown without chemical fertilizer in 2002.

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Panicle no. (m−2)</th>
<th>Spikelet no. (per panicle)</th>
<th>Total spikelets (×10³ m⁻²)</th>
<th>% filled grains</th>
<th>1000-kernel weight (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Takanari</td>
<td>222.0 c</td>
<td>188.4 a</td>
<td>41.8 a</td>
<td>67.2 c</td>
<td>20.0 c</td>
</tr>
<tr>
<td>Asanohikari</td>
<td>246.1 bc</td>
<td>104.5 b</td>
<td>25.0 c</td>
<td>91.3 a</td>
<td>22.1 b</td>
</tr>
<tr>
<td>Nipponbare</td>
<td>277.5 a</td>
<td>99.6 b</td>
<td>27.0 bc</td>
<td>83.5 a</td>
<td>22.4 ab</td>
</tr>
<tr>
<td>Koshihikari</td>
<td>259.0 ab</td>
<td>98.4 b</td>
<td>25.7 c</td>
<td>85.4 ab</td>
<td>22.7 a</td>
</tr>
<tr>
<td>Aikoku</td>
<td>229.4 c</td>
<td>108.1 b</td>
<td>25.1 c</td>
<td>80.7 b</td>
<td>22.4 ab</td>
</tr>
<tr>
<td>Sekitori</td>
<td>270.1 ab</td>
<td>108.8 b</td>
<td>29.7 b</td>
<td>79.8 b</td>
<td>19.7 c</td>
</tr>
</tbody>
</table>

Means with the same letters in each respective column are not significantly different at the 5% level, as determined by Tukey's test (n = 3).

Fig. 11. Dry weight (A1) at heading, time from transplanting to heading (A2), crop growth rate (A3), mean LAI (A4), net assimilation rate (A5) from transplanting to heading, increase in dry weight from heading to harvest (B1), time from heading to harvest (B2), crop growth rate (B3), mean LAI (B4), and net assimilation rate (B5) from heading to harvest in rice plants grown without chemical fertilizer in 2002. Columns with the same letters are not significantly different at the 5% level, as determined by Tukey's test (n=3).
might have resulted from the long time between transplanting and heading (Figs. 3A2, 3B2, 3C2). However, the CGR tended to be higher in Takanari and the NA cultivars than in the SA cultivars during this period (Figs. 3A3, 3B3, 3C3). Thus, not only the length of time before heading but also the CGR might have been responsible for the greater dry matter production in Takanari and the NA cultivars. Both a higher LAI (Figs. 3A4, 3B4, 3C4) and maintenance of high NAR (Figs. 3A5, 3B5, 3C5), in spite of a higher LAI, resulted in a higher CGR in Takanari and the NA cultivars.

The production of dry matter after heading was largest in Takanari and smallest in the SA cultivars (Figs. 4A1, 4B1, 4C1). The higher CGR during ripening was responsible for the largest production of dry matter, after heading, in Takanari (Figs. 4A3, 4B3, 4C3). The CGR in Koshihikari tended to be higher than that in the SA cultivars. The shorter duration of the ripening period was responsible for the smaller production of dry matter in the SA cultivars than in the NA cultivars (Figs. 4A2, 4B2, 4C2). The difference, in terms of dry matter production, among cultivars was more marked at the late ripening stage (Fig. 5). It seems plausible that the differences among cultivars, in terms of dry matter production after heading, were caused mainly by the differences in dry matter production at the late ripening stage. Takanari was able to produce the heaviest dry matter as a result of the highest CGR. Koshihikari was able to produce heavier dry matter than SA cultivars because of its higher CGR.

The interception of light by the canopy has a significant effect on the CGR. We found clear differences in the relative positions of leaves and panicles among selected cultivars in the canopy (Fig. 6). The light extinction coefficient ($k$) tended to be smaller in Takanari and largest in Aikoku (Fig. 7). As reported previously, the $k$ value is lower in improved cultivars (Hayami, 1982; Ishii et al., 1986; Saito et al., 1990; Kiniry et al., 1999, 2001). The improved interception of solar radiation by the canopy might be responsible for the larger CGR before heading through the maintenance of a higher NAR, even when the LAI is large in Takanari and Nipponbare and after heading through the higher NAR in Takanari. The light extinction coefficient of the canopy is affected by the inclination and distribution of leaves and by the distribution of panicles in the canopy (Saito et al., 1990; San-oh et al., 2006a). The panicles protruded over the leaves in Aikoku. This affects the $k$ value (Saito et al., 1990) although we did not compare leaf angles in the present study.

Responsiveness to nitrogen has been recognized as a varietal characteristic (Osada, 1995) and as one of the most important factors in dry matter (biomass) production (Wang et al., 2006). There was a close correlation between the amount of accumulated nitrogen and dry weight at harvest (Fig. 13). Differences among cultivars, in terms of nitrogen accumulation, were marked after heading and, in particular, at the late ripening stage (Fig. 9). Cultivar-specific differences in nitrogen accumulation were also evident in an earlier study by Wada et al. (1990), but these differences were restricted to the early growth stage and no differences were apparent at the ripening stage. We identified a significant difference in nitrogen accumulation among cultivars at the late ripening stage.
accumulation among cultivars, even at the late stage of ripening. There were significant differences in both root length density (cm cm\(^{-3}\)) and total root length among cultivars at the ripening stage (Table 6). Root length density and total root length were significantly greater in Takanari than in other cultivars (Table 6). There was a close correlation between the total root length and the accumulation of nitrogen at the ripening stage (Fig. 14). These observations suggest that the characteristics of the root systems in the new cultivars, in particular Takanari, might be attributed to the greater accumulation of nitrogen (Ookawa et al., 2004; San-oh et al., 2006b) although the increase in root dry weight and root length did not result in the promotion in nitrogen absorption in some cultivars (Samejima et al., 2005). This hypothesis remains to be confirmed. It has been reported that the accumulation of nitrogen and movement of cytokinins from roots to shoots are enhanced in plants with a large amount of roots (Soejima et al., 1995; Ookawa et al., 2004; San-oh et al., 2006b). The characteristics of the large amount of roots might affect the duration of ripening through higher cytokinin activities (Oritani, 1995; Soejima et al., 1995; Ookawa et al., 2004). A comparison of the physiological activities of the roots of old and new cultivars might shed some light on these issues.

2. Plants grown without chemical fertilizer

Even though the plants were grown without chemical fertilizer, they could accumulate the relatively large amount of nitrogen probably from the soil and irrigation water (Kyaw et al., 2005), and the accumulated nitrogen was 69-80% of the plants with chemical fertilizer. As in the case of plants grown without chemical fertilizer, we observed larger dry matter production before heading in Takanari and the NA cultivars (Fig. 11A1). The actual process of the production differed from that in the plants with chemical fertilizer. The time from sowing to heading was longer for them than for the other cultivars. The enhanced dry matter production might have resulted from the long period of time from transplanting to heading (Fig. 11A2). The CGR also tended to be higher in Takanari and the NA cultivars than in the SA cultivars during this period (Fig. 11A3). Thus, not only the duration of the period before heading but also the CGR appear responsible for the greater production of dry matter in Takanari and the NA cultivars even though the differences between mean LAs and NARs, were not significant (Figs. 11A4, 11A5). The production of dry matter after heading differed in some cases from that plants that were grown without chemical fertilizer. Production was greatest in Koshihikari and smallest in the SA cultivars (Fig. 11B1), but there were no significant differences, in terms of dry matter production, among Takanari, the NA cultivars and the SA cultivars. The significantly greater production of dry matter and accumulation of nitrogen by Takanari during the ripening stage were not observed in the absence of chemical fertilizer, which is quite different from the plants with chemical fertilizer (Fig. 12). The smaller dry matter production after heading decreased the percentage of filled grain and a kernel weight significantly (Table 7). There have been many reports indicating that new and improved cultivars can maintain high levels of leaf nitrogen and, therefore, high rates of leaf photosynthesis, when top-dressing of nitrogen is applied, with a higher resultant grain yield than that of older cultivars (Takeda et al., 1983; Kuroda and Kumura, 1990; Sasaki and Ishii, 1992; Sasaki et al., 1996; Fukushima, 2007). The effects of the chemical fertilizer top-dressing might appear more remarkable in Takanari, the high-yielding modern cultivar.

Nitrogen accumulation tended to be smaller in SA cultivars than other cultivars (Fig. 12). There was a
Fig. 16. Difference in accumulated nitrogen (A) and dry weight (B) between rice plants with and without chemical fertilizer and apparent fertilizer nitrogen use efficiency for dry matter production (C) in 2002.

Apparent fertilizer NUE = (total above-ground dry weight of plants with chemical N fertilizer – total above-ground dry weight of plants without chemical N fertilizer) / total applied chemical N fertilizer.

The greatest increase in dry weight by the application of chemical N fertilizer, followed by Asanohikari (Fig. 16B). Apparent fertilizer NUE was the highest in Takanari and the smallest in Koshihikari.

Conclusion

In this study, in plants grown with chemical fertilizer, the greater accumulation of dry matter in the newly released cultivar Takanari resulted from a consistently higher increase in the accumulation of dry matter after heading, greater accumulation of nitrogen, and better light-intercepting characteristics than those of the other cultivars. Moreover, the apparent fertilizer NUE in Takanari was higher than in the other cultivars. These indicate that the new cultivar, in particular Takanari can use applied chemical fertilizer nitrogen very efficiently for the production of both dry matter and grain. Koshihikari, by contrast, had an elevated CGR, with enhanced accumulation of nitrogen during ripening, in the absence of chemical fertilizer but not under the conditions with chemical fertilizer. These characteristics of Koshihikari should be noted in efforts to decrease rates of nitrogen application. The mechanism responsible for the efficient accumulation of nitrogen under the conditions with and without chemical fertilizer remains to be investigated.

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** In Japanese with English summary.
*** In Japanese.
**** In German.