Varietal Differences in Morphological Traits, Dry Matter Production and Yield of High-Yielding Rice in the Tohoku Region of Japan

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Abstract: A two-year field experiment was conducted with japonica type high-yielding variety “Fukuhibiki,” indica type high-yielding variety “Takanari,” large grain type high-yielding variety “Bekoaoba” and conventional japonica type varieties “Akitakomachi” and “Hitomebore” in the Tohoku region (colder area of Japan). The panicles of Takanari and Bekoaoba located lower in the canopy, and the flag leaf of those varieties intercept more solar radiation, because the flag leaf was long and the first internode of panicle did not emerge above the lamina joint of the flag leaf in Takanari and the panicle hung lower in Bekoaoba. The three high-yielding varieties produced a large sink size, due to the large potential sink size in Takanari, the very large grain size in Bekoaoba and the rather large number of spikelets per panicle and somewhat large grain size in Fukuhibiki. Based on dry matter production, the three high-yielding varieties had a high harvest index, although there were little varietal differences in top dry weight at maturity. Unhulled rice weight of the three high-yielding varieties was heavier than that of other varieties at 30 days after heading (30 DAH). However, there were no varietal differences in the increase in unhulled rice weight from 30 DAH to maturity (later than 50 DAH), probably due to the continual growth of the grains located lower until the late ripening period in all varieties. In conclusion, the traits related to high yield varied greatly among varieties. However, the three high-yielding varieties had a large sink size, heavy unhulled rice weight at 30 DAH and high harvest index.

Key words: High-yielding variety, Indica type, Japonica type, Large grain, Rice, Tohoku region.

Super high-yielding rice having more than 10 t ha⁻¹ yield and for multipurpose use is needed to improve the food self-sufficiency and to use paddy fields efficiently in Japan. Many kinds of high-yielding rice varieties are grown in farm fields or are used for research. Elucidation of the mechanism of high-yielding in the varieties with differential yield related traits is important to attain a super high yield. In warm or temperate areas of Japan, indica type varieties, which often record high yields, have mainly been analyzed (Takeda et al., 1984a, 1984b; Saitoh et al., 1993; Xu et al., 1997). In colder areas of Japan such as the Tohoku region, japonica type and large grain type varieties often record high yields (Wang et al., 1997; Kuroda et al., 1999; Nagata et al., 2007). Mae et al. (2006) reported that a large grain type variety Akita63 produced a high yield due to high nitrogen use efficiency. However, the morphological traits and ripening process related to high yielding in the Tohoku region are not fully understood. The aim of this study was to clarify the varietal differences of yielding related traits in the Tohoku region. This is our first report on super high-yielding rice in the Tohoku region. Our second report (Fukushima et al., 2011) describes the cultivation technology and the strategies for super high-yielding rice.

Materials and Methods

1. Varieties used and cultivation method

In this study we used Fukuhibiki, a japonica type high-yielding variety in the Tohoku region (Higashi et al., 1994); Takanari, an indica type high-yielding variety for warmer areas in Japan (Imbe et al., 2004); Bekoaoba, a large grain type high-yielding variety in the Tohoku region (Nakagomi et al., 2006); and Akitakomachi and Hitomebore, conventional japonica type varieties in the Tohoku region. Field experiments were conducted in a paddy field (gray lowland soil) at the National Agricultural Research Center for Tohoku Region (Daisen city, Japan; 39°29’N, 140°29’E) in 2008 and 2009. The dates of seeding and
transplanting were 16 Apr. and 16 May in 2008 and 15 Apr. and 14 May in 2009. The seedlings at a leaf age of 4.0 to 5.0 were transplanted by hand, three seedlings per hill, at a hill spacing of 15 cm and a row spacing of 30 cm. A compound fertilizer containing 16% N, 16% P₂O₅ and 16% K₂O was applied as basal dressing at a rate of 6 g m⁻² of N, and ammonium sulfate was applied as topdressing at 2 g m⁻² of N about 20 days before heading. This amount of nitrogen is conventional in the rice cultivation in the Tohoku region, but is not enough to attain high rice yield in high-yielding varieties. A randomized complete block design with three replications was used. Each plot was approximately 25 m². In both years, 30% of the seedlings of Takanari were transplanted supplementally, since some of them died probably due to the coldness.

2. Morphological traits

Morphological traits of panicle, leaves and stems were measured following the method of Fukushima (2007). Six main shoots per plot were sampled about a week after heading. The number of branches and spikelets including degenerated spikelets was counted based on the definition of Matsuba (1991). The number of vascular bundles in the neck internodes was counted by microscopic observation of the cross section. The length and width of the first (flag), second and third leaves and the length and diameter of every internode were measured.

3. Vertical position of panicles in the canopy

Morphological traits of ten shoots selected randomly from each plot were measured under the paddy field condition at 30 days after heading (DAH). The length of the emerged first internode was defined as the length of first internode above the lamina joint of flag leaf (Fig. 1). Panicle height was defined as the height from the neck node to the highest part of the bending panicle. The length of flag leaf above the panicle was defined as the length from the highest part of the bending panicle to the top of the flag leaf.

4. Dry matter production

Twenty hills were harvested from each plot at the maximum tiller number stage (about 55 days after transplanting) and at the full heading stage (about 3 DAH). The shoots and panicles were counted. About 10% of the whole sample was then separated into leaf blades, leaf sheaths plus stems, and panicles. The green leaf blade area was measured with an automatic leaf area meter (LI-3000A, LI-COR, USA in 2008 and AAM-9, Hayashi Denko, Japan in 2009). The dry weight of each sample was determined after oven drying at 70°C to a constant weight. The leaf area index (LAI) was calculated as the leaf blade area of the sub-sample divided by the dry weight of the sub-sample, multiplied by the dry weight of the whole sample. The dried samples of the plant parts of each plot were powdered with a vibrating sample mill for measuring the content of nitrogen and nonstructural carbohydrate (NSC). The nitrogen content was measured by the Dumas combustion method (Varionax, Elementar, Germany). The NSC contents of the stems and leaf sheaths were measured by the gravimetric method (Ohnishi and Horie 1999).

5. Yield and yield components

Forty hills from each plot were harvested at 30 DAH and at maturity (more than 50 days after heading). All panicles harvested at 30 DAH and at maturity per plot were counted to calculate the number of panicles per area. After threshing, the total unhulled rice was weighed and the half of the unhulled rice and all of the leaves and stems were weighed after oven drying at 70°C to a constant weight to calculate the dry weights of unhulled rice, leaves and stems. The remaining half of the unhulled rice harvested at maturity was hulled and weighed as the gross hulled rice yield. Then, grains thicker than 1.7 mm in Takanari, thicker than 1.8 mm in Akitakomachi, Hitomebore and Fukuhibiki, and thicker than 2.0 mm in Bekoaoba were screened by a grain sorter and weighed as the hulled rice yield. Thousand grain weight was calculated using 20 g of the hulled rice. In this study, we focused mainly on the gross hulled rice yield, since it was more important for multipurpose use. The gross hulled rice yield, hulled rice yield and thousand grain weight were adjusted to 15% moisture content. The number of spikelets per area was calculated as the number of spikelets per panicle divided by the number of panicles per area. Percentage of ripened grain was calculated as the...
number of hulled grains per area divided by the number of spikelet per area. Sink size was defined as single grain weight multiplied by the number of spikelets per area.

6. Ripening process of individual grains

Two hills from each plot were harvested at 20, 30, 40 and 55 DAH, and six panicles with about average weight were selected. Then, five grains (hulled rice) from the top of the second and third primary branch from the top of the panicle were weighed as upper grains, and those from the base of the panicle were weighed as lower grains after oven drying at 70°C to a constant weight.

Results

1. Heading date and climatic conditions

The heading date was a little early in Akitakomachi and Fukuhibiki and very late in Takanari. Accordingly, the temperature during the ripening period was low in Takanari, especially from 30 DAH to maturity (Table 1). The solar radiation before heading was the highest in Takanari, but that after 30 days after heading was the lowest in Takanari.
2. Morphological traits of the panicles, leaves and stems

Panicle length was the longest in Takanari, and culm length was shorter in the three high-yielding varieties than in the two conventional japonica varieties, and it was the shortest in Takanari (Table 2). The number of differentiated and surviving spikelets per panicle was in the order of Takanari > Fukuhibiki > Bekoaoba > Akitakomachi > Hitomebore. The number of second and third order spikelets per panicle was larger in the three high-yielding varieties, and was extremely large in Takanari, which also had a large number of degenerated spikelets and a large number of large vascular bundles in the neck internode. These results show that the morphological traits of panicles of Takanari were very different from those of the other four varieties.

Varietal differences in morphological traits of leaves and stems in 2008 were similar to those in 2009, and only the data in 2008 are shown in Fig. 2. The leaf blade was the longest in the third leaf and next longest in the second leaf in Akitakomachi, Hitomebore, Fukuhibiki and Bekoaoba. In Takanari, the second and third leaf blades were the longest and the first leaf blade was relatively longer than that of the other four varieties. The leaf blade was wider at a higher leaf position in all varieties. The first and second leaf blades were noticeably wider in Takanari. By contrast, the width of leaf blade of Bekoaoba was not different from that of two conventional japonica varieties. The higher the internode position, the longer the internode in all varieties. The ratios of the lengths of the first and second internodes to the total length were higher in Takanari than in the other varieties. The higher the internode position, the thinner the internode in all varieties. The internodes at every position were the thickest in Takanari, particularly the upper internodes. By contrast, the lower internodes of Bekoaoba were thicker than those of the two conventional varieties, but the upper internodes were not thicker in Bekoaoba. These results indicate that, the upper leaves and upper internodes of Takanari were especially larger than those in the other four varieties.
3. Vertical position of panicles in the canopy

The first (neck) internode emerged higher above the lamina joint of the flag leaf (first leaf) in Akitakomachi and Hitomebore than in Fukuhibiki and Bekoaoba, and was below the lamina joint in Takanari (Table 3; Fig. 3). The panicle height shown in Fig. 1 was the highest in Takanari and the lowest in Bekoaoba, showing that the panicle of Bekoaoba hung lower. The length of the flag leaf was the longest in Takanari. As a result, the length of the flag leaf above the panicle was the longest in Takanari and the next longest in Bekoaoba. The flag leaf was erect in all varieties at the heading stage. At 30 DAH, however, it leaned considerably in Akitakomachi and Hitomebore, and a little in Fukuhibiki but remained erect in Takanari and Bekoaoba.

4. Dry matter production before the full heading stage

There was little varietal difference in dry matter production at the maximum tiller number stage, but the top dry weight and LAI at the full heading stage tended to increase as the heading date became later (Table 4). Leaf nitrogen (%) was slightly lower in the late heading variety Takanari, although there were no varietal differences in total nitrogen (g m⁻²) at the full heading stage. NSC (%) and g m⁻²) at the full heading stage tended to be higher in Bekoaoba and Takanari.

5. Yield and yield components

The number of shoots per area and the number of panicles per area were larger in the two conventional varieties than in the three high-yielding varieties (Table 4). The percentage of productive shoots was the lowest in Takanari. The number of spikelets per panicle was in the order of Takanari > Fukuhibiki > Bekoaoba > Akitakomachi = Hitomebore. The thousand grain weight was the heaviest in Bekoaoba (Table 5). Accordingly, the sink size (single grain weight x the number of spikelets per area) was larger in the three high-yielding varieties than in the two conventional varieties. The gross hulled rice yield tended to be higher in the three high-yielding varieties than in the two conventional varieties. Of the three high-yielding varieties, Fukuhibiki, which produced relatively small sink size, showed a high percentage of sink filling (gross hulled rice yield/sink size). Consequently, the hulled rice yield tended to be high in Fukuhibiki. Takanari and Bekoaoba produced a lot of poorly ripened rice.
6. Ripening process

Harvest index (unhulled rice weight at maturity/ top dry weight at maturity) was higher in the three high-yielding varieties than in the two conventional varieties, although there were no varietal differences in top dry weight at maturity (Table 6).

Dry matter increase during ripening period (ΔW) was slightly smaller in Takanari and Bekoaoba than in the other varieties. Especially dry matter increase during late ripening period (ΔW30-60) was smaller in the late heading variety Takanari than in the other four varieties. The weight of stems and leaves decreased in all varieties from heading to 30 DAH. Of them, the decrease of leaf and stem weight (ΔS0-30) tended to be larger in Bekoaoba.

### Table 4. Differences in dry matter production at the maximum tiller number stage and heading stage in five rice varieties.

| Year | Variety      | Maximum tiller number stage | Full heading stage |
|------|--------------|------------------------------|-------------------|
|      | Plant height | No. of shoots | LAI | Top dry weight | No. of panicles | LAI | Top dry weight | LAI | Total nitrogen | Leaf nitrogen | Sink size |
| 2008 | Akitakomachi | 58 bc          | 576 a | 2.25 a | 233 a | 431 b | 74.8 c | 3.65 a | 988 ab | 9.7 a | 2.50 a | 37.8 a | 215 a |
|      | Hitomebore   | 56 ab          | 667 a | 2.38 a | 237 a | 455 a | 68.2 b | 4.07 a | 902 ab | 8.9 a | 2.28 a | 39.2 a | 256 a |
|      | Fukuhibiki   | 62 c           | 553 a | 2.68 a | 260 a | 340 a | 62.0 b | 3.88 a | 863 ab | 9.0 a | 2.32 a | 40.0 a | 222 a |
|      | Takamari     | 52 ab          | 604 a | 2.79 a | 244 a | 309 a | 51.1 a | 4.79 a | 1063 b | 10.5 a | 2.24 a | 41.4 ab | 206 ab |
|      | Bekoaoba     | 60 bc          | 534 a | 2.33 a | 275 a | 315 a | 59.0 ab | 4.12 a | 991 ab | 10.0 a | 2.44 a | 47.2 b | 307 b |
| 2009 | Akitakomachi | 55 ab          | 487 a | 1.94 a | 200 a | 391 c | 80.5 b | 4.48 a | 835 a | 9.6 a | 2.69 b | 38.5 ab | 198 a |
|      | Hitomebore   | 51 a           | 545 a | 1.77 a | 176 a | 425 d | 78.6 b | 4.47 a | 832 a | 8.9 a | 2.46 ab | 37.3 a | 193 a |
|      | Fukuhibiki   | 60 b           | 429 a | 1.91 a | 182 a | 331 bc | 77.9 b | 4.79 a | 832 a | 9.9 a | 2.59 b | 40.3 abc | 208 ab |
|      | Takamari     | 51 a           | 472 a | 1.91 a | 157 a | 247 a | 53.2 a | 5.03 a | 974 b | 9.7 a | 2.21 a | 46.8 c | 296 c |
|      | Bekoaoba     | 57 ab          | 437 a | 1.91 a | 234 a | 292 ab | 66.9 b | 4.30 a | 858 ab | 9.5 a | 2.54 ab | 44.6 bc | 244 bc |

### Table 5. Differences in yield and yield components among five rice varieties at maturity.

| Year | Variety      | No. of panicles (m$^{-2}$) | No. of spikelets per panicle | Thousand grain weight (g) | Percentage of ripened grain (%) | No. of spikelets (m$^{-2}$) | Sink size (g m$^{-2}$) | Percentage of sink filling (%) | Gross hulled rice yield (g m$^{-2}$) | Hullled rice yield (g m$^{-2}$) |
|------|--------------|-----------------------------|-----------------------------|---------------------------|-------------------------------|-----------------------------|---------------------------|-------------------------------|-----------------------------------|----------------------------------|
| 2008 | Akitakomachi | 414 c                       | 76 a                        | 23.0 b                    | 92.3 b                        | 31634 ab                    | 726 a                      | 93.1 b                        | 690 a                             | 670 a                             |
|      | Hitomebore   | 464 d                       | 73 a                        | 23.6 b                    | 88.3 b                        | 33980 ab                    | 804 ab                     | 91.8 b                        | 738 ab                            | 709 a                             |
|      | Fukuhibiki   | 335 b                       | 107 b                       | 25.4 c                    | 86.4 b                        | 35739 b                     | 909 bc                     | 88.7 ab                        | 804 bc                            | 783 b                             |
|      | Takamari     | 295 a                       | 146 c                       | 21.9 a                    | 75.9 a                        | 42734 c                     | 934 c                      | 81.9 a                        | 765 bc                            | 709 a                             |
|      | Bekoaoba     | 301 ab                      | 97 b                        | 34.3 d                    | 70.3 a                        | 29219 a                     | 1007 c                     | 81.3 a                        | 818 c                             | 708 a                             |
| 2009 | Akitakomachi | 395 c                       | 82 a                        | 22.4 a                    | 91.6 b                        | 32186 a                     | 721 a                      | 94.3 b                        | 670 a                             | 600 a                             |
|      | Hitomebore   | 440 c                       | 75 a                        | 23.2 a                    | 90.2 b                        | 33804 b                     | 764 a                      | 92.9 b                        | 710 a                             | 689 a                             |
|      | Fukuhibiki   | 314 b                       | 105 b                       | 25.0 b                    | 90.4 b                        | 32957 a                     | 822 ab                     | 92.0 b                        | 756 a                             | 743 a                             |
|      | Takamari     | 251 ab                      | 166 c                       | 22.2 a                    | 76.2 a                        | 41372 b                     | 922 b                      | 82.1 a                        | 756 a                             | 702 a                             |
|      | Bekoaoba     | 278 a                       | 98 b                        | 34.6 c                    | 73.2 a                        | 27171 a                     | 941 b                      | 82.9 a                        | 780 a                             | 689 a                             |

Sink size=Single grain weight x No. of spikelets per area. Percentage of sink filling= Gross hulled rice yield/Sink size. Means followed by the same letters are not significantly different at the 0.05 level by Tukey’s test (n=3). *, Significant at the 0.05 level; **, Significant at the 0.01 level; NS, Not significant by ANOVA.
From 30 DAH to maturity, the weight of stems and leaves increased in Akitakomachi and Hitomebore, slightly increased in Fukuhibiki and Bekoaoba but continued to decrease in Takanari.

The unhulled rice weight at 30 DAH was heavier in the three-high yielding varieties than in the two conventional varieties. However, the increase in unhulled rice weight during the late ripening period did not vary with the variety. Consequently, the unhulled rice weight at maturity was heavier in the three high yielding varieties than in the two conventional varieties.

Fig. 4 shows the growth pattern of a single grain (hulled rice). The grain located in the upper part of the panicle (upper grain) matured earlier than that located in the lower part of panicle (lower grain) in all varieties. The upper grain matured earlier in Takanari than in the other four varieties. Although the lower grain was also apt to mature earlier in Takanari, it continued to grow after 30 DAH as in the other four varieties.

### Discussion

1. **Morphological traits of panicles, leaves and stems**

   Generally, Fukuhibiki, Takanari and Bekoaoba are classified as large panicle-type varieties. However, our results indicated that the branch structure of the panicles in Takanari was quite different from that in the other four

### Table 6. Differences in the ripening traits at different stages among five rice varieties.

| Year | Variety  | TDWm (g m⁻²) | Harvest index | ΔWH-30 (g m⁻²) | ΔW30-M (g m⁻²) | ΔW (g m⁻²) | ΔSH-30 (g m⁻²) | ΔS30-M (g m⁻²) | RW30 (g m⁻²) | ΔRW30-M (g m⁻²) | RWm (g m⁻²) |
|------|----------|--------------|---------------|----------------|----------------|------------|----------------|----------------|-------------|----------------|----------|
| 2008 | Akitakomachi | 1343 ab | 0.47 a | 244 a | 201 b | 445 ab | -134 a | 76 c | 503 a | 126 a | 629 a |
|      | Hitomebore | 1398 ab | 0.47 a | 242 a | 222 b | 465 ab | -154 a | 86 c | 523 ab | 136 a | 660 ab |
|      | Fukuhibiki | 1369 ab | 0.53 c | 285 a | 222 b | 507 b | -148 a | 56 c | 556 b | 166 a | 721 bc |
|      | Takanari   | 1450 b  | 0.51 b | 318 a | 70 a  | 387 ab | -120 a | -45 a | 624 c | 114 a | 738 c  |
|      | Bekoaoba   | 1323 a  | 0.55 d | 203 a | 129 ab | 332 a | -274 a | 14 b | 619 c | 116 a | 734 c  |
| 2009 | Akitakomachi | 1315 a | 0.46 a | 229 a | 251 a | 480 a | -112 ab | 116 b | 473 a | 135 a | 608 a  |
|      | Hitomebore | 1358 a | 0.48 ab | 340 a | 186 a | 526 a | -63 a | 62 ab | 522 ab | 124 a | 645 a  |
|      | Fukuhibiki | 1260 a  | 0.54 c | 296 a | 132 a | 428 a | -152 ab | 31 ab | 574 b | 101 a | 676 a  |
|      | Takanari   | 1351 a  | 0.50 b | 255 a | 123 a | 377 a | -130 ab | -7 a | 544 ab | 150 a | 674 a  |
|      | Bekoaoba   | 1251 a  | 0.56 c | 236 a | 157 a | 393 a | -186 b | 13 a | 556 ab | 144 a | 701 a  |

TDW, Top dry weight; TDWm, TDW at maturity; Harvest index, Unhulled rice weight at maturity/TDWm; ΔWH-30, TDW at 30 DAH–TDW at the full heading stage; ΔW30-M, TDWm - TDW at 30 DAH; ΔW, TDWm –TDW at the full heading stage; ΔSH-30, Stem and leaf weight at 30 DAH –stem and leaf weight at the full heading stage; ΔS30-M, Stem and leaf weight at maturity - stem and leaf weight at 30 DAH; RW30, Unhulled rice weight at 30 DAH; ΔRW30-M, RWm-RW30; RWm, Unhulled rice weight at maturity. Means followed by the same letters are not significantly different at the 0.05 level by Tukey’s test (n = 3). *, Significant at the 0.05 level; **, Significant at the 0.01 level; NS, Not significant by ANOVA.

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**Fig. 4.** Differences in single grain weights at different stages among five rice varieties in 2008.

DAH, days after heading; AKT, Akitakomachi; HIT, Hitomebore; FUK, Fukuhibiki; TAK, Takanari; BEK, Bekoaoba.

Bars indicate standard errors (n = 3).

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From 30 DAH to maturity, the weight of stems and leaves increased in Akitakomachi and Hitomebore, slightly increased in Fukuhibiki and Bekoaoba but continued to decrease in Takanari.

The unhulled rice weight at 30 DAH was heavier in the three-high yielding varieties than in the two conventional varieties. However, the increase in unhulled rice weight during the late ripening period did not vary with the variety. Consequently, the unhulled rice weight at maturity was heavier in the three high yielding varieties than in the two conventional varieties.

Fig. 4 shows the growth pattern of a single grain (hulled rice). The grain located in the upper part of the panicle (upper grain) matured earlier than that located in the lower part of panicle (lower grain) in all varieties. The upper grain matured earlier in Takanari than in the other four varieties. Although the lower grain was also apt to mature earlier in Takanari, it continued to grow after 30 DAH as in the other four varieties.
varieties (Table 2). The size of the upper leaves and internodes of Takanari was also clearly larger than that of the other four varieties (Fig. 2). These results show that the morphological traits of the panicles, leaves and stems in Takanari were quite different from those in the other four varieties and those in Bekoaoba and Fukuhibiki were relatively similar to those in conventional japonica varieties except for the large grain size in Bekoaoba.

The number of large vascular bundles in the neck internode was more than two times greater in Takanari than in the other four varieties (Table 2). Kamura (1995) suggested that the high conductive ability of the large number of vascular bundles might contribute to the high yield of indica varieties. In the Tohoku region, however, varieties with a small number of vascular bundles in the neck internodes, such as Fukuhibiki and Bekoaoba, showed high yield. These results suggest that the conductivity of neck internodes might limit the yield in warmer areas, where ripening duration is short, but it does not limit the yield in colder areas such as the Tohoku region, where ripening duration is long.

2. Vertical position of panicles in the canopy

Low vertical positioning of panicles in the canopy is effective for increasing dry matter production during the ripening period (Saitoh et al. 2002). In fact, most of the high-yielding rice varieties bred recently have low vertical positioned panicles (Peng et al. 2008, Takita 2009) and Takanari and Bekoaoba have panicles in the lower part of the canopy. In the present study we found that this was because the flag leaves were long and the first (neck) internode did not emerge above the lamina joint of the flag leaf in Takanari and the panicles bended down lower in Bekoaoba (Table 3; Fig. 3).

From a morphological point of view, the length of the emerged first internode was calculated as the difference between the length of the first internode and the length of the first leaf sheath (Fig. 1). The first internode of Takanari was only 10% shorter, but the first leaf sheath of Takanari was about 20% longer than those of the other four varieties (Table 3; Fig. 2). This result shows that the long first leaf sheath contributes to the low panicle position in Takanari. In other words, the position of the first leaf blade (flag leaf) in Takanari is higher, since the first leaf sheath is long in Takanari. The panicle of Bekoaoba bended down severely. This is probably not due to the heaviness of the panicle but to the easily bending of rachis, since the heavy panicle of Fukuhibiki and Takanari did not bend down as much as that of Bekoaoba.

We analyzed the effects of the vertical position of the panicle in the canopy on the increase of top dry weight ΔW. The varieties with a lower panicle position did not always show a large ΔW (Table 6), probably because the LAI of less than 5 in this experiment was too small to cause mutual shading (Table 4). In addition, the canopy structure during the early ripening period might be important although this study measured the morphological traits at 30 DAH. The effect of canopy structure during whole ripening period on ΔW should be investigated with higher nitrogen application.

3. Yield formation from the view of yield components

The number of spikelets per area was the largest in Takanari (Table 5), although the percentage of productive shoots was the lowest (Table 4) and the number of degenerated spikelets per panicle was the largest (Table 2). These results indicate that the large potential sink size might result in the large sink size in Takanari. Fukushima and Akiita (1997) and Fukushima (1999) suggested that the development of the primordia of tiller and primary rachis branches is more vigorous in indica varieties, including Takanari, than in japonica varieties. In this study, the development in indica type variety Takanari might be more vigorous than that in the japonica type varieties and the large grain-type variety. In contrast, Bekoaoba had a large sink size owing to the heavy grain (Table 5). Fukuhibiki had a large sink size due to the large number of spikelets per panicle and slightly large grains.

Regarding nitrogen-use efficiency, Yoshida et al. (2006) indicated that improved indica types including Takanari have high spikelet production efficiency per nitrogen content. Mae et al. (2006) also showed that the high nitrogen use efficiency of the large grain-type variety "Akita 63" resulted in the large sink size. In our study, total nitrogen (g m\(^{-2}\)) and leaf nitrogen (%) at the full heading stage hardly varied with the variety (Table 4). This result suggests that the three high-yielding varieties could produce a larger sink size in the condition of similar nitrogen content.

In conclusion, the three high-yielding varieties had a large sink size in common, although the process of sink formation varied greatly with the variety.

4. Yield formation from the view of dry matter production and ripening process

The three high-yielding varieties produced heavy unhulled rice at 30 DAH and had a high harvest index in common, although ΔW and the top dry weight at maturity (TDWm) was not heavier in the three high-yielding varieties than in the two conventional varieties (Table 6). These results imply that the remobilization of assimilate in the stem and leaf sheath during the early ripening period was important to obtain a high yield. Bekoaoba had a high NSC content and large ΔSN\(_{530}\). However, Fukuhibiki and Takanari did not have a large ΔSN\(_{530}\). These results suggested that the high remobilization ratio contributed to the high rice yield of Bekoaoba.

The duration of grain growth is longer in japonica type
than in indica type varieties (Yoshida and Hara 1977) and is not related to the grain size (Kato 1989). Our study indicated that the increase of unhulled rice weight during the late ripening period (ΔRW30-M) did not vary with the variety. This was probably because the lower grain continued to grow until the late ripening period in all varieties, although the upper grains matured earlier in the indica type variety Takanari (Fig. 4).

5. Conclusion

This study elucidated that the morphological traits and dry matter production related to a high yield varied greatly with the variety. However, the three high-yielding varieties had a large sink size, heavy unhulled rice weight at 30 DAA and high harvest index in common. Although the grain yields in the three high-yielding varieties did not differ significantly under standard nitrogen application in this study, Nagata et al. (2007) reported that Bekoaoba had the highest yield among the three high-yielding varieties under high nitrogen application in the Tohoku region. The effects of cultivation technology such as nitrogen application and planting density on the growth and yield of high-yielding varieties are reported in the accompanying paper (Fukushima et al., 2011).

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