ABSTRACT
Rice varietal differences were compared between japonica type (JAT) and indica type (INT) and between panicle number type (PNT) and panicle weight type (PWT) in terms of tiller and panicle development. Rice varieties PNT-JAT Hinohikari, PWT-JAT Akenohoshi, PNT-INT IR36, and PWT-INT Takanari were used in the field experiments. Tiller bud formation and tiller leaf emergence occurred slightly later in the PWT than in the PNT varieties. These parameters occurred slightly earlier in the INT than in the JAT varieties. The maximum number of tillers was greater in IR36 than in Takanari, Hinohikari, and Akenohoshi. The number of panicles per unit area (PN) was greater in IR36 and Hinohikari than in Akenohoshi and Takanari. The widths of the shoot apical meristem (SAM) just before panicle initiation were in the order of Akenohoshi > Takanari > IR36. The number of spikelets per panicle (SN) was in the order of Takanari = Akenohoshi > IR36 > Hinohikari. In conclusion, the PWT varieties, which had relatively wider SAM, presented with the promotion of main shoot development and the suppression of tiller development. Consequently, PN decreased and SN increased in PWT varieties. INT varieties presented with the promotion of tiller and rachis branch development, which resulted in increases in both PN and SN. These developmental factors may determine varietal differences in the total number of spikelets per unit area.

Abbreviations: CGR: crop growth rate; DEL: differences between the numbers of emerged leaves in the tiller and those in the main shoot; DIL: differences between the number of initiated leaves in the tiller and those in the main shoot; INT: indica type; JAT: japonica type; MLAI: mean leaf area index; NAR: net assimilation rate; PN: the number of panicles per unit area; SN: the number of spikelets per panicle; PNT: panicle number type; PWT: panicle weight type; SAM: shoot apical meristem; TSN: the total number of spikelets per unit area

Rice is a staple food in many Asian countries including Japan. Factors determining varietal yield differences must be identified to improve crop productivity. In Japan, factors determining yield have been mainly used in the analysis of nitrogen uptake within conventional Japonica varieties (Murayama, 1967; Wada, 1969). From around 1980, however, varieties with extremely large panicles have been receiving increasing attention as high yield varieties. These varieties present high yield because of their large sink size (Fukushima et al., 2011). Sink size is determined by hull size and by the total number of spikelets per unit area (TSN) expressed as the product of the number of panicle per unit area (PN) and the number of spikelets per panicle (SN). Varieties with extremely large hulls have large sink size and high yield in the cooler region of Japan (Fukushima et al., 2011; Mae et al., 2006). On the other hand, varieties with very high SN also have large sink size and high yield in the temperate and warmer regions of Japan (Jiang et al., 1988; Takeda et al., 1984; Xu et al., 1997). In the present study, varieties with standard hull sizes and very high SN were defined as panicle weight type (PWT) varieties. The japonica type varieties widely cultivated in Japan were classified as panicle number type (PNT) varieties. Of the PWT varieties, yield is higher in the indica type (INT) varieties such as Takanari and Hokuriku 193 than it is in the japonica type (JAT) varieties such as Akenohoshi and Momiroman (Yoshinaga et al., 2013). To date, most studies on high-yield rice varieties have focused only on dry matter production and nitrogen uptake. On the other hand, Ishikawa et al. (1999) suggested that many secondary rachis-branches in PWT varieties were more important for determining TSN and yield. However, tiller and panicle development, which determines TSN, has not been fully investigated. Development of the vegetative branch, tiller, determines PN, whereas development of the reproductive branch, rachis branch, determines SN. The PN and SN determine TSN. The purpose of this study was to elucidate the factors determining the varietal differences in TSN by comparing...
Materials and methods

Varieties

The Hinohikari, Akenohoshi, IR36, and Takanari rice varieties were used. Hinohikari is an elite japonica variety in the warm region of Japan. IR36 is an indica variety bred by IRRI in the Philippines. Akenohoshi is classified as a japonica variety (Shinoda et al., 1989). Takanari is classified as an indica variety (Imbe et al., 2004), although both are progenies of japonica—indica crosses. In the present study, we classified Hinohikari as a PNT-JAT variety, Akenohoshi as a PWT-JAT variety, IR36 as a PNT-INT variety, and Takanari as a PWT-INT variety.

Cultivation

The experiments were conducted in 2001, 2003, and 2005 in a paddy field (gray lowland soil) at NARO Kyushu Okinawa Agricultural Research Center (Chikugo City, Japan; 33°11′ N latitude, 130°31′ E longitude) located in the warm region of Japan. Seeding and transplanting occurred on May 23 and June 19 in 2001 and June 17 in 2003, and May 18 and June 21 in 2005, respectively. The number of emerged leaves at transplanting ranged from 4.0 to 5.5. One seedling was transplanted per hill by hand at a hill spacing of 16 cm and a row spacing of 15 cm. A compound fertilizer containing 16% N, 16% P₂O₅, and 16% K₂O was used. Six g N m⁻² was applied as basal dressing and 3 g N m⁻² was applied August 6 and 16 in 6 August 2001 and 15 in 2003, and August 7 and 18 in 2005 as the first and second topdressings, respectively. A randomized complete block design with three replications was used. The plots were ~30 m² in area.

Dry matter production

Dry matter production was measured during the vegetative (from early to late tillering) and reproductive (from late tillering to full heading) phases. Twenty-four plants per plot were harvested at early tillering (July 10), middle tillering (July 18), late tillering (July 25), and full heading (~7 d after heading) in every three years. The tillers or panicles were counted first. Three plants from each subsample were dissected into leaf blades, leaf sheaths with stems, and panicles. The green leaf blade area was measured with an automatic leaf area meter (LI-3000A, LI-COR Biosciences, Lincoln, NE, USA). The dry weight of each sample was determined after oven-drying at 80°C to a constant weight. The leaf area index (LAI) was calculated as the leaf blade area of the subsample divided by the total dry weight of the subsample multiplied by the dry weight of the total sample. The crop growth rate (CGR), the net assimilation rate (NAR), and the mean leaf area index (MLAI) were calculated using the top dry weight and the LAI.

Yield and yield components

The yield and yield components were determined by the method of Kusuda (1995). Eighty hills per plot were harvested. The fresh stems on the stumps were counted as the number of panicles per unit area per plot. The plants were fully dried outside. After threshing, the unhulled rice grains were weighed. Approximately 7% of the unhulled rice grains were extracted as a subsample using a riffle sampler (Tsutsui Scientific Instruments Co., Ltd., Tokyo, Japan). The spikelets in the subsample were counted with a multi-auto counter (Fujiwara Scientific Co., Ltd., Tokyo, Japan). The remaining unhulled rice grains were hulled and divided by grain sorter into grains >1.7 mm thick (mature brown rice) and <1.7 mm thick (immature brown rice). The gross brown rice yield (mature and immature), the yield (mature brown rice), and the thousand-grain weight of the mature brown rice were measured. Their values were adjusted to a standardized 15% moisture content. The TSN was calculated as the number of spikelets of the subsample divided by the weight of the subsample multiplied by the weight of total unhulled rice per unit area. The SN was calculated as the TSN divided by the PN. The percentage of ripened grain was calculated as the number of grains >1.7 mm thick per unit area divided by the TSN.

Shoot apical meristem (SAM)

Nine main shoots per variety were sampled every 2 d from transplanting to the spikelet initiation stage. After the number of emerged leaves was recorded, the shoot apex covered with several young leaves was extracted and fixed in formaldehyde–acetic acid–ethanol (FAA). Three materials per day were embedded in paraffin wax. The embedded materials were longitudinally sectioned at 15 μm thickness. After panicle initiation, successive cross-sections were cut at 15 μm thickness with a rotary microtome (RM2235, Leica Camera AG, Wetzlar, Germany). The materials were stained for microscopic observation according to the Sharman method (Sharman, 1943). The tissue sections were photographed with a digital camera (DXM1200, Nikon Corporation, Tokyo, Japan). The numbers of initiated leaves in the main shoot and the tillers were determined by the method of Fukushima and Akita (1997b). The differences between the number of initiated leaves in the tiller and those in the main shoot (DIL) were defined as follows: DIL in the Nth tiller = number of tiller and panicle development between PNT and PWT varieties and between JAT and INT varieties.
initiated leaves in the Nth tiller + (N + 2) – number of initiated leaves in the main shoot. This calculation is based on Katayama’s synchronous tiller development theory (Fukushima & Akita, 1997b; Katayama, 1951). The SAM width was measured by the definition of Yamazaki (1963) using image analysis software (WinRoof, Mitani, Japan). The initiation and development of panicle were observed according to Matsushima (1957). The readily identifiable phase immediately before the first bract initiation stage was used as the starting point of the reproductive phase. From the early primary branch initiation stage to the late secondary branch initiation stage, the upper five SAMs of the primary branch, which grew in the vertical direction, were observed in cross-section and the average widths of the major and minor axes were calculated. The number of samples at each stage ranged from one to three.

**Tiller development**

The fifth (T5), sixth (T6), seventh (T7), and eighth (T8) tillers were investigated. All of these became productive. The numbers of emerged leaves in the main shoot, T5, T6, T7, and T8 were recorded weekly in five plants per plot. The differences between the numbers of emerged leaves in the tiller and those in the main shoot (DEL) were defined as follows: DEL in the Nth tiller = number of emerged leaves in the Nth tiller + (N + 2) – number of emerged leaves in the main shoot. This calculation is based on Katayama’s theory (Goto & Hoshikawa, 1988; Katayama, 1951).

**Panicle structure**

Five panicles in the main shoot per plot were collected 5 d after full heading. The numbers of rachis branches and spikelets, including degenerated rachis branches and spikelets, were counted according to the methods of Matsuba (1991) and Fukushima (1999a). The numbers of large vascular bundles in the neck internodes were counted by microscopic observation of the cross-sections. The vascular ratio was defined as the number of large vascular bundles divided by the number of primary branches.

**Results**

**Regional differences of climate condition and yield**

The results of the present study in the warm region of Japan were compared with those of studies conducted in the cool and temperate regions (Fukushima et al., 2011; Yoshinaga et al., 2013). The transplanting date of this study was >1 month later than those in the cool and temperate regions. The transplanting date of this study was >1 month later than those in the cool and temperate regions.
temperate regions. Accordingly, the heading date in the present study was later than those for studies on the cool and temperate regions (Table 1). Compared to the other trials in cool and temperate regions, in the present study, temperatures were very higher and the sunshine duration was substantially shorter 1–30 d after transplanting. In addition, temperatures were higher and sunshine duration was longer 30–1 d before heading. In all regions, Takanari presented higher TSN and yield than the control variety. The yield of Takanari in the present study was clearly lower than that for Takanari raised in the temperate region and slightly higher than that for Takanari grown in the cool region. The yield of the control variety in the present study was slightly lower than that of the varieties in the cool and temperate regions.

**Dry matter production**

The NAR did not differ among varieties from the early to middle tillering stages (Table 2). However, the NAR of Hinohikari and Akenohoshi were higher than those of IR36 and Takanari from the middle tillering to the full heading stages. In contrast, the MLAI of IR36 and Takanari were greater than those of Hinohikari and Akenohoshi from the early to middle tillering stages. CGR did not differ among the varieties from the middle tillering to the full heading stages. Nevertheless, the CGR of IR36 and Takanari were higher than those of Hinohikari and Akenohoshi from the early to middle tillering stages. Consequently, the top dry weights of IR36 and Takanari were greater than those of Hinohikari and Akenohoshi at the full heading stage. However, the LAI did not differ among varieties.

**Yield and yield components**

The heading date was ~5 d earlier in Hinohikari, Akenohoshi, and Takanari than in IR36 (Table 3). The maximum number of tillers per unit area was in the order of IR36 > Takanari ≥ Hinohikari ≥ Akenohoshi. The percentage of productive tillers was in the order of Hinohikari ≥ Akenohoshi ≥ IR36 = Takanari. Consequently, the PN was greater in Hinohikari and IR36 than it was in Akenohoshi and Takanari. The SN was in the order of Takanari > Akenohoshi > IR36 > Hinohikari. TSN, which is the product of PN and SN, was in the order of IR36 = Takanari ≥ Akenohoshi ≥ Hinohikari. The thousand-grain weight and the percentage of ripened grain, which are both yield components determined after heading, significantly differed among the varieties. As a result, the gross brown rice yield and the yield were in the order of Takanari ≥ IR36 ≥ Akenohoshi ≥ Hinohikari.

**SAM development during the vegetative phase**

The developmental patterns of SAM, tiller, and panicle remained nearly the same for three years. Therefore, the results are mainly shown for 2003. The SAM width at transplanting was in the order of IR36 = Takanari = Akenohoshi > Hinohikari (Figure 1). The SAM width then gradually increased for all varieties. The SAM width from early tillering to flag leaf initiation was in the order of Akenohoshi > Takanari = Hinohikari > IR36.

**Tiller bud development**

A longitudinal shoot section is shown in Figure 2. The actual timing of first leaf initiation in T5 of Hinohikari was later than that predicted by Katayama’s theory (Figure 3). When T5 emerged, however, the actual number of initiated leaves was slightly greater than that predicted by Katayama’s theory because the leaves initiated on the tiller bud earlier than they did on the main shoot. The average DIL of Hinohikari during tiller bud development were −0.07 in T5, −0.16 in T6, −0.21 in T7, and −0.38 in T8. As the tiller bud order ascended, tiller buds developed later than the main shoots. The other three varieties exhibited almost the same developmental pattern. Varietal differences in tiller bud development were recognized in the early stages. The numbers of initiated leaves on the tiller bud were in the order of IR36 > Takanari > Hinohikari > Akenohoshi when the number of initiated leaves on the main shoot was equal for all varieties (Figure 4). The average DIL of T6 during tiller

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**Table 2. Varietal differences in rice dry matter production.**

| Variety   | NAR (g m⁻² d⁻¹) | MLAI (m² m⁻²) | CGR (g m⁻² d⁻¹) | Traits in full heading stage |
|-----------|----------------|--------------|----------------|-----------------------------|
|           | E-M | M-L | L-H | E-M | M-L | L-H | E-M | M-L | L-H | Date | Top dry weight (g m⁻²) | LAI (m² m⁻²) |
| Hinohikari| 11.4 a | 11.1 a | 5.7 a | 0.72 b | 1.75 b | 3.58 b | 8.2 b | 19.6 a | 20.4 a | 2-Sep | 1025  a | 4.93 a |
| Akenohoshi| 13.1 a | 10.5 a | 6.3 a | 0.62 b | 1.60 b | 3.36 b | 8.1 b | 17.2 a | 20.8 a | 1-Sep | 1013 a | 4.65 a |
| IR36      | 10.1 a | 7.2 b | 4.4 b | 1.23 a | 2.95 a | 4.72 a | 12.2 a | 21.5 a | 21.0 a | 5-Sep | 1171 b | 5.63 a |
| Takanari  | 11.0 a | 7.5 b | 4.9 b | 1.18 a | 2.80 a | 4.39 a | 12.8 a | 21.3 a | 21.4 a | 1-Sep | 1111 b | 5.18 a |

E: Early tiller stage (10-Jul), M: Middle tiller stage (18-Jul), L: Late tiller stage (25-Jul), H: Full heading stage. Each value in the table is an average of three years. Values in a column labeled with the same letter are not significantly different at 0.05 probability level by Bonferroni’s correction.
bud development were 0.15 in IR36, −0.06 in Takanari, −0.16 in Hinohikari, and −0.61 in Akenohoshi. The same varietal differences were observed for the other tiller bud positions.

### Tiller development

The positional differences in tiller bud development were succeeded by those for tiller development. The numbers of emerged leaves in Hinohikari were in the order of T5 ≥ T6 = T7 ≥ T8 when the number of emerged leaves on the main shoot was equal (Figure 5). These differences were maintained from tiller emergence to flag leaf emergence. The average DEL were 0.91 in IR36, 0.64 in Takanari, 0.33 in Hinohikari, and 0.08 in Akenohoshi. The same varietal differences were observed for the other tiller positions.

### SAM development during reproductive phase

The SAM widths immediately before the first bract initiation stage were in the order of Akenohoshi > Hinohikari = Takanari > IR36 (Table 4, Figure 7). After first bract initiation, SAM width and height increased rapidly and the primary branch primordia initiated from the SAM (Figure 8). The SAM width of the primary branch gradually increased then decreased as the second branch primordia initiated. The SAM widths of the primary branch were in the order of Takanari = Akenohoshi ≥ IR36 ≥ Hinohikari at the early primary branch initiation stage, and Takanari = IR36 = Akenohoshi > Hinohikari at the early secondary branch initiation stage (Figure 9).

| Variety   | Heading date | Maximum date (m^2) | Percentage of productive tillers (%) | PN (m^2) | SN | TSN (m^2) | Thousand grain weight (g) | Percentage of ripened grain (%) | Gross brown rice yield (g m^2) | Yield (g m^2) |
|-----------|--------------|--------------------|--------------------------------------|----------|----|-----------|--------------------------|--------------------------------|-----------------------------|---------------|
| Hinohikari| 25-Aug b     | 533                | b                                    | 70.9     | a  | 373       | 31400                    | b                               | 23.4 a                     | 650 c          | 636 b         |
| Akenohoshi| 24-Aug b     | 447                | b                                    | 64.8     | ab | 283       | 39400                    | ab                              | 22.3 ab                     | 680 bc         | 654 b         |
| IR36      | 30-Aug a     | 908                | a                                    | 45.3     | b  | 411       | 44000                    | c                               | 20.9 b                     | 75.3 b         | 745 ab        |
| Takanari  | 25-Aug b     | 554                | b                                    | 46.9     | b  | 260       | 43500                    | a                               | 21.3 b                     | 78.8 ab        | 772 a         | 724 a         |

Each value in the table is the average of three years. Values in a column labeled with the same letter are not significantly different at 0.05 probability level by Bonferroni’s correction.

**Table 3. Varietal differences in rice yield and yield components.**

**Figure 1.** Changes in SAM width during vegetative phase of four rice varieties in 2003.

**Figure 2.** Longitudinal section of SAM on the main shoot and tiller buds in Takanari.

Number of emerged leaves on the main shoot (MS) was 6.4. Number of initiated leaves on MS, T5, T6, and T7 were 10.25, 3.50, 1.75, and 0.00, respectively.
Panicle structure

The numbers of differentiated spikelets per panicle were in the order of Takanari = Akenohoshi > IR36 > Hinohikari (Table 4). The numbers of degenerated spikelets per panicle were slightly higher in the PWT than the PNT varieties and slightly higher in the INT than the JAT varieties. Nevertheless, these differences were not significant. As a result, the numbers of surviving spikelets were in the order of Takanari = Akenohoshi > IR36 > Hinohikari (Table 4). The numbers of primary branches were in the order of Takanari > Akenohoshi > Hinohikari = IR36. The numbers of secondary branches were greater in Takanari and Akenohoshi than in IR36 and Hinohikari. The numbers of tertiary branches were in the order of Takanari = Akenohoshi ≥ IR36 > Hinohikari. The numbers of quadric branches were in the order of IR36 = Takanari ≥ Akenohoshi > Hinohikari although the differences among them were not significant. The number of differentiated spikelets per panicle/the number of primary branches (DSN/PBN) was greater in Akenohoshi, Takanari, and IR36 than in Hinohikari. This result corroborated the order of the SAM widths of the primary branches (Figure 9). The numbers of large vascular bundles in the neck internode were in the order of Takanari > IR36 > Akenohoshi > Hinohikari. The vascular ratios were higher in the INT varieties IR36 and Takanari than in the JAT varieties Hinohikari and Akenohoshi.

Discussion

Effects of dry matter production and nitrogen uptake on TSN

In this study, TSN was in the order of IR36 = Takanari ≥ Akenohoshi ≥ Hinohikari and yield was in the order of Takanari ≥ IR36 ≥ Akenohoshi = Hinohikari (Table 3). These results support the hypothesis that TSN is mainly responsible for determining yield. The effects of dry matter production and nitrogen uptake on TSN were addressed to elucidate the factors determining varietal differences in TSN.

CGR and MLAI were significantly larger in the INT than the JPT varieties during the early vegetative phase (Table 2). Relative differences in CGR and MLAI decreased during the reproductive phase. On the other hand, there were no significant differences in dry matter production between the INT and the JAT varieties during both the vegetative and reproductive phases in the cool and temperate regions of Japan (Fukushima et al., 2011; Yoshinaga et al., 2013). In the present study, temperature during the vegetative phase was ~8–9° higher than that in the cool...
and temperate region studies (Table 1). Relative temperature differences among regions declined during the reproductive phase as temperatures increased in the cool and temperate regions. These results suggest that there were no major differences in dry matter production among varieties during the reproductive phase in this study, although the leaf areas of the INT varieties might enlarge faster and produce more dry matter under high-temperature conditions during the vegetative phase. Takai et al. (2006) reported that CGR during the late reproductive phase is closely correlated with TSN and yield, suggesting that canopy photosynthesis during the late reproductive period may be essential for yield increase. On the other hand, Ishikawa et al. (1999) indicated that CGR during the reproductive phase is not correlated with TSN, suggesting that panicle structure is more important for determining varietal differences in TSN. Several other studies also suggest that CGR during the reproductive stage is not closely correlated with TSN, although it might be slightly greater in high yield than control varieties (Fukushima et al., 2011; Jiang et al., 1988; Takeda et al., 1984; Xu et al., 1997; Yoshinaga et al., 2013). Nitrogen uptake is closely correlated with TSN in PNT-JAT varieties (Wada, 1969) and could be an important factor in determining the varietal differences in TSN. However, TSN is clearly greater in PWT-INT and PWT-JAT than in the control PNT-JAT varieties under the same nitrogen uptake levels (Kamiji et al., 2011; Yamamoto et al., 1991; Yoshinaga et al., 2013). In conclusion, dry matter production and nitrogen uptake cannot fully explain the large varietal differences in TSN. Therefore, tiller and panicle development may be a more important candidate in determining varietal TSN differences.

Effects of tiller development on PN

Tiller and tiller bud development determine PN. Katayama (1951) proposed the synchronous tiller development theory in which the Nth tiller emerges almost simultaneously with the (N + 3)th leaf in the main shoot and the tiller leaf emergence rate is the same as that of the main shoot (Hanada, 1993). Later, Sekiya (1958), Nishikawa and Hanada (1959), and Yamazaki (1960) suggested that the Katayama’s theory is attributed to the regular formation of tiller bud: the Nth tiller bud is formed when the Nth leaf of the main shoot has fully emerged. These studies focused mainly on just a few JAT-PNT varieties. Nevertheless, Fukushima and Akita (1997b) showed that tiller buds developed faster in INT than JAT varieties.

In the present study, there were small, regular gaps in tiller development among varieties occurring at the early stage of tiller bud formation (Figures 4 and 6). The INT and PNT varieties presented with comparatively faster tiller bud development. Consequently, their tiller leaves emerged relatively earlier. This study also showed that higher-order tiller development happened later as the SAM width in the main shoot enlarged. For the same reason, the large SAM in PWT varieties could delay tiller development.

These varietal differences in tiller and tiller bud development may account for the maximum number of tillers per unit area. On the other hand, the percentage of productive tillers was lower in INT than JAT varieties as reported by Kubota et al. (1988) and Ishikawa et al. (1999). There could be a compensation effect for reducing excess tillers in INT varieties during tiller development. Nevertheless, the rapid tiller bud and tiller development is inferred to be important for increasing PN.

Effects of panicle development on SN

The SAM size at the panicle initiation stage is considered important for determining panicle branch structure. Yamagishi et al. (1992) reported that SAM size at the panicle initiation stage was correlated with SN. Fukushima and Akita (1997a) stated that the panicle vascular systems were substantially different between the japonica variety Musashikogane and the indica variety IR36. Consequently, the authors developed a hypothesis that the development of high-order rachis branches occurred more rapidly in INT varieties with high vascular ratios than in JAP varieties with low vascular ratios. Fukushima (1999a, 1999b) elucidated that the SAM size at the panicle initiation stage was more closely correlated with the primary branch number than...
the SN and that INT varieties with high vascular ratios did not always have large SAM at the panicle initiation stage but produced large numbers of high-order rachis branches.

In the present study, with the increase in the SAM width of the main shoot, the numbers of spikelets per panicle increased in the comparison between the JAT varieties Hinohikari and Akenohoshi and in the comparison between the INT varieties IR36 and Takanari. However, these differences were not observed in the comparison between the JAT varieties with low vascular ratios and the INT varieties with high vascular ratios (Table 4). Although the SAM width of the main shoot was smaller in IR36 than in Hinohikari, the SAM width of the primary rachis branch, the DSN/PBN, and the number of spikelets per panicle in Takanari were almost the same as those in Akenohoshi. In addition, the number of quadric branches proceeded faster in INT varieties with high vascular ratios than in JAP varieties with low vascular ratios. In conclusion, both the accelerated rachis branch development in INT and the large SAM width of the main shoot were considered important for increasing SN.

**Effects of tiller and panicle development on TSN**

The purpose of this study was to elucidate the factors determining the varietal differences in TSN, which is the product of PN and SN. Akenohoshi, a PWT-JAT variety,
which had a large SAM during the vegetative phase, suppressed tiller development but produced the large SAM just before panicle initiation, which resulted in few PN but very many SN. On the other hand, the PWT-INT variety Takanari, which had a moderate SAM size, presented with slight tiller promotion and high rachis branch promotion. Consequently, it had a moderate number of tillers, few PN, and very many SN. The PNT-INT variety IR36 had a small SAM during the vegetative phase and presented with tiller and high-order branch development promotion. As a result, it had very many tillers and many PN and SN. The promoted tiller and rachis branch development in INT varieties might be mutually correlated, as suggested by Fukushima and Akita (1997b). Although the numbers of spikelet per panicle in the main shoots did not significantly differ between Akenohoshi and Takanari (Table 4), SN (=TSN/PN) was significantly greater in Takanari than in Akenohoshi (Table 3). Probably because the relatively promoted tiller development in Takanari resulted in a comparatively greater number of spikelets per panicle in tillers.

In conclusion, PWT varieties, which had larger SAM, presented with suppressed tiller development and promoted main shoot development. As a result, their PN decreased and their SN increased. INT varieties presented with promoted tiller and rachis branch development and increases in both PN and SN. These developmental factors may determine varietal differences in TSN. A limitation of this study was that only a few rice cultivars were tested. Therefore, future research should attempt to corroborate the findings of the present study using several varieties and also evaluate the genetic parameters.

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Disclosure statement

No potential conflict of interest was reported by the author.

References

Fukushima, A. (1999a). Branching structure of panicle with reference to the number of spikelets in rice. *Japanese Journal of Crop Science, 68*, 71–76.
Fukushima, A. (1999b). Differentiation and development of the branching of panicle with reference to the number of spikelets in rice. *Japanese Journal of Crop Science, 68*, 77–82.
Fukushima, A., & Akita, S. (1997a). Varietal difference of the course and differentiation time of large vascular bundles in the rachis in rice. *Japanese Journal of Crop Science*, 66, 24–28.

Fukushima, A., & Akita, S. (1997b). Differential developmental pattern of tiller bud in rice cultivars. *Japanese Journal of Crop Science*, 68, 202–207.

Fukushima, A., Shiratsuchi, H., Yamaguchi, H., & Fukuda, A. (2011). Varietal differences in morphological traits, dry matter production and yield of high yielding rice in the Tohoku region of Japan. *Plant Production Science*, 14, 47–55.

Goto, Y., & Hoshikawa, K. (1988). Tilling behavior in *Oryza sativa* L. 1. Growth correlation between the main stem and tillers. *Japanese Journal of Crop Science*, 57, 496–504.

Hanada, K. (1993). Tillers. In T. Matsuo & K. Hoshikawa (Eds.), *Science of the rice plant. 1. Morphology* (pp. 225–258). Tokyo: Food and Agriculture Policy Research Center.

Ime, T., Akama, Y., Nakane, A., Hata, T., Ise, K., Ando, I., … Koga, Y. (2004). Development of multipurpose high-yielding rice variety “Takanari”. *Bulletin of the National Institute of Crop Science*, 5, 35–51.

Ishikawa, T., Fujimoto, H., Kabaki, N., Maruyama, S., & Akita, S. (1999). Dry matter production before heading and determination of number of spikelets of rice cultivar “Takanari”. *Japanese Journal of Crop Science*, 68, 63–70.

Jiang, C. Z., Hirasawa, T., & Ishihara, K. (1988). Physiological and ecological characteristics of high yielding varieties in rice plants I. Yield and dry matter production. *Japanese Journal of Crop Science*, 57, 132–138.

Kamiji, Y., Yoshida, H., Palta, J. A., Sakurateda, T., & Shiraiwa, T. (2011). N applications that increase plant N during panicle development are highly effective in increasing spikelet number in rice. *Field Crops Research*, 122, 242–247.

Katayama, T. (1951). *Studies on tilling of rice, wheat, and barley* (pp. 1–117). Tokyo: Yokendo.

Kubota, F., Tanaka, N., & Arima, S. (1988). Study on productive ecology of high yielding japonica-indica hybrid cultivar “Suweon258”. *Japanese Journal of Crop Science*, 57, 287–297.

Kusuda, O. (1995). Improvement of survey method in yield and yield components on rice plants. *Syokutou*, 29, 138–143.

Mae, T., Inaba, A., Keneta, Y., Masaki, S., Sasaki, M., Aizawa, M., … Makino, A. (2006). A large-grain rice cultivar, Akita 63, exhibits high yields with high physiological N-use efficiency. *Field Crops Research*, 97, 227–237.

Matsuba, K. (1991). The morphogenetic mechanism of formation of the panicle branching system in rice plants. (*Oryza sativa* L.). *Bulletin of the Chugoku National Agricultural Experiment Station*, 9, 11–58.

Matsushima, S. (1957). Analysis of developmental factors determining yield and yield prediction in lowland rice. *Bulletin of the National Institute of Agricultural Sciences*, A5, 1–271.

Murayama, N. (1967). Nitrogen nutrition of rice plant. *Japan Agricultural Research Quarterly*, 2(2), 1–5.

Nishikawa, G., & Hanada, K. (1959). Studies on branching habits in crop plants. 1. On the differentiation and development of tillering buds in lowland rice seedlings grown under different seeding spaces. *Japanese Journal of Crop Science*, 28, 191–193.

Sekiya, F. (1958). Studies on the tillering primordium and tillering bud in rice seedlings. 7. Developmental process of tillering primordium and tillering bud. *Japanese Journal of Crop Science*, 27, 75–76.

Sharman, B. C. (1943). Tannic acid and iron alum with safranin and orange G in studies of the shoot apex. *Stain Technology*, 18, 105–111.

Shinoda, H., Toriyama, K., Fujii, K., Shibata, M., Yamamoto, T., Sekizawa, K., … Yamada, T. (1989). A high-yielding rice variety “Akenohoshi”. *Bulletin of the Chugoku National Agricultural Experiment Station*, 4, 13–27.

Takai, T., Matsuura, S., Nishio, T., Ohsumi, A., Shiraiwa, T., & Horie, T. (2006). Rice yield potential is closely related to crop growth rate during late reproductive period. *Field Crops Research*, 96, 328–335.

Takeda, T., Oka, M., Uchimura, K., & Agata, W. (1984). Characteristics of dry matter and grain production of rice cultivars in the warmer part of Japan. III. Comparison between dry matter production of Japanese and new Korean cultivars. *Japanese Journal of Crop Science*, 53, 22–27.

Wada, G. (1969). The effect of nitrogenous nutrition on the yield-determining process of rice plant. *Bulletin of the National Institute of Agricultural Sciences*, A16, 27–167.

Xu, Y., Ookawa, T., & Ishihara, K. (1997). Analysis of the dry matter production process and yield formation of the high-yielding rice cultivar Takanari, from 1991 to 1994. *Japanese Journal of Crop Science*, 66, 42–50.

Yamagishi, J., Yajima, T., Etoh, K., Suzuki, H., & Inanaga, S. (1992). Relation of number of spikelets per panicle to the characteristics of shoot and the size around growing point at panicle initiation stage in rice varieties. *Japanese Journal of Crop Science*, 61, 568–575.

Yamamoto, Y., Yoshida, T., Enomoto, T., & Yoshikawa, G. (1991). Characteristics for the efficiency of spikelets production and the ripening in high-yielding Japonica-Indica hybrid and semidwarf Indica rice varieties. *Japanese Journal of Crop Science*, 60, 365–372.

Yamazaki, K. (1960). Studies on the morphogenesis of crop plants under different growing conditions II. The formation of lateral buds in rice and wheat. *Japanese Journal of Crop Science*, 28, 262–265.

Yamazaki, K. (1963). Studies on leaf formation in rice plants II. The development of leaves in relation to their position on a stem. *Japanese Journal of Crop Science*, 31, 81–88.

Yoshinaga, S., Takai, T., Arai-Sanoh, Y., Ishimaru, T., & Kondo, M. (2013). Varietal differences in sink production and grain-filling ability in recently developed high-yielding rice (*Oryza sativa* L.) varieties in Japan. *Field Crops Research*, 150, 74–82.