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Effects of Top Dressing on Growth and Panicle Dry Weight as Affected by Soil Water Stress at the Early Panicle-Development Stage in Rice (*Oryza sativa* L.)

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Abstract: Rice yield is reduced by a short period of water stress at the early panicle-development stage. This study was conducted to examine the factors that reduce the panicle dry weight of rice subjected to water stress and the alleviating effects of top dressing after the stress. Akihikari, Nipponbare and Akebono were grown in 4-L pots under submerged soil conditions. One half of the pots were subjected to the same degree of water stress during panicle development and the other half was grown without water stress. On the day after the stress treatment, chemical fertilizer was applied to one half of each water treatment. Panicle dry weight at maturity was decreased by water stress and the top dressing after the stress alleviated the decrease. The top dressing increased panicle dry weight under the two water treatments in all three cultivars. Increase of panicle dry weight was dependent on that of total dry weight from drainage to full heading, from full heading to maturity, and from drainage to maturity. Leaf area duration (LAD) and net assimilation rate (NAR) were responsible for changes in total dry weight. Effect of water stress was prominent before full heading, while that of top dressing after full heading. It was concluded that reduction of LAD and NAR may be involved in reduction of panicle dry weight by water stress at the early panicle-development stage, and that top dressing after the water stress may mitigate the effect of water stress on panicle dry weight through the improvement of LAD and NAR.

Key words: Leaf area duration, Net assimilation rate, Rice, SPAD, Total dry weight.

Rice yield is reduced by intermittent water stress due to irregular rainfall and lack of irrigation water in drought-prone areas (Garrity et al., 1986; Lafitte et al., 2006). Various studies on rice yield have indicated that the effect of temporary water stress on yield varies on the plant developmental stage when water stress occurs (O'Toole, 1982; Tsuda et al., 1994; Tsuda and Hiraiwa, 1996; Pantuwan et al., 2002). Meiosis and heading stages are most critical established because water stress at these stages leads to high sterility thus a large yield reduction (O'Toole, 1982; Tsuda et al., 1994). On the other hand, less attention has been paid to water stress at early panicle-development stage since its effects on yield are small. However, the yield decreases due to the water stress at the early panicle-development stage (Tsuda and Takami, 1991; Tsuda et al., 1993, 1994).

Shoot apices produce primordia of primary and secondary branches, then spikelet primordia successively after panicle initiation in rice (Hoshikawa, 1975). These

developmental stages are considered to be a vegetative process rather than reproductive process in the sense that there are no specific processes such as pollen formation. At these stages, water status of young panicle was similar to that of vegetative organ under the soil water stress conditions, whereas panicle water potential at meiosis stage was maintained higher than leaf water potential (Tsuda and Takami, 1993; Tsuda et al., 1994). We considered that yield responses could be related to vegetative responses such as dry matter production when rice plants were subjected to water stress at early panicle-development stages.

The maintenance of leaf area under intermittent water stress is considered to alleviate yield reduction since it may assure photosynthesis after the water stress (Turner, 1982; Tuberosa et al., 2003). Rice plants do not increase leaf area after the flag leaves expanded, and the leaf area remained after water stress at the early panicle-development stage may be related to yield. In general, top dressing of fertilizer

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Abbreviations: CWS, cumulative water stress; DAS, days after sowing; FN, flooded plot without top dressing; FT, flooded plot with top dressing; LAD, leaf area duration; NAR, net assimilation rate; SN, stress plot without top dressing; ST, stress plot with top dressing.

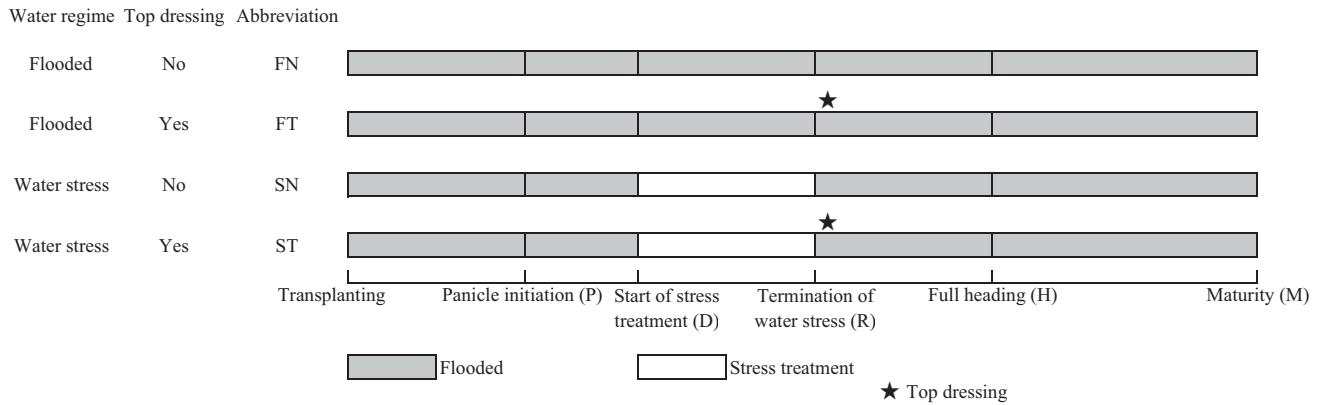


Fig. 1. Schematic description of water stress treatment and top dressing.

Four plots were allotted to each cultivar. FN and FT indicate flooded plot without and with top dressing, and SN and ST stress plot without and with top dressing. Water was drained at the early panicle-development stage (D), and water stress was terminated by flooding when cumulative water stress (CWS) exceeded 5.5 MPa d (R) in SN and ST. Top dressing was applied to FT and ST plots at R.

increases and maintains the leaf area, and photosynthesis (Matsushima, 1973; Cho and Murata, 1980; Okumura et al., 1982; Sasaki and Ishii, 1992), so may alleviate the damage due to water stress.

In this study, we examined whether changes in panicle dry weight due to water stress at the early panicle-development stage could be related to those of leaf area and net assimilation rate, and whether top dressing after the stress alleviates the damage in rice.

Materials and Methods

Three rice cultivars Akihikari, Nipponbare and Akebono, which are early, medium and late maturing respectively, were used. Germinated seeds were planted at a rate of one seed per hole in Minoru pot (Minoru Industrial Co. Ltd.) on 25 May in 2006 and grown at the Experimental Field, Okayama University. Each seedling was planted in a 4-L pot filled with sieved soil of the paddy field on 15 June. Controlled availability fertilizer (LP140E80, N:P:K=14:14:14) was incorporated into the soil at a rate of 7g per pot as a basal fertilizer. The pots were kept under a rain shelter the roof of which was covered with transparent vinyl, and the plants were grown under submerged soil conditions.

Leaf age, number of stems and plant length were measured in five plants of each cultivar. At the panicle initiation decided based on the leaf age: 10, 13 and 14 in Akihikari, Nipponbare and Akebono respectively, several tillers were collected for the observation of shoot apices every two or three days. After confirming the secondary branch primordia by the anatomical observation under a stereoscopic microscope in each cultivar, a half of the pots were drained and not watered thereafter, and referred to as water stress plot (Fig. 1). However, exception, the small amount of water was applied to prevent extreme water stress or plant death. The other half of the pots were kept

under submerged soil conditions, and were referred to as the flooded plot.

After the drainage, leaf water potential (Ψ) was measured on the uppermost expanded leaf using a pressure chamber before sunrise. The number of plants measured was two plants for each cultivar in the flooded plot, and nine for Akihikari and ten for Nipponbare and Akebono in water stress plot. Using measured values of Ψ , cumulative water stress (CWS, MPa d) as an index of soil water stress proposed by Tsuda (1988) was calculated: $CWS = \sum(\Psi_{0i} - \Psi_i)$, where Ψ_{0i} and Ψ_i were Ψ for flooded and water stress plots on i -th d after the drainage, respectively. When a value of CWS exceeded 5.5MPa d, pots of water stress plot were watered to terminate water stress treatment, and kept under submerged conditions to maturity that was 42 or 43 d after full heading. On the day water stress was terminated, chemical fertilizer (N: P: K=16: 16: 16) was top dressed on a half of each of flooded and water stress pots at a rate of 3 g per pot. These pots were referred to as top dressed and pots not top dressed as not top dressed. The experiment was conducted as a completely randomized design with three factors; cultivar, water treatment and top dressing.

Leaf chlorophyll was measured with a chlorophyll meter (SPAD-502, Konica Minolta Sensing, Inc.) for five plants in each plot. The measurements were conducted on the uppermost three leaf blades on a tiller of an individual plants. Values of three readings on the position 1/4, 1/2 and 3/4 from the base to tip along a leaf blade were averaged. The measurements were conducted at drainage of water, full heading and maturity.

Five plants in each plot were harvested at drainage and at maturity, and three plants at full heading. Harvest at maturity was conducted 42 or 43 d after the full heading. Plants were separated into leaf blade, stem including leaf sheath (hereafter referred to as stem) and dead part, and

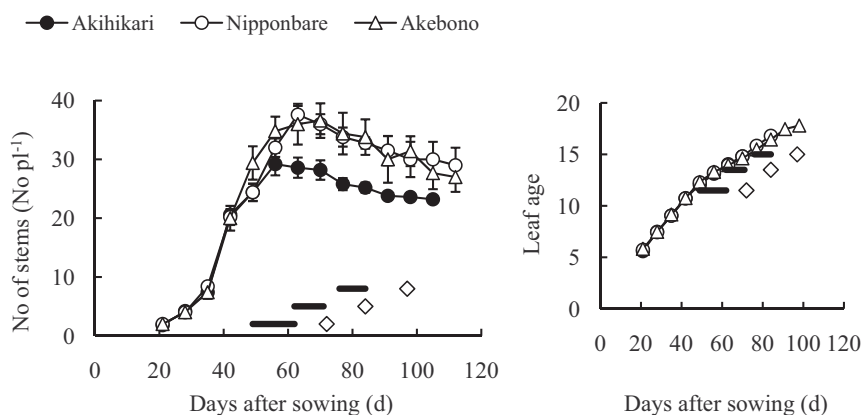


Fig. 2. Changes in stem number per plant and leaf age in flooded without top dressing (FN) in the three rice cultivars and the water stress periods. Values and vertical bars are means and standard errors of five plants. Horizontal bars and empty lozenges indicate water stress period and full heading time, and they are for Akihikari, Nipponbare and Akebono from left to right.

panicle when existed. The leaf area of individual plants was measured with an automatic area meter (AAM-8, Hayashi Denko Co. Ltd.). Each plant part was dried in a heated drier at 80°C for more than three days and dry weight was measured. At maturity, yield and yielded components were determined on three plants in each plot.

Leaf area duration (LAD) was calculated as $(LA_1 + LA_2) \times (t_2 - t_1) / 2$, where LA_1 and LA_2 were leaf area at sampling times, t_1 and t_2 , respectively. We excluded the days at which Ψ_i was lower than Ψ_{oi} in water stress plots since leaf rolling was severe and that photosynthesis seemed negligible. Increase in total dry weight from t_1 to t_2 divided by LAD for each growth period was referred to as net assimilation rate (NAR).

Multiple regression was applied to determine the relationship between two factors, “x” and “y” in each cultivar (Bland and Altman, 1995). When we used factor “y” as outcome variable, the other factor “x” and the cultivars were referred to as predictor variables. Cultivar was treated as categorical factor using dummy variable with two degrees of freedom. The P value from the t test for the regression slope of “x” was used to determine the significance of the analysis. The magnitude of correlation coefficient between the factors “x” and “y” in each cultivar was calculated as square root of (sum of squares for “x”) / (sum of squares for “x” + residual sum of squares).

Results

Changes in stem number in flooded plot are shown in Fig. 2. Stem number increased at a similar rate until 42 d after sowing (DAS) in the three cultivars. Stem number increased for a longer period in Nipponbare and Akebono than in Akihikari. The maximum tiller number stage was at 56 DAS in Akihikari, one to two weeks earlier than in Nipponbare and Akebono. Water was drained at 49, 62

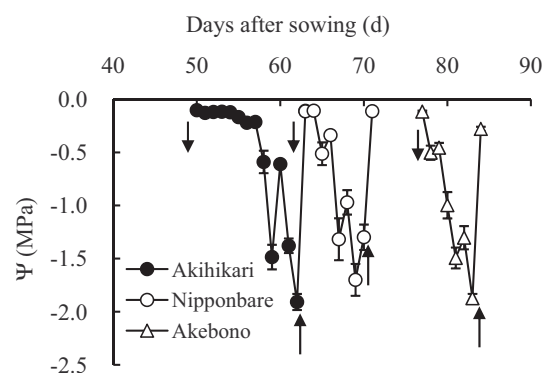


Fig. 3. Changes in leaf water potential before sunrise (Ψ) during water stress period in the three rice cultivars. Values and vertical bars are means and standard errors, respectively, of nine or ten plants. Downward and upward arrows indicate time of withholding irrigation and termination of water stress by irrigation for each cultivar, respectively.

and 76 DAS in Akihikari, Nipponbare and Akebono, respectively. The full heading time was 72, 84 and 97 DAS in Akihikari, Nipponbare and Akebono respectively in flooded plots. Although heading time was not affected by top dressing, it was delayed for three to five days by water stress. The duration from the end of water stress to the full heading was from 10 to 13 d in flooded plots and from 15 to 17 d in water stress plots in top dressed and not top dressed plots, showing a small difference among the three cultivars.

Under a submerged soil condition, Ψ was high ca. -0.1 MPa in the three cultivars. After the drainage, Ψ in water stress plots decreased gradually and recovered to the high values after the termination of water stress by irrigation (Fig. 3). Small increases in Ψ during the treatment were due to the application of water to prevent

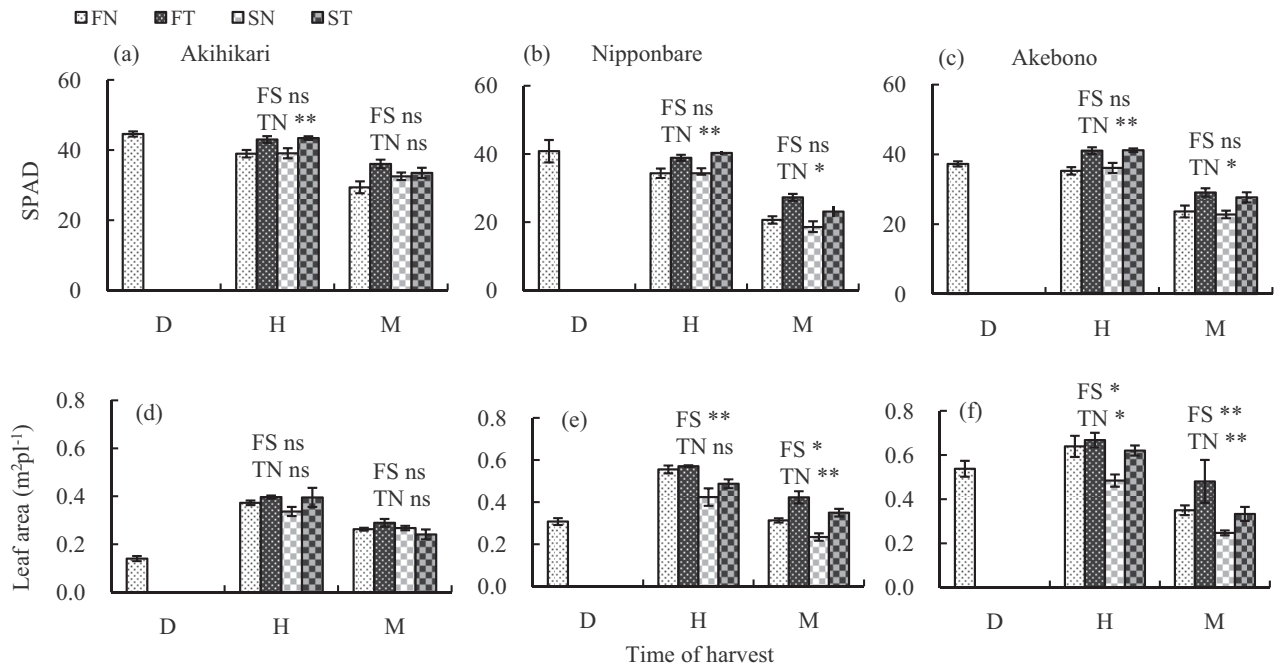


Fig. 4. Effects of water stress and top dressing on chlorophyll concentration (SPAD) and leaf area in the three rice cultivars. (a) and (d), Akihikari; (b) and (e), Nipponbare; (c) and (f), Akebono; (a), (b) and (c), SPAD; (d), (e) and (f), leaf area. Values and vertical bars are means and standard errors, respectively, of five plants for SPAD, and of five plants at drainage (D) and maturity (M), and three plants at full heading (H) for leaf area. FN and FT indicate flooded plot without and with top dressing, and SN and ST stress plot without and with top dressing, respectively. FS and TN indicate the effects of water treatment and top dressing by ANOVA: * and **, significant at 1% and 5%; ns not significant at 5%. There was no significant interaction.

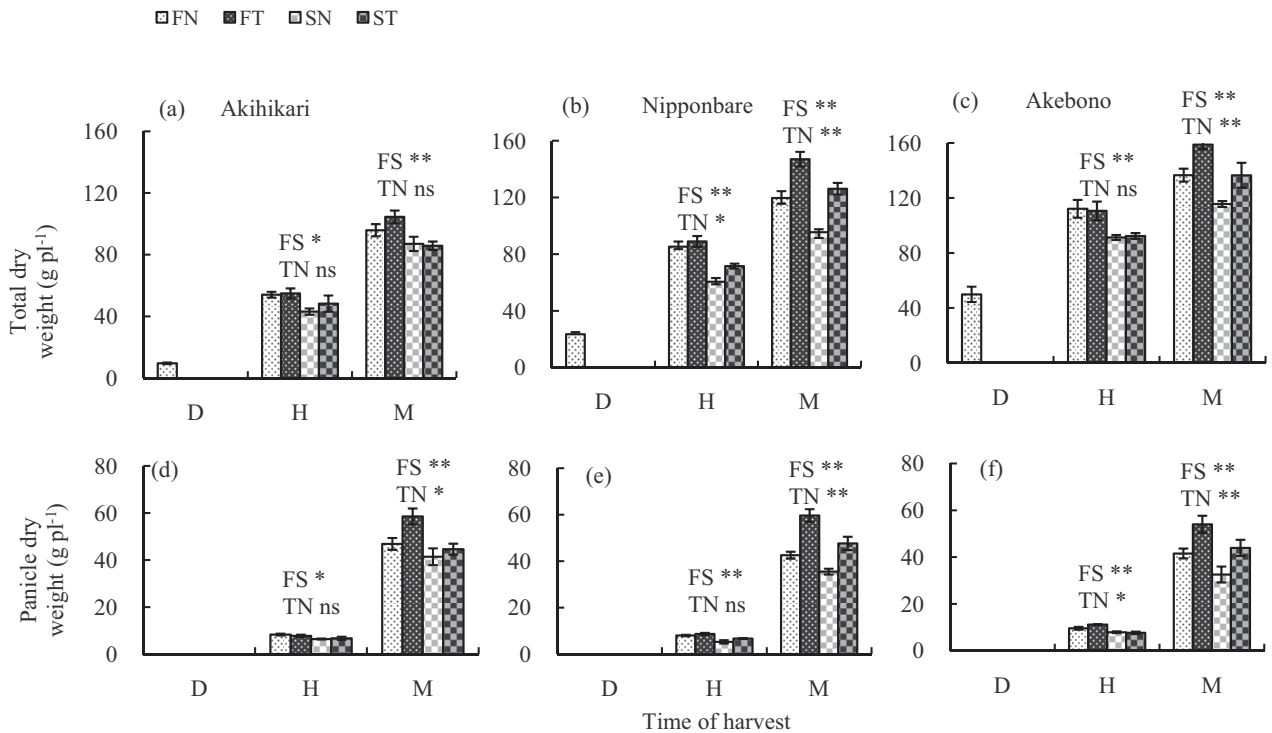


Fig. 5. Effects of water stress and top dressing on total and panicle dry weight in the three rice cultivars. (a) and (d), Akihikari; (b) and (e), Nipponbare; (c) and (f), Akebono; (a), (b) and (c), total dry weight; (d), (e) and (f), panicle dry weight. Values and vertical bars are means and standard errors, respectively, of five plants at drainage (D) and maturity (M), and three at full heading (H). FN and FT indicate flooded plot without and with top dressing, and SN and ST stress plot without and with top dressing, respectively. FS and TN indicate effects of water treatment and top dressing, respectively, by ANOVA: * and **, significant at 1% and 5%; ns not significant at 5%. There was no significant interaction.

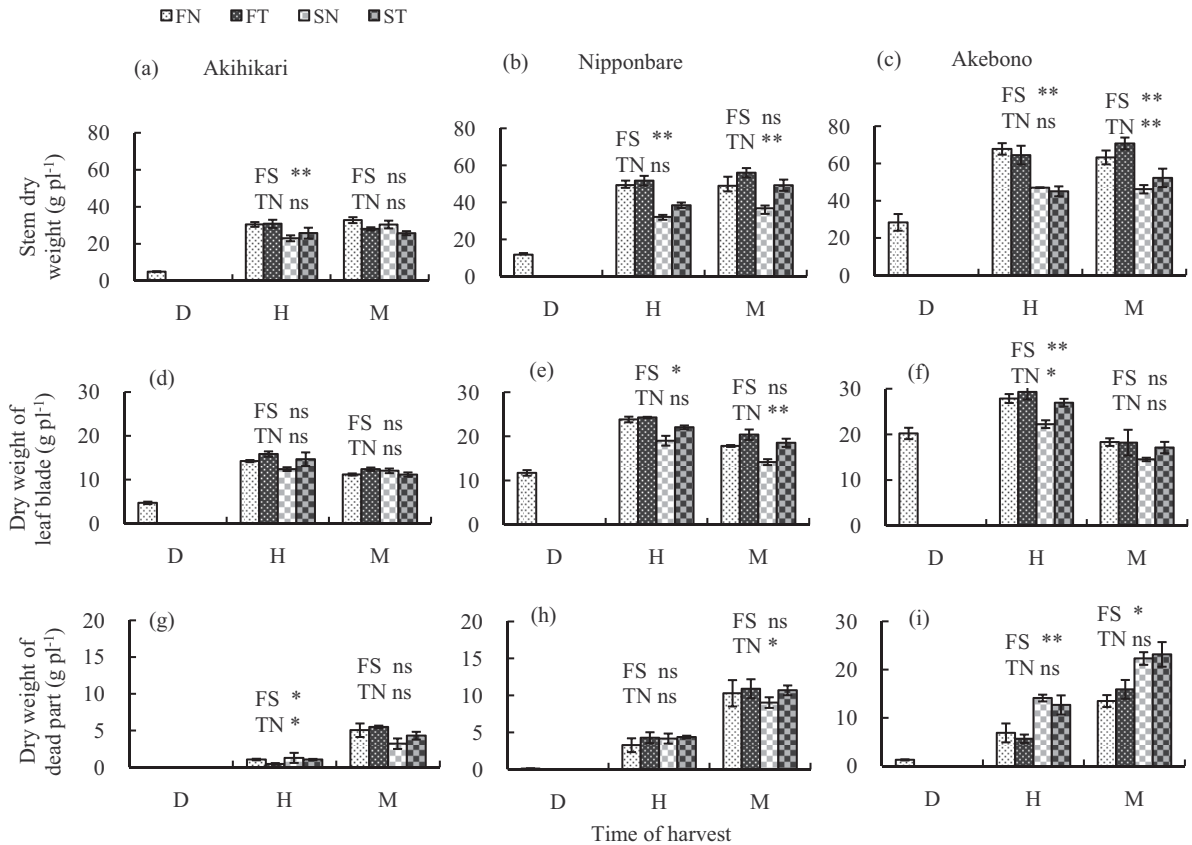


Fig. 6. Effects of water stress and top dressing on dry weight of stem, leaf blade and dead part in the three rice cultivars. (a), (d) and (g), Akihikari; (b), (e) and (h), Nipponbare; (c), (f) and (i), Akebono. (a), (b) and (c), stem dry weight; (d), (e) and (f): dry weight of leaf blade, (g), (h), (i): dry weight of dead part. Values and vertical bars are means and standard errors, respectively, of five plants at drainage (D) and maturity (M), and three at full heading (H). FN and FT indicate flooded plot without and with top dressing, respectively, and SN and ST stress plot without and with top dressing, respectively. FS and TN indicate effects of water treatment and top dressing, respectively, by ANOVA: * and **, significant at 1% and 5%; ns not significant at 5%. There was no significant interaction.

plant death. Although it took longer from the drainage to the initiation of Ψ decrease in Akihikari, applied soil water stress expressed as CWS was similar in all cultivars from 5.5 MPa d in Nipponbare to 5.8 MPa d in Akebono. Meteorological conditions during stress treatment at Okayama weather station were the following: mean temperature; 25.1, 29.5 and 30.2°C, relative humidity; 81, 68 and 62%, sunshine hours; 1.5, 7.5 and 8.4 hr, for Akihikari, Nipponbare and Akebono, respectively.

Leaf chlorophyll referred to as SPAD values was higher in Akihikari at the start of the treatment, and decreased as plants developed in the three cultivars (Fig. 4). ANOVA indicated that the effect of water stress on SPAD was not significant in all three cultivars, while top dressing increased SPAD significantly except for Akihikari at maturity. On the other hand, the effect of water stress was significant in leaf area (Fig. 4). Leaf area was reduced by water stress and increased by top dressing in Nipponbare and Akebono with the exception of Nipponbare at full heading. Water stress and top dressing did not change leaf area significantly in Akihikari.

At full heading and maturity, total dry weight of plant was decreased by water stress in all three cultivars (Fig. 5). Top dressing increased total dry weight in Nipponbare and Akebono, but not in Akihikari. Panicle dry weight at maturity was reduced by water stress and increased by top dressing in flooded and water stress plants. The degree of the reduction by water stress was 12, 17 and 22% in the not top dressed plants in Akihikari, Nipponbare and Akebono, respectively. Panicle dry weight at maturity was increased about 30% by top dressing averaging two water treatments in all three cultivars. Yield components did not show clear responses to water stress and top dressing. For example, number of spikelets per plant affected by only water stress in Nipponbare, while by top dressing only in Akebono, no effect being found in Akihikari (data not shown).

Stem dry weight at full heading was reduced clearly by water stress but not by topdressing in all three cultivars (Fig. 6). Leaf dry weight at full heading was reduced by water stress and increased by top dressing in Nipponbare and Akebono. Dry weight of dead part increased as plants developed. At full heading it was increased by water stress

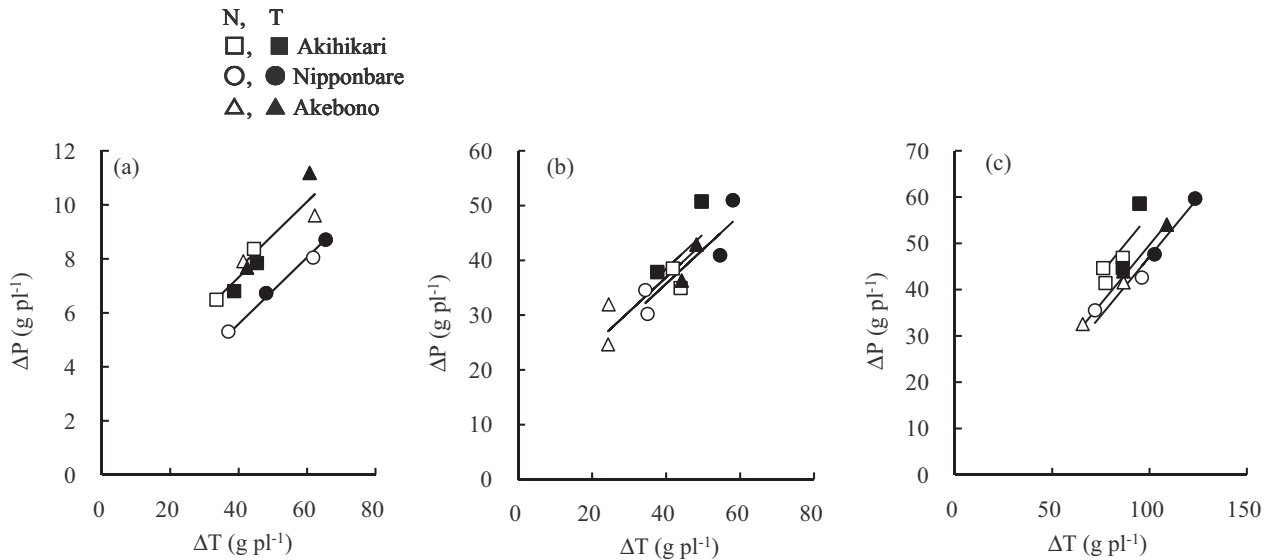


Fig. 7. Relationships between increase in total dry weight (ΔT) and that in panicle dry weight (ΔP) from drainage to full heading (a), from full heading to maturity (b) and from drainage to maturity (c). The coefficients of multiple correlation are 0.936 ($P < 0.001$), 0.848 ($P < 0.01$), and 0.958 ($P < 0.001$) in (a), (b) and (c) respectively. Symbols are Akihikari (\square , \blacksquare), Nipponbare (\circ , \bullet) and Akebono (\triangle , \blacktriangle). Open and closed symbols indicate plots without and with topdressing, respectively.

but unaffected by top dressing in Akebono, and affected neither by water stress nor top dressing in Nipponbare. In Akihikari, dry weight of plant parts was changed little by water stress and top dressing.

The relationships between the increase in panicle dry weight (ΔP) and that in total dry weight (ΔT) was examined for each growth period that is, from the drainage to full heading, from full heading to maturity, and from the drainage to maturity (Fig. 7). It seemed that ΔP increased in proportion to ΔT in each cultivar, so multiple regression was used to determine the relationship between ΔT and ΔP in each cultivar. There was a strong positive correlation between ΔT and ΔP in each cultivar for each growth period. Therefore, the change in ΔT was responsible for that in ΔP . In Fig. 7, closed and open symbols indicate top dressed and not top dressed plots, respectively. Based on the coordinate points of the data, the changes in ΔT and ΔP were mainly due to water stress from the drainage to full heading, while they were due to top dressing from full heading to maturity. Thus, ΔT and ΔP from the drainage to maturity were affected by both water stress and top dressing.

To find out the factors that affected ΔT , we estimated leaf area duration (LAD). LAD was closely related to LA, which was estimated as $(LA_1 + LA_2)/2$, with correlation coefficients higher than 0.954 ($P < 0.0001$) for each growth period, based on multiple regression analysis (data was not shown).

The relationships between LAD and ΔT , and between NAR and ΔT were examined in Figs. 8, 9, respectively. To examine the two relationships, we applied multiple

regression. There were highly significant correlations for ΔT with LAD and NAR for each growth period (Figs. 8, 9). Similar to the relationship between ΔT and ΔP , water stress and top dressing affected LAD and NAR differently depending on the growth periods: the effect of water stress was clear from drainage to full heading, while that of top dressing from full heading to maturity.

Discussion

Panicle dry weight at maturity was reduced by water stress at early stage of panicle-development (Fig. 5), similar to earlier studies (Tsuda and Takami, 1991; Tsuda et al., 1993; 1994). Top dressing after the stress increased panicle dry weight (Fig. 5). What factors were responsible for the decrease in yield by water stress and the increase by the top dressing?

There was a significant relationship between ΔT and ΔP (Fig. 7). The regression coefficient between ΔT and ΔP from drainage to maturity did not vary across water stress and top dressing in each cultivar, indicating that changes in ΔT were responsible for those in ΔP (Fig. 7c). Further, LAD and NAR were responsible for ΔT (Figs. 8, 9). However, water stress and top dressing affected them differently for each growth period.

Generally, top dressing increases nitrogen content of leaf, and thus chlorophyll content and photosynthesis rate, as well as leaf area. In this study, the SPAD value, which was an indicator of chlorophyll contents, at full heading was increased by top dressing and leaf area was also increased (Fig. 4). On the other hand, ΔT , LAD and NAR from the drainage to full heading were not affected by top dressing

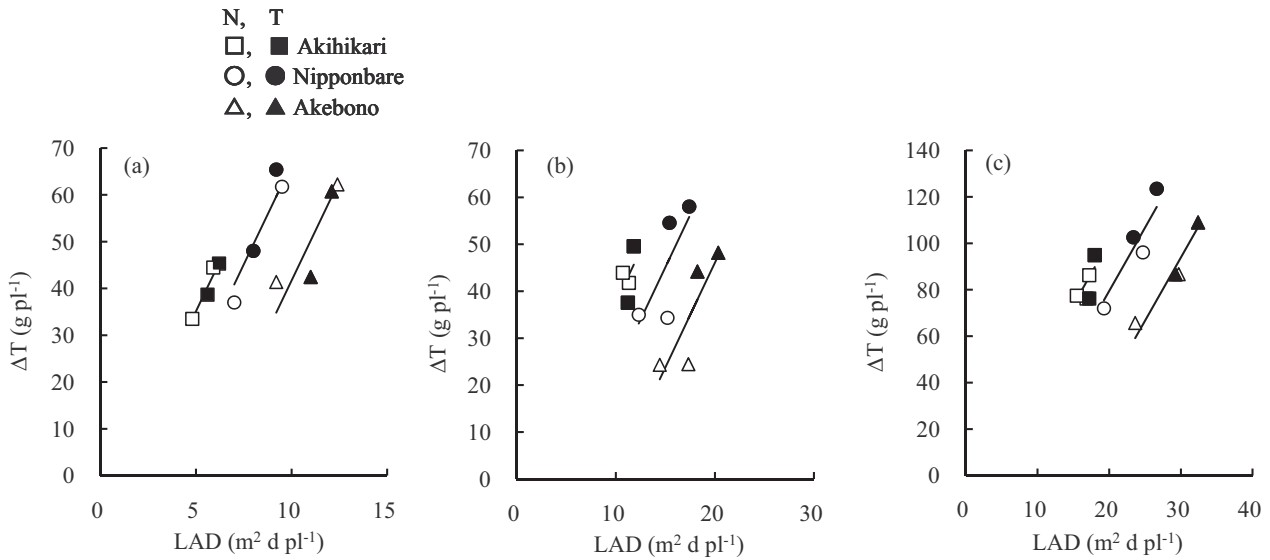


Fig. 8. Relationships between leaf area duration (LAD) and increase in total dry weight (ΔT) from drainage to full heading (a), from full heading to maturity (b) and from drainage to maturity (c). The coefficients of multiple correlation are 0.915 ($P < 0.001$), 0.783 ($P < 0.01$), and 0.929 ($P < 0.001$) in (a), (b) and (c) respectively. Symbols are Akihikari (\square , \blacksquare), Nipponbare (\circ , \bullet) and Akebono (\triangle , \blacktriangle). Open and closed symbols indicate plots without and with topdressing, respectively.

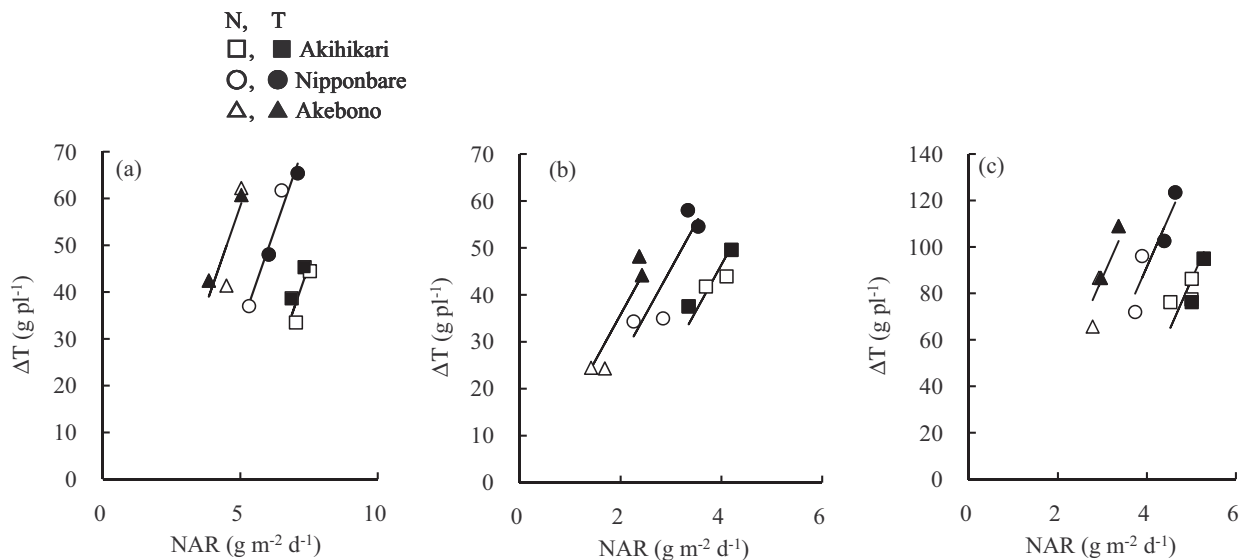


Fig. 9. Relationships between net assimilation rate (NAR) and increase in total dry weight (ΔT) from drainage to full heading (a), from full heading to maturity (b) and from drainage to maturity (c). The coefficients of multiple correlation are 0.915 ($P < 0.001$), 0.900 ($P < 0.001$), and 0.874 ($P < 0.001$) in (a), (b) and (c) respectively. Symbols are Akihikari (\square , \blacksquare), Nipponbare (\circ , \bullet) and Akebono (\triangle , \blacktriangle). Open and closed symbols indicate plots without and with topdressing, respectively.

(Figs. 4, 5, 8, 9). Time from the drainage to full heading was 21–23 d whereas that from topdressing to heading was about 2 wk, which might not be enough to exhibit the effects of top dressing due to the large effect by water stress. The effect of top dressing was prominent after full heading or in the ripening period.

The green leaf area is the difference between the gain

due to production of new leaf area and the loss due to death (Thomas and Howarth, 2000). Leaf area at full heading was reduced by water stress with no change in dead part in Nipponbare, but with increase in dead part in Akebono (Figs. 4, 6). This suggested that the reduction of leaf area may be mainly due to new leaf area production and leaf death in Nipponbare and Akebono, respectively.

On the other hand, top dressing may increase leaf area by delaying leaf senescence during the ripening period (Figs. 4, 6). We might be able to control leaf area by manipulating either production or senescence of leaf.

In this study, the larger leaf area could be related to improvement of yield under a single stress cycle condition, suggesting that a large leaf area improve the yield under conditions similar to this study. However, it is considered that larger leaf area is not always a beneficial under drought conditions (Turner, 1982). For example, a crop with a large leaf area may exhaust soil water earlier, resulting in a large yield reduction under terminal drought where the crop depends exclusively on the water stored in the soil. Therefore, we should be careful to apply methods of increasing leaf area to yield improvement under drought in rice.

The reduction of panicle dry weight by water stress was 12, 17 and 22% in Akihikari, Nipponbare and Akebono, respectively. According to the method proposed by Tsuda et al. (1993), water stress susceptibility was calculated as the degree of reduction of panicle dry weight divided by CWS was 0.0214, 0.0309 and 0.0379 MPa⁻¹ d⁻¹ in the three cultivars, respectively. The difference in the water stress susceptibility was similar to that reported by Tsuda and Takami (1991), but it does not necessarily mean that the difference was due to the trait of the cultivars. The reason was that meteorological conditions during the water stress treatment were quite different between Akihikari and other two cultivars, suggesting that the difference in water stress susceptibility may be partly depend on meteorological conditions.

In summary, the changes in leaf area and net assimilation rate caused by water stress and top dressing are responsible for the changes in panicle dry weight in rice. Top dressing improved panicle dry weight in the plants subjected to temporary water stress, indicating that top dressing was a good management practice not only under submerged soil conditions but also after temporary water stress.

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