Effects of different water management practices on the dry matter production process and characteristics in NERICAs

Mayumi Kikuta\textsuperscript{a,b}, Daigo Makihara\textsuperscript{a}, Naoya Arita\textsuperscript{c}, Akira Miyazaki\textsuperscript{d} and Yoshinori Yamamoto\textsuperscript{d}

\textsuperscript{a}International Center for Research and Education in Agriculture (ICREA), Nagoya University, Nagoya, Japan; \textsuperscript{b}Applied Social System Institute of Asia (ASSIA), Nagoya University, Nagoya, Japan; \textsuperscript{c}Graduate School of Integrated Arts and Sciences, Kochi University, Nankoku, Japan; \textsuperscript{d}Faculty of Agriculture, Kochi University, Nankoku, Japan

\textbf{ABSTRACT}

In this study, we aimed to clarify the effects of different water management strategies on dry matter production and yield performance of New Rice for Africa (NERICA) varieties. Dry matter production of NERICA 1 and NERICA 5 was compared with that of Yumehatamochi, a Japanese upland variety, and Hinohikari, a Japanese lowland variety under three water regimes, i.e. continuously flooded, supplemental irrigation, and non-irrigation (rainfed). Total carbohydrate content in the panicles under different water regimes was more closely related to post-heading photosynthates than pre-headling reserve assimilates. Dry matter production during ripening tended to decrease under low soil water conditions, whereas the dry matter translocated from the leaf and stem to the panicle tended to increase. Consequently, the distribution ratio of post-heading photosynthates in the total carbohydrate content declined in response to the reduction in available soil moisture. These results indicate that the total carbohydrate content vary depending on the soil water conditions. In NERICAs, dry matter production during ripening was lower than that in Japanese varieties, indicating that their dependence on pre-heading reserve assimilates was greater. In particular, post-heading photosynthate content of NERICA 1 was strongly affected by the variation in water management in comparison with that of other varieties. The decrease in crop growth rate during ripening in NERICA 1 can be mainly attributed to the lower post-heading photosynthate content. Thus, the ability of NERICA 1 to assimilate carbon after heading was considered to be potentially low, which has to be improved to achieve higher yield.

\textbf{Introduction}

Rice consumption in sub-Saharan Africa is increasing at a fast rate (Otsuka & Kijima, 2010). Although rice production in this area increased in the 2000s compared with that in the 1970s, the demand has exceeded the production (Somado et al., 2008). In the 2000s, New Rice for Africa varieties (NERICAs) were developed by crossing \textit{Oryza glaberrima} and \textit{O. sativa} by the Africa Rice Center (formerly, the West Africa Rice Development Association) to improve rice production in sub-Saharan Africa (Jones, Dingkuhn, et al., 1997; Jones, Mande, et al., 1997) and have been released in several African countries. The NERICAs were developed with the aim to combine the advantageous traits of \textit{O. glaberrima} and \textit{O. sativa} (Diagne et al., 2010; Jones, Dingkuhn, et al., 1997; Jones, Mande, et al., 1997; Kaneda, 2007). Although NERICAs were mainly developed for cultivation in upland ecosystems, they have also been cultivated in lowlands and wetlands (Fujie et al., 2010). This suggests that NERICAs have the capacity to adapt to a wide range of soil water conditions.

However, several studies have reported inconsistency in the growth and yield of NERICAs under various soil water conditions. For instance, in Uganda, the yield of NERICA under lowland conditions was higher than that under upland conditions, unless rainfall supplied sufficient water (Awio et al., 2015; Matsumoto et al., 2014). Shaibu et al. (2015) also indicated that the yield of NERICAs under continuously flooded condition is higher than that under alternate wetting and drying system (AWD) in Malawi. In contrast, Matsunami et al. (2009) reported that adequate rainfall resulted in better NERICA performance under upland conditions than under lowland condition in Japan.

Previously, we reported that the response of spikelet number per panicle to low soil water conditions varied among NERICA varieties, which partially explained the inconsistency in NERICA performance across uplands and lowlands (Kikuta et al., 2017). However, rice yield is determined by both sink size (spikelet number m\textsuperscript{-2} × grain weight per grain) (Kusutani et al., 1993; Saitoh et al., 1991) and source capacity (the...
capacity to supply carbohydrates to the grains) (Murata & Matsushima, 1975). Therefore, it is important to compare source-capacity-related traits of NERICA varieties under low soil water conditions. Source capacity is defined by the amount of photosynthates after heading (post-heading photosynthetic) and reserve carbohydrates in leaf sheaths and culm assimilated before heading (pre-heading reserve assimilates) (Matsushima, 1957; Murata & Matsushima, 1975; Yoshida, 1972). Generally, the carbohydrate content in rice grain is largely dependent on post-heading photosynthates, rather than pre-heading reserve assimilates (Cock and Yoshida 1972; Yoshida, 1972). Pre-heading reserve assimilates are translocated to the panicles to compensate for the deficiency in post-heading photosynthates (Nagata et al., 2001).

Research on dry matter production characteristics during yield establishment in rice has mainly focused on lowland varieties (Gendua et al., 2009; Kusutani et al., 1993; Miah et al., 1996; Saitoh et al., 1991; Song et al., 1990; Yamamoto, 1991). In lowland rice, compensatory carbohydrate supply from pre-heading reserve assimilates occurs when carbohydrate supply from post-heading photosynthates is insufficient due to water stress (Kobata & Takami, 1981).

A few studies have focused on dry matter production characteristics of upland varieties. Yun et al., (1997) reported that an upland variety was more dependent on pre-heading reserve assimilates than a lowland variety under upland conditions. In addition, Hasegawa (1962) and Wada et al. (2002) reported that the proportion of post-heading photosynthates in the grain decreased under upland conditions compared with that under lowland conditions. As plant morphological characteristics such as tiller number and culm diameter are different between upland and lowland rice varieties, the responses of dry matter production characteristics during yield establishment under different soil water conditions might differ between the varieties. To clarify whether there are differences among NERICA varieties in the response of source-capacity-related traits to low soil water conditions, we compared the responses of dry matter production characteristics in NERICAs with those of Japanese upland and lowland varieties under different water availability conditions. Furthermore, we discussed the characteristics of NERICA that need improvement in relation to increasing grain yield under different water managements.

Materials and methods

Experimental design

The experiment was conducted at the Education and Research Centre for Subtropical Field Science of the Faculty of Agriculture, Kochi University, Japan (33°55’N, 133°68’E) in 2011 and 2012. During both years, four varieties were used, namely NERICA 1 (upland rice, non-glutinous), NERICA 5 (upland rice, non-glutinous), Yumenohatamochi (Japanese upland rice, glutinous), and Hinohikari (Japanese lowland rice, non-glutinous).

In 2011, three water management regimes were set up; i.e. continuously flooded (FL, the water table was maintained at approximately 5 cm above the soil surface during the growth period), supplemental irrigation (IR, when the soil water potential at 10-cm depth reached approximately 40 kPa, before leaf rolling of all varieties, irrigation water was applied), and non-irrigation (NIR, rainfed condition) (Figure 1). The study site received considerable amount of rainfall, exceeding 1500 mm during the 2011 growing period, causing the soil water potential under NIR and IR to be comparable. Therefore, in 2012, the experiment was conducted with only FL and NIR. The four varieties were laid out with two replications according to a randomized block design during both years, and the size of each plot was 3.75 m × 3.75 m for each variety.

All plots received 100 kg N ha⁻¹, 100 kg P ha⁻¹, and 100 kg K ha⁻¹ as a slow-release compound fertilizer (14-14-14, NPK) before final puddling. Seedlings were manually transplanted with two seedlings per hill at 22.2 hills m⁻² (spacing; 30 cm × 15 cm) on 1 June 2011 and on 30 May 2012. All plots were maintained flooded for three weeks after transplanting to ensure plant establishment, and water managements were started from 21 June 2011 [20 days after transplantation (DAT)] and 22 June 2012 (23 DAT). In IR and NIR, the water from the field was drained and saved above the soil surface at the start of the treatments. Insects and diseases were well controlled by chemicals.
and weeds were controlled by hand weeding to avoid yield loss when necessary during both years.

Monthly mean temperature, rainfall, and solar radiation during the growing period were obtained from the Automated Meteorological Data Acquisition System (AMeDAS) in Gomen Station (Nankoku City, Kochi, Japan; 33°35′ N, 133°39′ E). The climatic data have been shown in our previous report (Kikuta et al., 2017). The soil water potential in all treatments was measured using a tensiometer (DIK-3150; Daiki Rika Kogyo Co., Ltd., Saitama, Japan) installed at 10-cm soil depth, either daily or every two days after the onset of water management.

**Measurements**

**Shoot dry weight**

Three plants were selected for counting the productive tiller number from 20 hills (i.e. in total, six plants per variety under each water condition) three times at full heading, 20 days after heading, and maturity, and the average was taken. The plants were separated into four parts: leaf sheath and culm, leaf blade, panicle, and dead portion. The leaf area in one hill per plot was measured using a leaf area meter (AAM-7; Hayashi Denkoh Co. Ltd., Japan), and the leaf area index (LAI) was computed. The sampled plant parts were oven-dried at 80°C for 2 h, and then at 65°C for 48 h to determine the dry weight. The leaf area in the other two hills was calculated from the dry weight and specific leaf area of the leaf blade. The dry matter translocated from the leaf and stem to the panicle during ripening (ΔT) was computed from the dry weight of the leaf sheath and stem from full heading to maturity. ΔW, representing newly assimilated carbohydrates during the ripening period, was computed as the increment in total dry weight from heading to maturity. ΔW + ΔT was used as a parameter representing source capacity.

**Bleeding rate**

In 2012, the bleeding rate, an indicator for root activity (Yamaguchi et al., 1995), was measured at heading, 20 days after heading, and maturity using the methodology described by Morita and Abe (1999, 2002). The plants selected for determining the dry weight were cut at 15 cm above the soil surface to measure the bleeding rate from the root zone in all plots. Cotton towels that had been weighed were placed on the cut portions and were covered with polyethylene bags and bound with a rubber band to prevent evaporation. After 1 h, the towels were collected and immediately weighed.

**Analysis of sugar and starch**

Dried samples of leaf and stem at full heading and maturity were ground (WT-150; MIKI Seisakusho, Japan) and milled to a fine powder (T1-100; CMT Co. Ltd., Japan). Sugars were extracted with 80% hot ethanol and starch was extracted with 4.6 N perchloric acid (HClO₄) from the residues of sugar extraction following the method of Murayama et al., (1955). The content of total starch and sugars were measured as glucose by the anthrone-sulfuric acid method using a spectrophotometer (UV-1200; Shimadzu, Japan). Starch content was expressed as the glucose content multiplied by 0.9.

**Yield and yield components**

At the maturity stage, 20 plants per plot were harvested and were air-dried in the glass house for two weeks. The panicles per hill were then counted. Three plants with average number and weight of panicles (i.e. six plants per water treatment) were selected from each plot to determine yield and yield components. Spikelets were counted and were separated into filled and unfilled using salt water (specific gravity is 1.06 for non-glutinous and 1.03 for glutinous spikelets). The 1000-grain weight was calibrated to that of brown rice with 15% grain water content using a grain moisture tester (PB-3000 series; Grain Moisture Tester, Kett Electric Laboratory, Tokyo, Japan). Sink size per square meter was calculated as the product of number of spikelets and weight of one grain (Kusutani et al., 1993; Saitoh et al., 1991).

**Statistical analyses**

Water management regime was the main factor and variety was the split-plot factor. Means of growth and yield parameters were separated using LSD test at P < 0.05 in JMP Pro 13.0.0 (SAS Institute Inc., NC, USA).

**Results**

**ANOVA results**

During both the years, the variety of rice significantly affected all yield- and growth-related parameters (Table 1). Treatment also significantly affected all yield- and growth-related parameters, except ΔT in both years, NAR in 2011, and average LAI in 2012. Furthermore, yield and ΔW + ΔT were significantly affected by the interaction between variety and treatment in both years, whereas the sink size was significantly affected only in 2012.
Yield and sink size

For all varieties, yield was the highest under FL, followed by IR and NIR, except for Yumenohatamochi in 2012 (Table 2). Under IR and NIR, the relative yield of Yumenohatamochi tended to be higher than that of NERICA 1, NERICA 5, and Hinohikari in both years. Under FL in both years, Hinohikari had higher yield than Yumenohatamochi, NERICA 1, and NERICA 5. Under NIR, the yield of NERICAs tended to be lower than that of Japanese varieties, except for Hinohikari in 2012, whereas under IR in 2011, there was no varietal difference.

The sink size was the highest under FL, followed by IR and NIR, except for Yumenohatamochi in 2012 (Table 2). Under IR and NIR, the sink size of NERICAs tended to be smaller than that of the two Japanese varieties, except for Hinohikari in 2012. Furthermore, under NIR, the sink size of NERICA 5 was larger than that of NERICA 1.

Dry matter production characteristics

Under all treatments, ΔW + ΔT of the NERICAs tended to be lower than that of Yumenohatamochi and Hinohikari, except for NERICA 1 under FL and Hinohikari under NIR in 2012 (Table 3). Under IR and NIR, the relative value of ΔW + ΔT for Yumenohatamochi tended to be higher than that of the other three varieties. ΔW + ΔT for NERICA 1, NERICA 5, and Hinohikari tended to be the highest under FL, followed by IR and NIR. Among the treatments, the highest ΔW was observed under FL, followed by IR and NIR. ΔW of NERICA 1 was lower than that of Yumenohatamochi under IR and NIR in both years and under FL in 2012. In NERICA 5, Yumenohatamochi, and Hinohikari, the lowest ΔT was observed under FL; however, this was not the case in NERICA 1. Yumenohatamochi had the highest percent of ΔW to ΔW+ΔT, whereas NERICA 1 had the lowest value among the four varieties under all treatments. In both years, there was a significant negative correlation between ΔW and ΔT in all the water management regimes across the varieties (Figure 2). ΔW+ΔT significantly positively correlated with ΔW in both years (Figure 3). On the contrary, no significant correlation was found between ΔW + ΔT and ΔT.

Crop growth rate (CGR) during the ripening stage

Among the treatments, FL resulted in the highest CGR, except in Yumenohatamochi in 2012 (Table 4). Irrespective of the water management regime, the CGR

Table 1. Analysis of variance to determine the effects of variety (V) and water management treatment (T) on the parameters related to yield, yield physiology, and dry matter production for NERICA 1, NERICA 5, Yumenohatamochi, and Hinohikari grown under three different water management regimes during 2011 and 2012: continuously flooded, supplementary irrigation, and non-irrigation.

| Variety (V) | Treatment (T) | V × T |
|------------|---------------|-------|
| Yield (g m⁻²) | *** | ** |
| Sink size (g m⁻²) | *** | *** |
| ΔW + ΔT (g m⁻²) | *** | *** |
| ΔW (g m⁻²) | *** | *** |
| ΔT (g m⁻²) | ** | n.s. |
| ΔG (g m⁻²) | ** | n.s. |
| NAR (g m⁻²) | ** | n.s. |
| Δv. LAI | *** | n.s. |

n.s.: not significant, *: significant at P < 0.05, **: significant at P < 0.01, ***: significant at P < 0.001. ΔW: newly assimilated carbohydrates from heading to maturity. ΔT: pre-heading reserve assimilates translocated from the leaf and stem to the panicle during ripening. ΔW+ΔT: source capacity; CGR: crop growth rate; NAR: net assimilation rate; a.v. LAI: average leaf area index.

Table 2. Yield and sink size in NERICA 1 (N1), NERICA 5 (N5), Yumenohatamochi (YHM), and Hinohikari (HH) grown under three water management regimes: continuously flooded (FL), supplemental irrigation (IR), and non-irrigation (NIR), in 2011 and 2012.

| Variety | FL | IR | NIR | IR/FL | NIR/FL |
|---------|----|----|-----|-------|--------|
| Yield (g m⁻²) | N1 | 413 b | 346 a | 287 c | 84 | 69 |
| N5 | 440 b | 348 a | 298 bc | 79 | 68 |
| YHM | 434 b | 392 a | 379 ab | 90 | 87 |
| HH | 508 a | 406 a | 402 a | 80 | 79 |
| Sink size (g m⁻²) | N1 | 580 b | 417 b | 355 c | 72 | 69 |
| N5 | 726 a | 516 ab | 480 b | 71 | 68 |
| YHM | 636 ab | 582 a | 534 a | 92 | 87 |
| HH | 728 a | 571 a | 516 a | 78 | 79 |

Within each column, values followed by the same letter are not significantly different at P < 0.05. Numbers in italics indicate the relative value of each yield parameter under IR or NIR to that under FL for each variety.
of NERICA 1 tended to be lower than that of Yumenohatamochi, although there was no significant difference among the varieties under FL in 2011 and NIR in 2012. The net assimilation rate (NAR) was higher under FL than under IR and NIR, except in Hinohikari in 2011. Regardless of the treatment, NERICA 1 had lower NAR than that of Yumenohatamochi and NERICA 5, with the exception of that under FL in 2011 and NIR in 2012. In all treatments, the average LAI tended to be lower in the NERICAs than in Yumenohatamochi and Hinohikari. The average LAI tended to be less affected by water management than NAR. The CGR significantly positively correlated with the NAR (Figure 4). However, no clear relationship was observed between the CGR and average LAI. The CGR during the ripening stage significantly positively correlated with $\Delta W$ in all the water management regimes across the varieties (Figure 5).

### Bleeding rate during the ripening stage

The bleeding rate under FL during the ripening stage showed two patterns: 1) NERICA 1 and Hinohikari showed

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**Table 3. $\Delta W$, $\Delta T$, and $\Delta W + \Delta T$ in NERICA 1 (N1), NERICA 5 (N5), Yumenohatamochi (YHM), and Hinohikari (HH) grown under three water management regimes: continuously flooded (FL), supplemental irrigation (IR), and non-irrigation (NIR), in 2011 and 2012.**

| Variety | FL  | IR  | NIR | IR/FL | NIR/FL | FL  | IR  | NIR | IR/FL | NIR/FL |
|---------|-----|-----|-----|-------|--------|-----|-----|-----|-------|--------|
| $\Delta W + \Delta T$ ($g m^{-2}$) |     |     |     |       |        |     |     |     |       |        |
| N1      | 536 | 474 | 324 | 88    | 60     | 602 | 468 | 78  |       |        |
| N5      | 589 | 447 | 458 | 76    | 78     | 498 | 472 | 95  |       |        |
| YHM     | 635 | 592 | 581 | 93    | 92     | 614 | 644 | 105 |       |        |
| HH      | 684 | 623 | 616 | 91    | 84     | 681 | 363 | 53  |       |        |
| $\Delta W$ ($g m^{-2}$) |     |     |     |       |        |     |     |     |       |        |
| N1      | 265 | 190 | 86  | 72    | 32     | 343 | 200 | 58  |       |        |
| N5      | 492 | 287 | 220 | 58    | 45     | 450 | 408 | 91  |       |        |
| YHM     | 685 | 616 | 532 | 90    | 78     | 611 | 597 | 98  |       |        |
| HH      | 593 | 352 | 368 | 59    | 62     | 670 | 308 | 46  |       |        |
| $\Delta T$ ($g m^{-2}$) |     |     |     |       |        |     |     |     |       |        |
| N1      | 270 | 284 | 238 | 105   | 88     | 259 | 268 | 104 |       |        |
| N5      | 93  | 160 | 288 | 163   | 243    | 48  | 64  | 135 |       |        |
| YHM     | -50 | -24 | 49  | 52    | 198    | 4   | 47  | 130 |       |        |
| HH      | 91  | 271 | 206 | 300   | 227    | 11  | 55  | 494 |       |        |
| $\Delta W/\Delta W + \Delta T$ (%) |     |     |     |       |        |     |     |     |       |        |
| N1      | 50  | 40  | 27  | -     | -      | 57  | 43  | -   |       |        |
| N5      | 83  | 64  | 48  | -     | -      | 90  | 86  | -   |       |        |
| YHM     | >100| >100| 92  | -     | -      | 99  | 93  | -   |       |        |
| HH      | 87  | 56  | 64  | -     | -      | 98  | 85  | -   |       |        |

Within each column, values followed by the same letter are not significantly different at $P < 0.05$. $\Delta W$: newly assimilated carbohydrates from heading to maturity; $\Delta T$: pre-heading reserve assimilates translocated from the leaf and stem to the panicle during ripening; $\Delta W + \Delta T$: source capacity. A negative value indicates an increase in dry weight. Numbers in italics indicate the relative value of each yield parameter under IR or NIR to that under FL for each variety.

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**Figure 2. Relationship between $\Delta W$ and $\Delta T$ in NERICA 1 (□, ■), NERICA 5 (○, ●), Yumenohatamochi (◇, ◆), and Hinohikari (△, ▲) grown under different soil water management regimes: continuously flooded, supplemental irrigation, and non-irrigation, in 2011 and 2012. * and *** indicate significant at 5% and 0.1%, respectively. The open symbols and solid line represent data in 2011, and the closed symbols and dotted line represent data in 2012. $\Delta W$: newly assimilated carbohydrates from heading to maturity; $\Delta T$: pre-heading reserve assimilates translocated from the leaf and stem to the panicle during ripening.**
a dramatic decrease in bleeding rate with time and 2) the bleeding rate of Yumenohatamochi and NERICA 5 remained stable or slightly decreased (Figure 6). In all varieties, the bleeding rate under NIR was lower than that under FL, regardless of the growth stage. The change in bleeding rate under NIR showed a trend similar to that under FL, except in Hinohikari under NIR, the bleeding rate at the full heading stage was obviously lower than that under FL. The relative value of bleeding rate under NIR to that under FL significantly positively correlated with the relative value of NAR under NIR to that under FL (Figure 7).

**Non-structural carbohydrates (NSC)**

The NSC content in the leaf sheath and culm was generally the highest at the full heading stage in all treatments, and decreased at 20 days after the full heading stage (Table 5). At maturity, all varieties showed higher NSC in comparison with that at 20 days after full heading. At the full heading stage, NERICA 1 and Hinohikari had significantly higher NSC than that of NERICA 5 and Yumenohatamochi in all treatments in 2012, and a similar trend was observed in all treatment in 2011. At 20 days after full heading, Hinohikari had the highest NSC among the four varieties under all treatments. At maturity, NERICAs had lower NSC than that of Yumenohatamochi and Hinohikari under all treatments in both years, except that of NERICA 5 under FL in 2012. The decrease in NSC from the full heading stage to 20 days after full heading tended to be higher in NERICA 1 than in the Japanese varieties, although there was no significant difference among the varieties under IR in 2011 and
In addition, this decrease in NSC significantly positively correlated with $\Delta T$ from the full heading stage until 20 days after full heading in all water management regimes across the varieties (Figure 8).

**Discussion**

**Involvement of source factor in yield reduction**

The yield of the four varieties varied in response to different water management strategies (Tables 1 and 2). In most cases, yield decreased under low soil water conditions. In addition, the sink size and source capacity also decreased under such conditions (Tables 2 and 3). These results showed that the yield under lower soil water conditions, IR and NIR, was limited by both sink size and source capacity. Moreover, there were varietal differences in both the factors, which were more apparent under low soil water conditions.

Under low soil water conditions, $\Delta W$, which was the highest under FL in all varieties, tended to decrease, whereas $\Delta T$ increased (Table 3, Figure 2). Therefore, the proportion of post-heading photosynthates and pre-heading reserve assimilates in total carbohydrates accumulated in the panicles...
varied depending on water management (Table 3). These results were in agreement with those of previous studies, which showed that pre-heading reserve assimilates are translocated from the leaf and stem to the panicle when the production of photosynthates is suppressed by stresses after heading (Nagata et al., 2001), such as water stress (Kobata & Takami, 1979, 1981) and light interception (Soga & Nozaki, 1957; Yoshida, 1972). Our findings indicate that the proportion of source contents that filled up in the panicles changed gradually in response to different water managements.

Total carbohydrates in the panicle ($\Delta W + \Delta T$) were more closely associated with $\Delta W$ than with $\Delta T$ (Figure 3).

Figure 6. Changes in bleeding rate in NERICA 1 (N1), NERICA 5 (N5), Yumenohatamochi (YHM), and Hinohikari (HH) during the ripening stage under two soil water management regimes: continuously flooded (FL) and non-irrigation (NIR), in 2012. FH: full heading stage. DAFH20: 20 days after full heading. MT: maturity stage.

Figure 7. Relationship between relative values\(^1\) of net assimilation rate (NAR) and bleeding rate at maturity stage in NERICA 1 (■), NERICA 5 (●), Yumenohatamochi (◆), and Hinohikari (▲) grown under different soil water conditions: continuously flooded (FL) and non-irrigation (NIR), in 2012. \(^1\) Relative values under FL being 100 (i.e. NIR/FL × 100). ** indicates significant at 1% level.
Furthermore, the higher $\Delta W$ was attributed to higher CGR, which can in turn be attributed to the NAR and average LAI (Figure 5). Our results support the findings by Song et al. (1990), who reported that $\Delta W$ is closely related to CGR in rice. In addition, Japonica-Indica hybrid rice produce higher amount of dry matter during ripening because of higher NAR under lowland conditions (Jiang et al., 1988; Saitoh et al., 1990). Further, in our study, CGR was determined mainly by NAR in all water management regimes (Figure 4). The NAR is determined by canopy structure, light-interception characteristics, and photosynthesis rate (Jiang et al., 1988), and it is strongly influenced by soil water conditions (Wada et al., 2002). Wada et al. (2002) determined the CGR of Japonica-Indica hybrid rice by average LAI under upland conditions. Considering these reports, the determinant factor for CGR might differ depending on the soil water condition. Additionally, in the present study, the CGR was more closely related to the

### Table 5. Accumulated non-structural carbohydrate (NSC) in the leaf and culm at full heading (FH), 20 days after full heading (DAFH20), and maturity stage (MT), and decrease in NSC from FH to DAFH20 in NERICA 1 (N1), NERICA 5 (N5), Yumenohatamochi (YHM), and Hinohikari (HH) grown under three water management regimes: continuously flooded (FL), supplemental irrigation (IR), and non-irrigation (NIR), in 2011 and 2012.

| Variety | FL | IR | NIR | IR/FL | NIR/FL |
|---------|----|----|-----|-------|--------|
| NSC (g m$^{-2}$) | | | | | |
| FH | | | | | |
| N1 | 102 a | 92 ab | 110 ab | 90 | 107 |
| N5 | 77 a | 62 b | 75 b | 81 | 98 |
| YHM | 65 a | 64 b | 71 b | 98 | 109 |
| HH | 106 a | 138 a | 133 a | 130 | 126 |
| DAFH20 | | | | | |
| N1 | 20 b | 14 b | 18 c | 66 | 88 |
| N5 | 22 b | 22 b | 20 c | 101 | 91 |
| YHM | 22 b | 33 b | 41 b | 148 | 182 |
| HH | 93 a | 111 a | 110 a | 119 | 118 |
| MT | | | | | |
| N1 | 57 c | 29 b | 29 c | 51 | 50 |
| N5 | 23 d | 23 b | 23 c | 97 | 98 |
| YHM | 93 b | 96 ab | 62 b | 103 | 67 |
| HH | 128 a | 124 a | 126 a | 97 | 98 |
| NSC$_{FH-DAFH20}^1$ (g m$^{-2}$) | | | | | |
| N1 | 8 a | 9 a | 8 a | 79 | 96 |
| N5 | 55 ab | 40 a | 55 ab | 73 | 101 |
| YHM | 43 ab | 31 a | 30 b | 72 | 70 |
| HH | 13 b | 27 a | 24 b | 214 | 188 |
| MT | | | | | |
| N1 | 57 c | 57 c | 57 c | 57 c | 57 c |
| N5 | 23 d | 23 b | 23 c | 97 | 98 |
| YHM | 93 b | 96 ab | 62 b | 103 | 67 |
| HH | 128 a | 124 a | 126 a | 97 | 98 |
| ΔNSC$_{FH-DAFH20}^1$ (g m$^{-2}$) | | | | | |
| N1 | 8 a | 9 a | 8 a | 79 | 96 |
| N5 | 55 ab | 40 a | 55 ab | 73 | 101 |
| YHM | 43 ab | 31 a | 30 b | 72 | 70 |
| HH | 13 b | 27 a | 24 b | 214 | 188 |

Within each column, values followed by the same letter are not significantly different at $P < 0.05$. Numbers in italics indicate the relative value of each yield parameter under IR or NIR to that under FL for each variety. 1) The decrease in NSC from FH to DAFH20.

![Figure 8](https://example.com/figure8.png)

Figure 8. Relationship between the decrease in non-structural carbohydrate (NSC) and $\Delta T$ in NERICA 1 (□, ●), NERICA 5 (○, ●), Yumenohatamochi (◇, ◆), and Hinohikari (△, ▲) during the half stage of ripening period under different soil water management regimes: continuously flooded, supplemental irrigation, and non-irrigation, in 2011 and 2012. ** indicates significant at 1%. The open symbols represent data in 2011 and the closed symbols represent data in 2012. The solid line indicates common regression line for all varieties in both years. 1) The decrease of NSC from FH to 20 days after full heading. 2) Translocated pre-heading reserve assimilates from the leaf and stem to the panicle from full heading to 20 days after full heading.
NAR than average LAI in each water treatment, although these relationships were not significant because of lack of replications (data not shown). To maintain a high NAR, it is important to maintain high root activity and nutrient supply to the aboveground parts (Osaki et al., 1997). In our study, we considered that the decrease in NAR with the decrease in soil moisture was related to root activity during ripening (Figures 6 and 7). The higher absorption of nitrogen through higher root activity contributed to the increase in RuBP carboxylase, resulting in improved photosynthetic capacity (Ito et al., 2006). Thus, the decrease in ΔW under low soil moisture might be attributed to the decrease in dry matter production during ripening, which could be explained by the decline in photosynthetic rate due to reduction in nutrient and water absorption in the root system.

**Varietal differences**

ΔW was lower in both NERICA varieties than in Yumenohtamochi and Hinohikari, and this tendency was more pronounced under low soil water condition in 2011 (Table 3). A similar trend was observed for CGR (Table 4). The differences between NRICAs and the Japanese varieties were mainly caused by smaller leaf area per unit area of NRICAs under all conditions and the decrease in photosynthetic rate under low soil water conditions (Table 4). Contrarily, ΔNSC, the decrease in NSC from full heading to 20 days after full heading, was higher in NRICAs than in the Japanese varieties (Table 5). In addition, ΔNSC was similar to ΔT during the same period (Figure 8), suggesting that the NSC were mostly translocated to the panicles. These results are in agreement with those reported by Inoue et al., (2015), who found that NRICAs have a high accumulation efficiency of degradable matter, which can be translocated to the panicles during the early grain-filling period. However, NSC in NRICAs during the late grain-filling period was lower than that in the Japanese varieties (Table 5), indicating that NRICAs did not re-accumulate carbohydrates in the leaf sheath and culms during the late grain-filling period. These results indicate that NRICAs have less surplus carbohydrates than Japanese varieties, suggesting that carbohydrate shortage might occur if the sink size is increased.

Yun et al. (1997) reported that an upland variety was more dependent on post-heading photosynthates than a lowland variety grown under upland condition. However, in Yumenohtamochi, the proportion of ΔW in total carbohydrates of panicle was higher than that of ΔT (Table 3). In addition, ΔW in Yumenohtamochi was not significantly affected by water management like the other varieties (Table 3). Specifically, ΔW in Yumenohtamochi under NIR in 2012 was comparable with that under FL. This can be attributed to deeper rooting characteristic (Hirasawa et al., 1998; Nemoto et al., 1998) and the ability to maintain root activity during ripening (Figure 6).

The reduction rate of ΔW under low soil moisture conditions to continuously flooded condition was higher for NERICA 1 than for NERICA 5 (Table 3). Furthermore, NERICA 1 had a lower proportion of post-heading photosynthates in total carbohydrates of the panicle than NERICA 5, irrespective of the water management strategy. Dry matter production during ripening was more strongly influenced by soil moisture condition in NERICA 1 than in NERICA 5. Thus, we found that there are genotypic differences in the dry matter partitioning characteristics among NRICAs. NERICA 1 tended to have lower CGR than NERICA 5 during the ripening stage (Table 4). Yang et al., (2004), who investigated varietal differences among nine rice varieties including NERICA 1, reported that NERICA 1 showed the lowest CGR during ripening. The root activity at full heading stage was higher in NERICA 1 than in other varieties in all treatments; however, it decreased drastically in comparison with that in the other varieties (Figure 6). On the contrary, root activity of NERICA 5 was maintained at the same level from full heading to maturity stages under FL and NIR. Root activity during ripening maintains photosynthetic capacity (Ito et al., 2006). Thus, the drastic decrease in NAR in NERICA 1 compared with NERICA 5 could be attributed to insufficient water and nutrient uptake necessary for the plant to grow due to the rapid decline in root activity at the late grain-filling stage. Although further study is needed to clarify the relationship between root activity and dry matter production in NERICA 1 during ripening, it was considered that the lower CGR in NERICA 1 during the ripening stage was not caused by water stress, but by a variety characteristic. Moreover, the low CGR of NERICA 1 during ripening was found to be more remarkable under low soil moisture conditions.

Generally, in lowland rice varieties, the proportion of pre-heading reserve assimilates in total carbohydrates in the panicles is lower than post-heading photosynthates, which has been reported to be approximately 20-40% in lowland rice varieties (Murata & Matsushima, 1975; Yoshida, 1972). Yun et al. (1997) reported that upland rice varieties depend more on stored carbohydrates than lowland varieties. Moreover, heavy panicle-type varieties with large sink size tend to have a higher proportion of pre-heading reserve assimilates in total carbohydrates in the panicles (Gendua et al., 2009; Kusutani et al., 1993; Miah et al., 1996; Saitoh et al., 1991; Song et al., 1990; Yamamoto, 1991). NERICA varieties are classified as
panicle weight-type (Tsunematsu & Takagi, 2004) because of the higher number of spikelets per panicle and fewer panicles (Kikuta et al., 2017; Matsunami et al., 2009; Wainaina et al., 2015). Thus, morphological characteristics of the panicles might explain the higher proportion of pre-heading reserve assimilates in the total carbohydrate in the panicles of NERICAs (Table 3).

Conclusions

Under different water management conditions throughout the growth period, the total carbohydrate content was determined by post-heading photosynthetic content rather than the translocation of pre-heading reserve assimilates. Source capacity and activity during ripening tended to decrease under low soil water conditions. As a result, the proportion of pre-heading reserve assimilates to total carbohydrate translocated to the panicles increased under low soil water conditions and thus the contents of the source in the panicle changed. Furthermore, we found that the source response varied depending on the variety, even among the NERICAs. The translocation rate in the NERICAs was faster than that in the Japanese varieties, resulting in lower accumulation of carbohydrates in the panicles during the late grain-filling period. These results indicate the significance of soil moisture stress during early grain filling in yield reduction in NERICAs. In particular, NERICA 1, a popular upland variety among NERICAs in sub-Saharan Africa, might have a lower ability to assimilate after heading. Therefore, the selection of a suitable NERICA variety on the basis of soil moisture conditions could be important to improve yield. Furthermore, our results imply that improving assimilation ability during ripening may contribute to yield increase in NERICA 1. However, further study on the potential and varietal differences in sink activity in NERICAs under low soil water conditions is warranted.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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