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Effects of Nitrogen Forms on Root System Development, Physiological Traits, and Dry Matter Production of Rice

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Abstract

The objectives of this study were to evaluate the effects of nitrogen forms on root system development (expressed as total root length, nodal root number, nodal root length, and lateral root length), water use, photosynthetic rate, and dry matter production under water deficit (WD) at 20% w/w and continuously waterlogged (CWL) conditions. Rice plants cv. Nipponbare were grown in plastic pots in a vinyl house. Six N forms were applied at the same rate of 360 mg N per pot, and were prepared as follows: N-NH_4^+ alone (A); N-NH_4^+ with nitrification inhibitor (A+DCD); N-NO_3^- alone (N); N-NO_3^- with nitrification inhibitor (N+DCD); combined N-NH_4^+ and N-NO_3^- (AN); and combined N-NH_4^+ and N-NO_3^- with nitrification inhibitor (AN+DCD). The nitrification inhibitor, dicyandiamide (DCD) ($C_2H_4N_4$), was applied at the rate of 100 mg pot^{-1}. The results of the experiment showed that under both WD and CWL conditions, significant increases were seen in the root system development as expressed through total root length, nodal root number, nodal root length, and lateral root length in the N-NO_3^- treatments with and without DCD compared to the application of N-NH_4^+ treatments with and without DCD. This led to an increase in water use, and eventually a significant increase in dry matter production. Similarly, the A treatments with and without DCD also significantly increased root system development as compared with the AN and AN+DCD treatments. Furthermore, under both CWL and WD conditions, the positive and notably significant correlations between the total root length and water use, as well as between the total root length and shoot dry weight, were found only in the A and A+DCD treatments. These results indicate that rice prefers sole ammonium over the mixed ammonium-nitrate treatment, and sole nitrate applications under both WD and CWL conditions.

Keywords

Ammonium, continuously waterlogged, nitrate, rice, root system development, water deficit

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Introduction

Water deficit can be defined as the absence of adequate moisture necessary for a plant to grow normally and complete its life cycle (Zhu, 2002). The lack of adequate moisture leading to water stress is a common occurrence in rain-fed areas, brought about by infrequent rains and poor irrigation. In the rain-fed lowland ecosystem in South and Southeast Asia, rice yield is very low, averaging only 1.5 tons ha^{-1} (Wade *et al*., 1995) as compared to a range of 3-9 tons ha^{-1} in areas where the water supply is sufficient (IRRI, 1997).

Nitrogen (N) is one of the essential macronutrients for plant growth, and one of the main factors considered in the production of high-yielding rice cultivars. Plants can absorb the two inorganic forms of N as ammonium (NH_4^+) and nitrate (NO_3^-) nutrition. The different N forms influence plant growth, but contrasting results have been observed depending on the plant species used. Some upland plants such as maize and wheat have been shown to prefer nitrate to ammonium (Guo *et al*., 2007a). These plants suffered ammonium toxicity when supplied with high ammonium rates as the sole nitrogen source in the root medium. In contrast, having a higher ammonium assimilation capacity than other plant species, rice plants avoid ammonium toxicity and exhibit a preference for ammonium nutrition (Guo *et al*., 2007a). In a paddy field, NH_4^+ rather than NO_3^- tends to be the main source of nitrogen for rice (Wang *et al*., 1993). However, in well-drained soils, NH_4^+ converts rapidly to nitrite (NO_2^-) and then to NO_3^-. Therefore, the main form of nitrogen in upland soils is NO_3^- no matter what form of N fertilizer is applied (Duan *et al*., 2006). Yuan *et al*. (2005) also reported that rice grown in aerobic soil conditions was mainly fed by NO_3^- rather than NH_4^+ nutrition, but that rice usually grows better in NH_4^+ or a mix of $NH_4^+$and NO_3^- forms than in the NO_3^- form.

The rice root system structure and its response to various soil conditions have been studied intensively, including water deficit conditions (Thiem and Yamauchi, 2017), re-watered conditions (Kamoshita *et al*., 2000), and fluctuating soil moisture conditions (Niones *et al*., 2012) in rice fields. The availability of N forms in the soil is dependent on soil moisture conditions, which affect root dry weight (Yang *et al*., 2012), root volume, and total root length (Gao *et al*., 2010) of rice. However, the extent of the effects depends on the cultivar (Song *et al*., 2011). This study, therefore, examined if the root system development, water use, photosynthetic rate, and dry matter production of rice grown under water deficit and continuously waterlogged conditions would be affected by different N form treatments.

Materials and Methods

Plant materials

Nipponbare is a Japanese standard japonica cultivar of rice (Kano-Nakata *et al.*, 2011). The experiments were conducted in a vinyl greenhouse located in an experimental field of Nagoya University, Japan (136°56′6″ E, 35° 9′ 5″ N) on June 2, 2012. The seeds were soaked in water mixed with a fungicide (benomyl (benlate), 0.15% w/v and incubated in a seed germinator maintained at 28°C for 72 h prior to sowing. Three pre-germinated seeds were grown in plastic pots (20 cm in height and 16 cm in diameter) filled with 4.0 kg of air-dried sandy loam soil. The seedlings were thinned to one seedling per pot at 3 days after sowing (DAS).

Experimental design, treatments, and cultural management practices

The soil moisture treatments, water deficit (WD) conditions at 20% w/w and continuously waterlogged (CWL) were similar to those used by Kano-Nakata *et al*. (2011). In the CWL treatment, the water level was maintained at 2 cm above the soil surface from 5 DAS until the end of the experiment at 50 DAS. In the WD conditions, each pot was weighed daily and the amount of water lost was replenished once a day and recorded as evapotranspiration. Four pots without plants were also prepared to measure the amount of water lost through evaporation. Whole plant transpiration was estimated as the difference in water loss between the pots with and without plants. Water use was calculated as the accumulated daily whole plant transpiration rate from 7 DAS until the termination of the experiment (50 DAS).

Six N form treatments were utilized in this experiment, and were at the same rate used by Yamauchi *et al*. (1988) at 360 mg N per pot. The experimental pots were prepared as follows: N-NH_4^+ alone (A); N-NH_4^+ with nitrification inhibitor (A+DCD); N-NO_3^- alone (N); N-NO_3^- with nitrification inhibitor (N+DCD); combination of N-NH_4^+ and N-NO_3^- (AN); and combination of N-NH_4^+ and N-NO_3^- with nitrification inhibitor (AN+DCD). The source of N-NH_4^+ was $(NH_4)_2SO_4$, while the source of N-NO_3^- was $Ca(NO_3)_2$. The nitrification inhibitor, dicyandiamide (DCD) ($C_2H_4N_4$), was applied at the rate of 100 mg pot^{-1}, which retarded the conversion of ammonium to nitrate (Jagrati, 2007). Phosphate (P), supplied by KH_2PO_4, and potassium (K), from KCl, were also added at the rates used by Yamauchi *et al*. (1988) at 480 mg pot^{-1} and 420 mg pot^{-1}, respectively. Each treatment was thoroughly mixed into the soil of each pot manually for 2 min before seed sowing.

Measurements

The photosynthetic rates were measured using a portable photosynthesis analyzer (LI-6400, LI-COR, Lincoln, NE, USA) on the abaxial side of the topmost fully-developed leaf of the main stem between 9 AM and 11 AM at 40 DAS using the following system settings: leaf temperature, 30°C; CO_2 concentration, 380 µL L^{-1}; relative humidity, 65 - 75%; and quantum flux density, 1200 µmol m^{-2} s^{-1}.

At 50 DAS the plants were harvested. Four pots (1 pot = 1 replication) were harvested for each of the treatment combinations. The shoots were cut at the stem base and oven-dried at 70°C for 3 days prior to the recording of the dry weight. The collected root samples were washed free of soil in running water. Cleaned root samples were stored in FAA (formalin: acetic acid: 70% ethanol in a 1:1:18 ratio by volume) solution for preservation before further measurements of various root components were collected. The lengths of nodal roots were measured using a ruler, and the total number of nodal roots at the base of each stem was manually counted. For the total root length measurements, roots were spread on transparent sheets with minimal overlapping. Digital images were then taken using an Epson scanner (ES2200) at 300 dpi resolution. The total length of each root sample was analyzed using Win RHIZO software v. 2007d (Regent Instruments, Quebec, Canada).

Statistical analysis

The experiments were arranged in a completely randomized design with four replications per treatment. The difference in average values between each of the nitrogen treatments was tested by the least significant difference (LSD) test at a 5% level of significance using CropStat version 7.2 (IRRI, 2009). The relationships between total root length and water use, and the relationships between total root length and shoot dry weight were determined using correlation analysis.

Results and Discussion

In this study, we tested both a range of nitrogen forms and combinations of the nitrogen forms with the nitrification inhibitor dicyandiamide (DCD). When the application of N-NH_4^+ is in the soil, it will undergo the nitrification process, whereby soil bacteria in the genus *Nitrosomonas* convert the ammonium to nitrite and then to nitrate. In our previous study (Thiem *et al*., 2015), we observed that in both the WD at 20% w/w and CWL conditions, the amount of N-NH_4^+ in the soil was higher in the A+DCD and AN+DCD treatments than in the A and AN treatments. In contrast, the amount of N-NO_3^- in the soil was lower in the A+DCD and AN+DCD treatments than in the A and AN treatments only under the WD at 20% w/w condition. These results indicated that DCD inhibited the conversion of ammonium to nitrate. In the present study, under both WD and CWL conditions, the shoot dry weight, photosynthetic rate, water use, and all root traits were numerically higher in the A+DCD treatment than in the A treatment, although they were not statistically different ($P<0.05$) (Figures 1, 2, and 3, and Table 1). Similarly, there were no significant differences in shoot dry weight, photosynthetic rate, water use, and all the root traits between the AN and AN+DCD treatments, as well as between the N and N+DCD treatments under both WD and CWL conditions. Our results, which indicate that DCD did not affect plant growth, were also reported by Li *et al*. (2009). We will address comparisons between the nitrogen form treatments with the addition of DCD to the nitrogen form treatments without the addition of DCD in the succeeding sections.

Response of rice shoot growth to the N forms

The effects of the nitrogen form treatments on the shoot dry weight of Nipponbare rice grown under WD at 20% w/w of soil moisture content (SMC) and CWL conditions are presented in Figure 1. The results indicate that the response of shoot dry matter to the nitrogen forms was significantly different (*P<0.05*) regardless of SMC. When comparing the N and N+DCD treatments, the A and A+DCD treatments significantly increased shoot dry weight by 1.1 - 1.9 g plant^{-1} and 2.8 - 2.9 g plant^{-1} under WD and CWL conditions, respectively. Similarly, when comparing the AN and AN+DCD treatments, the A and A+DCD treatments also significantly increased (*P<0.05*) shoot dry weight by 0.3 - 0.8 g plant^{-1} and 1.9 - 2.1 g plant^{-1} under WD and CWL conditions, respectively. In addition, there was a significant difference in shoot dry weight between AN and AN+DCD treatments, and between N and N+DCD treatments. These results indicate that Nipponbare prefers sole ammonium over the mixed ammonium-nitrate and sole nitrate applications. Li *et al.* (2009) also observed that under water stress conditions, ammonium nutrition increased the biomass of rice plants in both hydroponic and pot experiments in comparison with nitrate nutrition.

Response of rice water use to the N forms

Figure 2 shows the effects of the N form treatments on the water use of Nipponbare rice grown under WD at 20% w/w of SMC and CWL conditions. The results showed that water use differed significantly (*P<0.05*) among the different N form treatments under both WD and CWL conditions. Under the CWL condition, rice tended to consume more water than under the WD condition, regardless of the N form treatment. Water use of the A and A+DCD treatments was significantly higher than in the N and N+DCD treatments by 314.1 - 526.0 g plant^{-1} under WD conditions, and by 704.7 - 842.2 g plant^{-1} under CWL conditions. Similarly, water use was significantly higher for

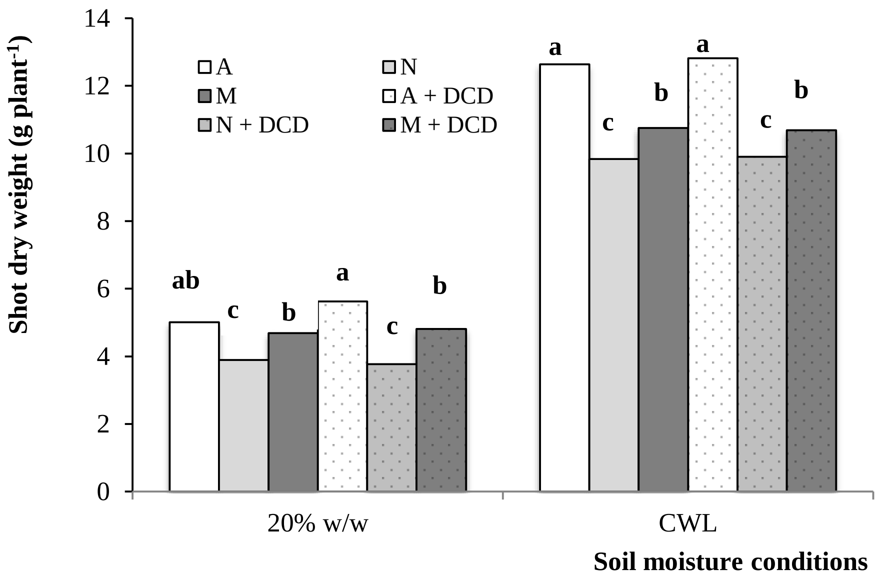

Figure 1. Effects of the nitrogen form treatments on shoot dry weight of rice under WD at 20% w/w of SMC and CWL conditions

Note: Columns with the same letter within each treatment are not significantly different at the 5% level.

the A and A+DCD treatments than in the AN and AN+DCD treatments by 148.0 - 205.5 g $plant^{-1}$ and 165.5 - 257.0 g $plant^{-1}$ under WD and CWL conditions, respectively. These results are consistent with Guo *et al*. (2008) who observed that ammonium nutrition improved water use efficiency of rice under water stress conditions. It was suggested that ammonium nutrition could enhance the drought tolerance of rice plants under non-flooded conditions, and this could be important in field situations.

Response of rice photosynthetic rate to the N forms

There were significant differences (*P<0.05*) in photosynthetic rates of plants grown under SMC of WD at 20% w/w and CWL conditions among nitrogen form treatments (Figure 3). Numerous studies have demonstrated that ammonium-supplied plants have a higher photosynthetic rate than nitrate supplied plants (Guo *et al*., 2007a, 2007b, and 2008). In the present study, when the N and N+DCD treatments were compared to the A and A+DCD treatments, the photosynthetic rate significantly increased by 2.6 - 3.4 μmol $m^{-2}s^{-1}$ under WD conditions and by 3.9 - 6.3 μmol $m^{-2}s^{-1}$ under CWL conditions. Similarly, a significant increase in photosynthetic rate was observed when the AN and AN+DCD treatments were compared with the A and A+DCD treatments under both WD and CWL conditions by 1.4 - 2.2 μmol $m^{-2}s^{-1}$ and 3.2 - 3.5 μmol $m^{-2}s^{-1}$, respectively.

Response of rice root system development to the N forms

The results of the effects of the nitrogen forms under WD and CWL conditions on root system development were expressed as the total root length, number of nodal roots, total nodal root length, and total lateral root, and are presented in Table 1. The results consistently demonstrate significant effects of the SMC and N form factors on all the above root traits. Therefore, there were also significant two-way interactions between the SMC and N forms on all the traits examined.

Song *et al*. (2011) studied the effects of nitrogen forms on root growth of two rice cultivars. They found that the response of root growth to nitrogen forms is dependent on the cultivars. In our present study, all root traits were significantly different among nitrogen form treatments (Table 1), under both WD and

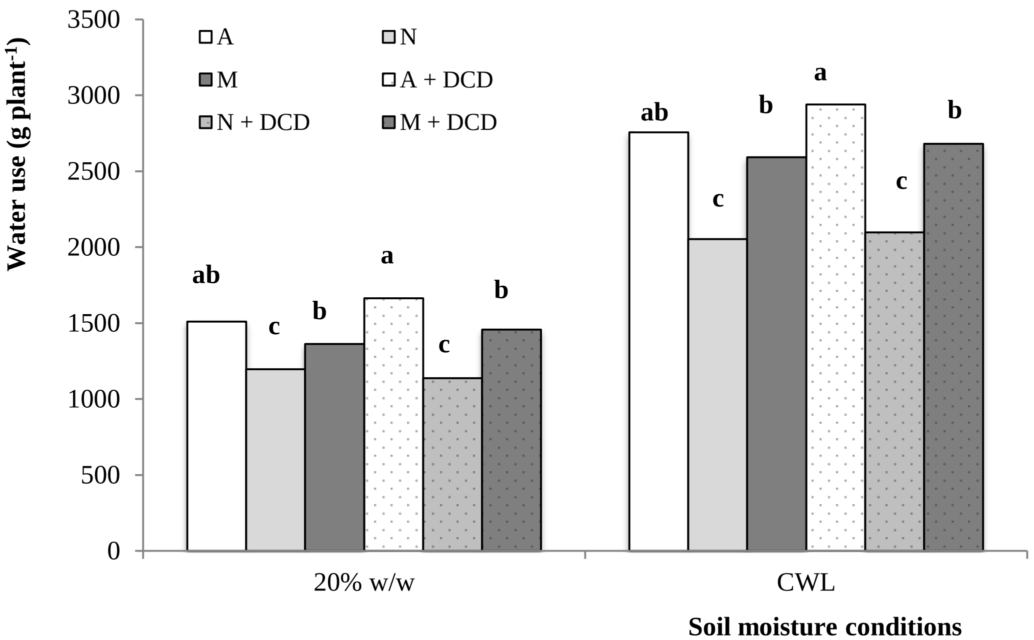

Figure 2. Effects of the nitrogen form treatments on water use of rice under WD at 20% w/w of SMC and CWL conditions

Note: Columns with the same letter within each treatment are not significantly different at the 5% level.

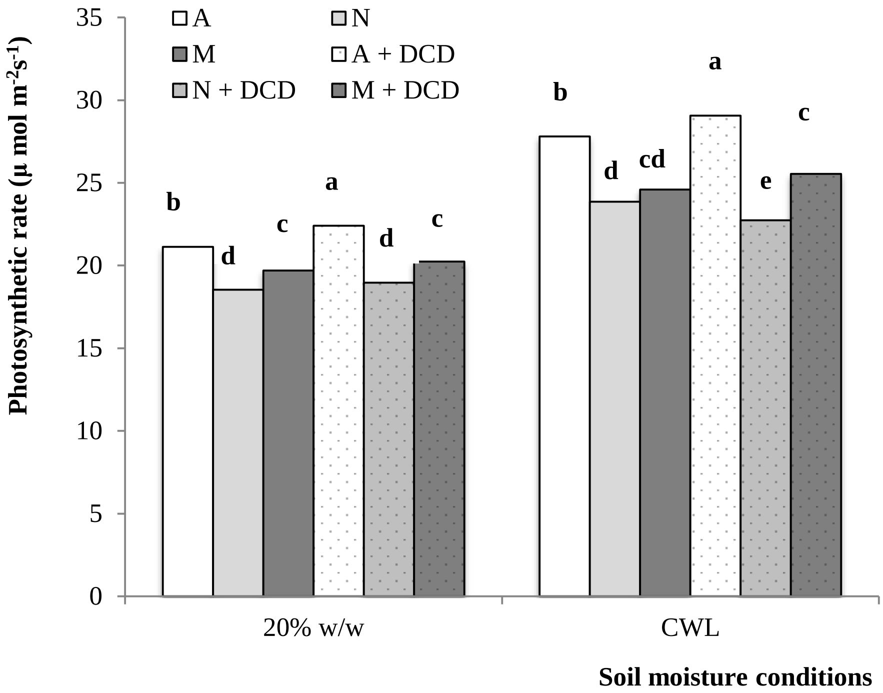

Figure 3. Effects of the nitrogen form treatments on the photosynthetic rate of rice under WD at 20% w/w of SMC and CWL conditions

Note: Columns with the same letter within each treatment are not significantly different at the 5% level.

CWL conditions. The total root length significantly increased in the A and A+DCD treatments in comparison with the N and N+DCD treatments by 5.2 - 6.1 m plant^{-1} under WD conditions, and by 26.7 - 28.2 m plant^{-1} under CWL conditions. Similarly, as compared with the AN and AN+DCD treatments, the A and A+DCD treatments significantly increased in total root length by 2.5 - 3.7 m plant^{-1} and 20.0 - 21.2 m plant^{-1} under WD and CWL conditions, respectively. The increased total root length for the A and A+DCD treatments compared to the N and N+DCD treatments was due to the combination of significant increases in nodal root number, nodal root length, and lateral root length: 28.5 - 35.5 no. plant^{-1}, 2.5 - 4.6 cm plant^{-1}, and 1.5 - 2.7 cm plant^{-1} under WD conditions, and 96.3 - 102.2 no. plant^{-1}, 16.2 - 16.4 cm plant^{-1}, and 10.3 - 11.9 cm plant^{-1} under CWL conditions, respectively. Similarly, the nodal root length and lateral root length for the A and A+DCD treatments were significantly higher than for the AN and AN+DCD treatments: 9.8 - 14.0 no. plant^{-1}, 3.2 cm plant^{-1}, and 1.7 cm plant^{-1} under WD; and 63.5 - 69.5 no. plant^{-1}, 10.6 - 13.7 cm plant^{-1}, and 7.5 - 9.3 cm plant^{-1} under CWL conditions, respectively. However, there were no significant differences in the nodal root lengths between the A and AN treatments, nor in the lateral root lengths between the A+DCD and AN+DCD treatments under WD conditions.

Relationships between total root length and water use

Figure 4 shows the relationship between the total root length and water use of rice plants with different nitrogen form treatments under WD and CWL conditions. In the N treatments with or without the addition of DCD, there was not a correlation between the total root length and water use. Similarly, total root length was also not found to be correlated with shoot dry weight for the AN treatments with or without the addition of DCD. However, the application of the A treatments with or without the addition of DCD increased the total root length (Table 1), which increased water use (Figure 2), and thus led to a positive correlation (*P<0.05*) between the total root length and water use under both WD and CWL conditions (Figures 4a and 4b).

Table 1. Effects of the nitrogen form treatments on root system development of rice under WD at 20% w/w of SMC and CWL conditions

Soil moisture conditions	Nitrogen form treatments	TRL (cm $plant^{-1}$)	NRN (no. $plant^{-1}$)	NRL (cm $plant^{-1}$)	LRL (cm $plant^{-1}$)
20% w/w	A	45.1a	155.8ab	22.4ab	22.7a
	N	39.9c	127.3c	19.9c	20.0c
	AN	42.6b	141.8b	21.6b	21.0b
	A+DCD	46.5a	160.3a	23.3a	23.2a
	N+DCD	40.4c	124.8c	18.7d	21.7b
	AN+DCD	42.8b	150.5b	20.1c	22.7a
CWL	A	93.9a	385.5a	60.4a	33.4a
	N	65.7c	283.3c	44.2d	21.5d
	AN	73.9b	322.0b	49.8b	24.1c
	A+DCD	94.3a	387.3a	60.7a	33.6a
	N+DCD	67.6c	291.0c	44.3d	23.3c
	AN+DCD	73.1b	317.8b	47.0c	26.1b
SMC		**	**	**	**
N		**	*	**	**
SMC&N		**	*	**	**

*Notes: TRL: total root length; NRN: number of nodal roots; NRL: nodal root length; LRL: lateral root length. Values followed by the same letter in each treatment column are not significantly different at the 5% level by Fisher's LSD test. * and ** denote the significance levels at the 5% and 1% levels, respectively.*

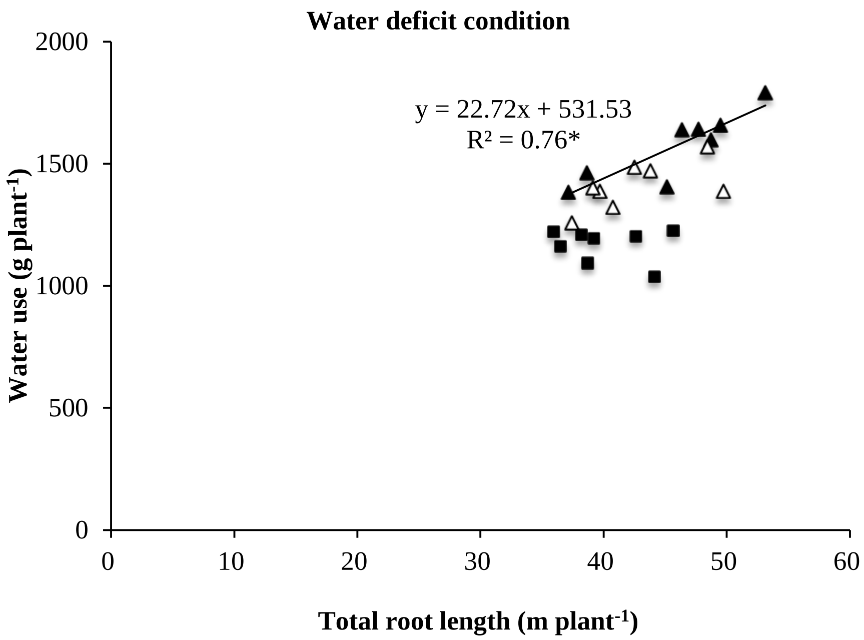

Figure 4a. Relationship between total root length and water use of rice grown under WD conditions with N form treatments

Notes: ▲: y = 22.72 x + 531.53, r = 0.87 for A treatments with or without DCD; ■: y = -3.40x + 1303.6, r = 0.12ns for N treatments with or without DCD; △: y = 13.67x + 825.68, r = 0.62ns for AN treatments with or without DCD; ns: not significant. * denotes the significance level at P<0.05.*

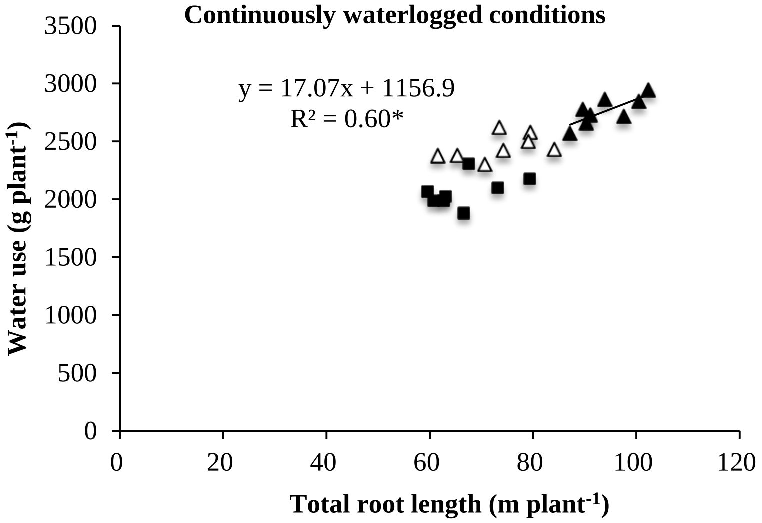

Figure 4b. Relationship between total root length and water use of rice grown under CWL conditions with N form treatments

Notes: ▲: y = 17.07x + 1156.9, r = 0. 78 for A treatments with or without DCD; ■: y = 8.78x + 1478.8, r = 0.45ns for N treatments with or without DCD; △: y = 6.67x + 1960.9, r = 0.46ns for AN treatments with or without DCD; ns: not significant. * indicates significance level at P<0.05.*

Relationships between total root length and shoot dry weight

The relationship between the total root length and shoot dry weight was significantly correlated under mild drought stress conditions (Kano-Nakata *et al.*, 2011). In this study, under both WD and CWL conditions, the total root length showed close correlations (at $P<0.05$ and 0.01, respectively) with shoot dry weight, and the curvilinear regression was highly significant for the A with and without DCD treatments. However, the relationship between the total root length and shoot dry weight was not significant in the N with and without DCD treatments as well as in the AN with and without DCD treatments (Figures 5a and 5b).

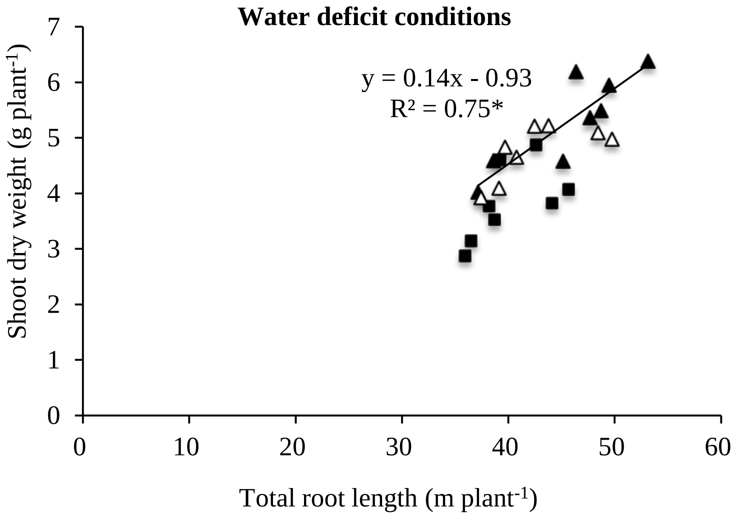

Figure 5a. Relationship between total root length and shoot dry weight of rice grown under WD conditions with N form treatments

Notes: ▲: y = 0.14x - 0.93, r = 0.87 for A treatments with or without DCD; ■: y = 0.11x - 0.75, r = 0.60ns for N treatments with or without DCD; △: y = 0.08x + 1.42, r = 0.69ns for AN treatments with or without DCD; ns: not significant. * denotes the significance level at P<0.05.*

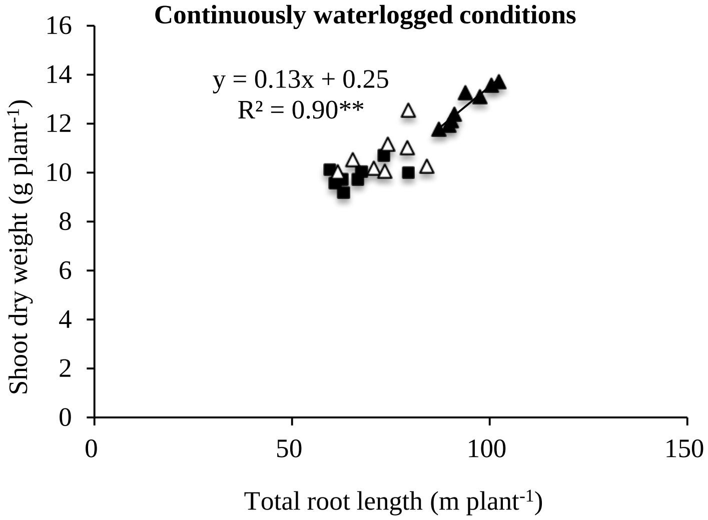

Figure 5b. Relationship between total root length and shoot dry weight of rice grown under CWL conditions with N form treatments

*Notes: ▲: y = 0.13x +0.25, r = 0.95** for A treatments with or without DCD; ■: y = 0.03x + 7.72, r = 0.49ns for N treatments with or without DCD; △: y = 0.05x + 7.11, r = 0.43ns for AN treatments with or without DCD; ns: not significant. ** denotes the significance level at P<0.01.*

Conclusions

The nitrogen form treatments affected the root system development, water use, photosynthetic rate, and dry matter production of rice under both water deficit and continuously waterlogged conditions. Among the six N form treatments, the application of ammonium forms increased the root system development, which then enhanced water uptake, and eventually increased the dry matter production of Nipponbare rice in comparison with the application of nitrate forms, as well as the mixture of nitrate and ammonium forms under both water deficit and continuously waterlogged conditions. Moreover, positive and notably significant relationships were found between the total root length and water use, as well as between the total root length and shoot dry weight in the application of ammonium forms of N.

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