Nitrate application induced a lower yield loss in rice under progressive drought stress

Bo Cheng (chengboo@webmail.hzau.edu.cn)
Huazhong Agriculture University https://orcid.org/0000-0001-6128-8827
Mingli Cai
Huazhong Agriculture University
CouGui Cao
Huazhong Agriculture University
Yang Jiang
Huazhong Agriculture University

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Abstract

Rice plants were subjected to nitrate application and water disruption-induced drought treatments in a screen-house using pot culture, the urea application and flood treatments were used as controls. Nitrate ($Ca(NO_3)_2$) application significantly increased the ratio of NO_3^--N to NH_4^+-N in the soil under both drought and flood treatments. Compared with urea application under flood treatment, both nitrate application and drought treatments caused yield losses. Under drought treatment, the yield loss of rice plant for nitrate application was 28.4% lower than that for urea application. The aboveground plant was smaller and more compact under nitrate application. Although nitrate application did not increase water uptake rate and xylem sap rate of the rice plant, nitrate application significantly stimulated the root growth of rice plant compared with urea application, especially under drought treatment, as indicated by higher root cap ratio, root biomass, root volume, root length, and density of lateral roots. Finally, the soil water potential decreased slower for nitrate application compared with urea application under drought treatment. The leaf water potential was higher for nitrate application compared with urea application under drought treatment. Our results indicated that rice plant developed a series of phenotypic adaptations to nitrate application and progressive drought, such as smaller and more compact aboveground plant, a less active but larger root system. These phenotypic adaptations made rice plant suffer less from the progressive drought stress resulting in a lower yield loss.

1. Introduction

Rice is one of the most important crops in Asia and consumes a large amount of irrigation water (Bouman. 2007). Increasing water shortage has threatened the sustainability of rice production (Davatgar et al. 2009). Drought stress caused by water shortage occurs frequently and becomes a major abiotic factor that restricts the plant growth and productivity (Sharp et al. 2004; Kano et al. 2011; Tran et al. 2014). Drought stress causes yield loss in the late growth stage of cereal crops (Liu et al. 2010). Lots of studies have been done to check the growth and physiological responses of rice to drought stress at early growth stage by subjecting rice to a simulated constant low water potential in solution or soil (Li et al. 2009; Gao et al. 2010; Yang et al. 2012; Ding et al. 2015). However, in the practical rice production, drought stress was often induced by a water disruption caused by water shortage or arid climate. For this water disruption-induced drought, the soil water potential was not constant but decreased over time, which was the progressive drought (Vrp et al. 2012). Studying the growth and physiological responses of rice to progressive drought stress at late growth stage is vital to understand the reason for the yield loss of rice in the practical production.

Rice exhibited a better performance under flooded environment with ammonium nutrition or nitrate-ammonium mixed nutrition because of its higher ammonium assimilation capacity than other rain-fed crops (Britto et al. 2001; Guo et al. 2007a). The ratio of nitrate to ammonium in the soil would increase from the flooded environment to the non-flooded environment (Guo et al. 2007a). Changes in soil N sources and water potential would influence the growth and yield formation of rice plants (Guo et al. 2007b; Guo et al. 2008). The integrated effect on rice growth and yield formation was highly dependent on the phenotypic adaptations of plant to soil N sources and water potential changes (Lin et al. 2005; Guo et al. 2007a; Guo et al. 2007b; Li et al. 2007; Guo et al. 2008; Li et al. 2009; Gao et al. 2010). Among the reported phenotypic adaptation, root traits have proved to be the most promising drought resistance traits (Lynch. 2007; Serraj et al. 2009; Vrp et al. 2011; Vrp et al. 2012). Maintaining the ability of rice to absorb water from soil under drought stress by accessing greater volumes of soil via deeper and more active root system was found to be an important way to improve rice drought resistance adaptability (Lilley and Fukai. 1994; Uga et al. 2013). Various results were observed about the effects of N sources on root growth of rice under drought stress. Some studies demonstrated that nitrate would stimulate root growth of rice under drought stress (Li et al. 2007; Li et al. 2008; Ogawa et al. 2014). However, other studies reported that nitrate would inhibit root growth and reduce root activity of rice under drought stress (Li et al. 2009; Gao et al. 2010; Yang et al. 2012; Ding et al. 2015). These various results are relative with different ways of N sources treatments. In the previous studies, commonly used method of studying the effect of N sources on rice growth was to subject the rice plants to ammonium or nitrate nutrient solutions for a period of time. However, in the paddy soil, the ammonium or nitrate nutrient changes were more complicated, and they have always been nitrate-ammonium mixed nutrition. What is more, in the practical rice production, the most commonly used N source fertilizer in the paddy soil was not ammonium, but urea [$CO(NH_2)_2$]. Besides, the effect of a short term ammonium or nitrate treatment on rice growth and yield formation is different from that of multiple ammonium or nitrate applications during the rice growth duration.

In this study, we maintained a certain amount of nitrate in the soil by applications of nitrate source fertilizer during the whole rice growth duration. The rice plants were subjected to two-stage water disruption-induced progressive drought after the flowering stage. We hypothesized that the nitrate application and drought stress would have integrated effects on rice growth and yield performance, which might be closely associated with a series of rice phenotypic adaptations under nitrate application. These phenotypic adaptations would affect the response of rice plant to the progressive drought and finally affect the yield performance. Therefore, this study aims to (1) investigate the phenotypic adaptations of rice plant to nitrate application and progressive drought (2) and to understand the combined impacts of these phenotypic adaptations on yield performance.

2. Materials And Methods

2.1 Experimental design

A pot experiment was conducted in a screen-house from June to October in 2013 at Huazhong Agricultural University, Wuhan City (29°58'N 113°53'E), Hubei Province, China. The treatments were laid out in a randomized block design with two water treatments (flood and drought) as the blocking factor and two N sources (nitrate and urea), replicated three times. We had 10 pots (10 samples) for each replication. The nitrate and urea source used in this study was $Ca(NO_3)_2$ and $CO(NH_2)_2$. The rice variety used in this study was Minghui63, a typical and elite indica rice, which was widely used in Asia for both production and breeding. Four ten-day-old seedlings were transplanted in each pot. Each pot (40 cm in diameter and 30 cm in height) was filled with 12 kg sieved and air-dried paddy soil. The background values of chemical properties of the soil were as follows: total N, 0.92 g kg^{-1}; NO_3^--N, 5.14 mg kg^{-1}; NH_4^+-N, 2.11 mg kg^{-1}; available phosphorus, 6.59 mg kg^{-1}; available potassium, 122 mg kg^{-1}; organic carbon, 13.15 g kg^{-1}; pH, 6.47. For the drought treatment, approximately 3 cm water above the soil surface was maintained until the flowering stage. After the flowering stage, the water supply was suspended for 7 days and the soil was naturally dried. Regular amount of water was recovered at the 9 days after the flowering stage, and then the water supply was suspended again for 7 days. Then approximately 3 cm water above the soil surface was maintained until rice maturity. The soil water potential was recorded every two hours from 6:00 am to 8:00 pm every day through tensiometers (Jet Fill 2725, Soil Moisture Equipment Corp., Goleta, CA, USA) placed at 15 cm below the soil surface. For the flood treatment, approximately 3 cm water above the soil surface was maintained until the maturing stage. N fertilizer nitrate [($Ca(NO_3)_2$] or urea [$CO(NH_2)_2$] was applied at a rate of 4 g N pot^{-1} with 50% at the basal stage, 20% at the mid-tillering stage and 30% at the panicle initiation stage, respectively. Phosphorus fertilizer (NaH_2PO_4) was applied at a rate of 2 g P_2O_5 pot^{-1} at the basal stage. Potassium fertilizer (KCl) was applied at a rate of 4 g K_2O pot^{-1} with 50% at the basal stage and 50% at the panicle initiation stage. Pests, weeds and diseases were strictly controlled during the growth season to avoid yield losses.

2.2 Data collection and analysis

At 16 days after the flowering stage, tiller number of the four plants per pot were counted and heights of the four plants per pot were measured. Leaf area of the 4 plants per pot was measured by a leaf area meter (Li-Cor 3100, LI-COR Inc., Lincoln, NE, USA). Leaf inclination was calculated from the angle between the leaf and horizontal direction, and the inclination of top three leaves of the four plants per pot were measured. SPAD values of 4 flag leaves per pot were measured using a chlorophyll meter (SPAD-502, Soil-Plant Analysis Development Section, Minolta Camera Co., Osaka, Japan). Water uptake rate was measured by weighing the pot between 9:00 am and 11:00 am. The pot was covered with two layers of plastic sheet to reduce water loss due to evaporation from the soil surface during the weighing process. Four flag leaves were sampled at midnight per pot and then cut into pieces, and leaf water potential was immediately determined using the dew point potentiometer (WP4C, Decagon Devices, USA). The plants per pot were de-topped at 2 cm above the base with a razor blade and then the xylem saps were collected using pre-weighed cotton balls from 7:00 pm to the next 7:00 pm. Xylem saps were collected and weighted. The xylem sap was normalized as xylem sap weight divided by the root fresh weight of the plant.

At 16 days after the flowering stage, rice roots of per pot were sampled and immersed in the water. The roots were separated gently using a tooth-pick to avoid injury before imaging. Morphological parameters (root volume, total root length and number of lateral roots) were measured using the LA1600 scanner (Regent Instruments, Sainte-Foy-Sillery-Cap-Rouge, QC, Canada) and WinRHIZO2008a software. The roots and aboveground plants were oven-dried at 70°C to determine the biomass. Root cap ratio was calculated as the root biomass divided by the aboveground plant biomass. Available N (NH_4^+-N and NO_3^--N) in the soil was determined by FIAStar-5000 continuous-flow analyzer.

The aboveground plants in the pots were taken at the maturity stage. The sampled plants were dissected and oven-dried at 70°C to determine its biomass.

The panicles were threshed, and the filled spikelets were weighed as the grain yield. Differences in grain yields between urea application under flood treatment and other treatments were calculated. Yield loss was calculated as the yield difference divided by the grain yield for urea application under flood treatment.

Means were compared and grouped using analysis of variance by SAS 9.4 (SAS Institute, Inc., Cary, NC, USA), and the least significant difference (LSD) post-hoc test, respectively. Data were presented as the means ± standard deviation (n = 3).

3. Results

3.1 Soil nutrient and water status

With nitrate application, the NO_3^--N in the soil was significantly higher than the NH_4^+-N in the soil (Fig. 1). With urea application, the NH_4^+-N in the soil was significantly higher than NO_3^--N in the soil (Fig. 1). The ratios of NO_3^--N to NH_4^+-N in the soil were 3.85 and 0.43 for nitrate application and urea application under drought treatment, respectively (Fig. 1). And the ratios of NO_3^--N to NH_4^+-N in the soil were 1.93 and 0.09 for nitrate application and urea application under flood treatment, respectively (Fig. 1). Daily mean soil water potential of drought treatment decreased rapidly once the water supply was suspended for both nitrate application and urea application during the two-stage drought treatment (Fig. 2). The daily mean soil water potentials for nitrate application decreased slower than those for urea application. The daily mean soil water potentials for nitrate application were 19.84% and 20.54% higher than those for urea application at the end of each stage of drought treatment, respectively.

3.2 Yield performance

Drought treatment significantly decreased the grain yield of rice plants (Table 1). Under flood treatment, the grain yield and biomass of the rice plants for nitrate application were lower than those for urea application. However, under drought treatment, grain yield for nitrate application was higher than that for urea application, and there was no significant difference in biomass between nitrate application and urea application. Drought treatment and nitrate application all brought yield losses when compared with urea application under flood treatment. It was interesting to note that, nitrate application induced a lower (28.4%) yield loss compared with urea application under drought treatment. Water treatment, N source and water treatment × N source all exerted significant influences on rice yield performance (Table 1).

Table 1
Yield performance for nitrate application and urea application under different water treatments.

Water treatment	N source	Grain yield (g pot^{-1})	Biomass (g pot^{-1})	Yield loss (%)
Drought	Nitrate	76.6 ± 3.1 c	214.7 ± 11.2 c	43.4 ± 1.6 b
	Urea	53.4 ± 2.8 d	225.6 ± 9.2 c	60.6 ± 1.2 a
Flood	Nitrate	106.6 ± 4.9 b	268.4 ± 8.7 b	21.3 ± 2.4 c
	Urea	135.4 ± 5.2 a	321.2 ± 12.5 a	–
Analysis of variance				
Water treatment		**	**	**
N source		**	*	**
Water treatment × N source		**	*	**
Data are presented as the means ± standard deviation (n = 3). Lowercase letters indicate LSD (*α = 0.05*) grouping of means across different treatments. Means with the same letter are not significantly different. The * indicate a significant source of variation at *α = 0.05* while ** at *α = 0.01.*				

3.3 Aboveground plant traits

Nitrate application induced a small rice plant reflected by the significantly reduced leaf area, tillers and plant height under different water treatments (Table 2). Nitrate application also caused a lower leaf SPAD under flood treatment. But there was no significant difference in leaf SPAD between nitrate application and urea application under drought treatment. Water treatment, N source and water treatment × N source all exerted significant influences on the leaf area and leaf SPAD (Table 2). N source significantly affected the tillers and plant height (Table 2). Nitrate application significantly increased the leaf inclination of leaves at different phyllotaxis under different water treatments compared with urea application (Fig. 3), which meant the canopy of rice plant was more compact for nitrate application. The phenotypic differences for nitrate application and urea application under drought treatment were shown in Fig. S1. The leaf water potential was 23.23% higher for nitrate application under drought treatment compared with urea application (Fig. 4). Under flood treatment, there were no significant differences in leaf water potential between nitrate application and urea application.

Table 2
Agronomic traits for nitrate application and urea application under different water treatments.

Water treatment	N source	Leaf area (cm^2 pot^{-1})	SPAD	Tillers (pot^{-1})	Plant height (cm)
Drought	Nitrate	5614 ± 36 d	31.3 ± 0.6 c	55.4 ± 2.3 b	111.8 ± 4.6 b
	Urea	7736 ± 73 b	32.2 ± 0.2 c	74.1 ± 3.4 a	127.4 ± 3.3 a
Flood	Nitrate	6125 ± 65 c	34.1 ± 0.8 b	53.6 ± 3.2 b	113.6 ± 5.3 b
	Urea	8342 ± 53 a	37.3 ± 1.0 a	72.2 ± 4.6 a	128.1 ± 5.6 a
Analysis of variance					
Water treatment		*	**	NS	NS
N source		**	*	**	*
Water treatment × N source		*	*	NS	NS

Data are presented as the means ± standard deviation (n = 3). Lowercase letters indicate LSD (*α = 0.05*) grouping of means across different treatments. Means with the same letter are not significantly different. The * indicate a significant source of variation at *α = 0.05* while ** at *α = 0.01*. NS means not significant.

3.4 Root traits and activity

Nitrate application significantly stimulated the root growth of rice plants compared with urea application, especially under drought treatment, as indicated by the higher root cap ratio, root biomass, volume, length, and density of lateral roots (Table 3). The density of lateral roots had the largest increase (72.1%) for nitrate application among these rice root traits compared with urea application under drought treatment. Water treatment, N source and water treatment × N source all exerted significant influences on the root traits (Table 3). Water uptake rate and xylem sap rate for nitrate application were lower compared with urea application under different water treatments (Fig. 5). Drought treatment decreased the water uptake rate and xylem sap rate compared with flood treatment. The differences in water uptake rate and xylem sap rate between nitrate application and urea application under drought treatment were smaller than those under flood treatment.

Table 3
Root traits for nitrate application and urea application under different water treatments.

Water treatment	N source	Root cap ratio	Root biomass (g pot^{-1})	Root volume (cm^3 pot^{-1})	Total root length (m)	Density of lateral roots (cm^{-1} of primary root)
Drought	Nitrate	0.26 ± 0.03 a	61.7 ± 2.2 a	497.2 ± 10.2 a	334.4 ± 8.6 a	10.5 ± 0.7 a
	Urea	0.17 ± 0.02 bc	44.4 ± 1.3 c	323.3 ± 9.4 c	225.5 ± 8.1 c	6.1 ± 0.4 c
Flood	Nitrate	0.22 ± 0.02 ab	50.8 ± 2.0 b	412.4 ± 6.6 b	297.7 ± 11.2 b	8.1 ± 0.4 b
	Urea	0.15 ± 0.01 c	42.2 ± 1.8 c	298.7 ± 9.7 c	194.1 ± 12.8 c	5.4 ± 0.2 c
Analysis of variance						
Water treatment		*	*	*	*	**
N source		**	**	**	**	**
Water treatment × N source		*	*	*	**	**

Data are presented as the means ± standard deviation (n = 3). Lowercase letters indicate LSD (*a = 0.05*) grouping of means across different treatments. Means with the same letter are not significantly different. The * indicate a significant source of variation at *a = 0.05* while ** at *a = 0.01*.

4. Discussion

Rice is a typical ammonium-loving crop. Lots of studies had demonstrated that rice could grow better and gain higher yield under ammonium-source fertilizer application under conventional flood environment (Britto et al. 2001; Guo et al. 2007a; Tabuchi et al. 2007; Kronzucker et al. 2010). In our study, the rice also gained a higher grain yield under urea application compared with nitrate application under flood treatment (Table 1). However, under drought treatment, grain yield was higher for nitrate application compared with urea application. As biomass was invariable between nitrate and urea as sources of N under drought treatment, partitioning of dry matter appeared to contribute to higher grain yield when nitrate was used as a source of N (Table 1), which meant the nitrate application improved the assimilate productivity of the rice plant under drought treatment compared with urea application. This is mainly due to the interactions between N sources and water treatments.

Both N sources and soil water status would affect the root growth of the plant. In our study, after the two-stage progressive drought treatment, we found the rice plant had a larger root system for nitrate application compared with urea application (Table 3). Some studies also indicated that nitrate nutrition would stimulate root growth of the plant under different soil water status. For example, enriched supply of nitrate was found to promote the lateral root elongation (Zhang and Forde. 1998; Zhang and Forde. 2000). And Ogawa et al. (2014) and Li et al. (2007) found that some rice lines had higher root length and higher root biomass under nitrate nutrition than under ammonium nutrition. Besides, Li et al. (2008) reported that the nitrate-ammonium mixed nutrition increased the root length, root surface area and root density compared with ammonium nutrition. However, different results were found when scientists subjected rice seedlings to polyethylene glycol-induced drought stress using hydroponic culture. Gao et al. (2010) demonstrated that rice seedlings supplied with ammonium nutrition had increased numbers of root tips and a larger root surface area compared with nitrate nutrition. And Ding et al. (2015) found that drought stress decreased the root elongation rate in rice seedlings when they were supplied with nitrate nutrition. These results indicated that the effect of N sources on rice root phenotypic traits were different, which depending on the methods of N sources and water treatments. Although various effects of N sources on root phenotypic traits were observed, the consensus in previous studies was that the nitrate nutrition would decrease the root activity of rice plant compared with ammonium nutrition (Li et al. 2009; Gao et al. 2010; Yang et al. 2012; Ding et al. 2015). Rice is an ammonia-loving crop that easily absorbs ammonia-nitrogen, and nitrate will reduce its root activity. Recent studies showed that the regulation mechanism of ammonia and nitrate nitrogen on rice root activity is closely related to pH and microorganism in the rhizosphere (Chen et al. 2017; Oldroy et al. 2020). In our study, to get as close to the actual condition as possible, we set the water disruption-induced drought treatment using soil culture and took the urea application as the control. What is more, instead of a period N sources treatment, multiple nitrate and urea applications during the rice growth duration were proceed in our study. Consistent with the previous studies, the root activity of rice plant for nitrate application was lower compared with urea application in our study (Fig. 5). Our results indicated that the nitrate application in the paddy soil obviously stimulated root growth of the rice plant compared with urea application, but did not improve the root activity.

Compared with the various results of effects of N sources on root growth of rice plant in the previous studies, the effects of N sources on abovegroud plant growth were relatively consistent. All the previous evidences pointed that nitrate nutrition would inhibite the aboveground plant growth of rice compared with ammonium nutrition (Lin et al. 2005; Guo et al. 2007a; Li et al. 2009). Similar phenomena was observed in our study. Whether under flood or drought treatment, the aboveground rice plant for nitrate application was smaller compared with urea application (Table 2). Moreover, our results also showed that the aboveground plant was not only smaller but also more compact for nitrate application, which was reflected by the angle between the canopy leaves and the stem became smaller (Fig. 3). A smaller and more compact plant was proved to have lower water demand and transpiration (Kondo et al. 2004; Giuliani and Edwards. 2013). Our results further revealed the rice plant for nitrate application had higher leaf water potential after the two-stage progressive drought treatment.

Compared with solution, soil has a stronger buffering effect on fertilizer application (Nye. 1966; Mendoza. 1989). In our study, nitrate application significantly increased the concentration of NO_3^--N in the soil (Fig. 1). However, there was still a certain amount of NH_4^+-N in the soil. Our result also showed that the drought treatment would also increase the ratio of NO_3^--N to NH_4^+-N in the soil, which is the same as previous studies (Hartmann et al. 2013; Tran et al. 2015). The available N nutrition in the soil was a nitrate–ammonium mixed nutrition. Some studies had checked the effects of nitrate–ammonium mixed nutrition (different ratios of nitrate to ammonium) on rice plant. Other previous studies indicated that the rice plant usually grew better under nitrate–ammonium mixed nutrition than under sole nitrate nutrition (Guo et al. 2007a; Guo et al. 2008). In our study, we did not combine the nitrate and urea nutrition source by ratios. Therefore, investigating the combined effects of nitrate nitrogen and urea on rice plants under drought stress is an important direction of the next step. Beyond that, the nitrate used in our study was $Ca(NO_3)_2$, which could increase the Ca^{2+} concentration in the soil. The intracellular Ca^{2+} has been found to regulate the responses of the plant to drought stress (Sanders et al. 1999; Saijo et al. 2000). Therefore, we could not rule out the possibility that both N source and Ca^{2+} affected the plant growth under drought stress in our study. For the soil water status, though the water supply was suspended at the same time and lasted for the same time for nitrate application and urea application under drought treatment. The soil water potential decreased slower for nitrate application compared with urea applicattion (Fig. 2). These indicated that the plants for nitrate application and urea application under drought treatment were actually facing different ratios of NO_3^--N to NH_4^+-N nutrition and different degrees of drought stresses.

5. Conclusions

According to ahead discussions, we combined our results and teased out the reasons for the lower yield loss of rice plant for nitrate application under drought treatment as follows. The nitrate application increased the ratio of NO_3^--N to NH_4^+-N in the soil resulting in smaller and more compact aboveground plant and less active but larger root system compared with urea application. These phenotypic changes reduced the water demand and water uptake of the rice plant, leading to slower decrease of the soil water potential. The slower decrease of soil water potential meant the rice for nitrate application actually suffered a relatively lighter drought stress compared with the rice plant for urea application, and it also verified by the higher leaf water potential of the rice plant for nitrate application under drought treatment. Our results indicated that with nitrate application treatment, the plant developed a series of adaptive traits for a high ratio of NO_3^--N to NH_4^+-N in the soil. In this sense, we inferred that nitrate application would improve the adaptability of rice to the changes in soil induced by drought treatment. In conclusion, the phenotypic adaptations to nitrate application made the rice plant suffered less from progressive drought stress resulting in a lower yield loss.

Declarations

Declaration of competing interest

Authors declare that there are no conflicts of interest.

Author contributions

Conceived and designed the experiments: JY, CCG and CML. Performed the experiments: JY, CCG and CML. Analyzed the data: JY, CB. Wrote the paper: CB, JY.

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Figures

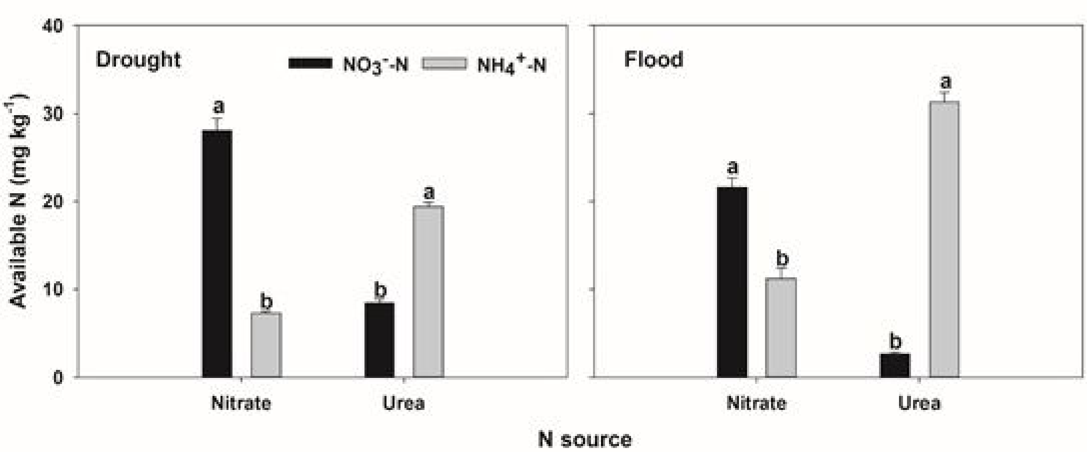

Figure 1

Available N in the soil for nitrate application and urea application under different water treatments. Lowercase letters indicate LSD (α=0.05) grouping of means within the same N source. Column with the different letter is significantly different. The vertical bars indicate standard deviations.

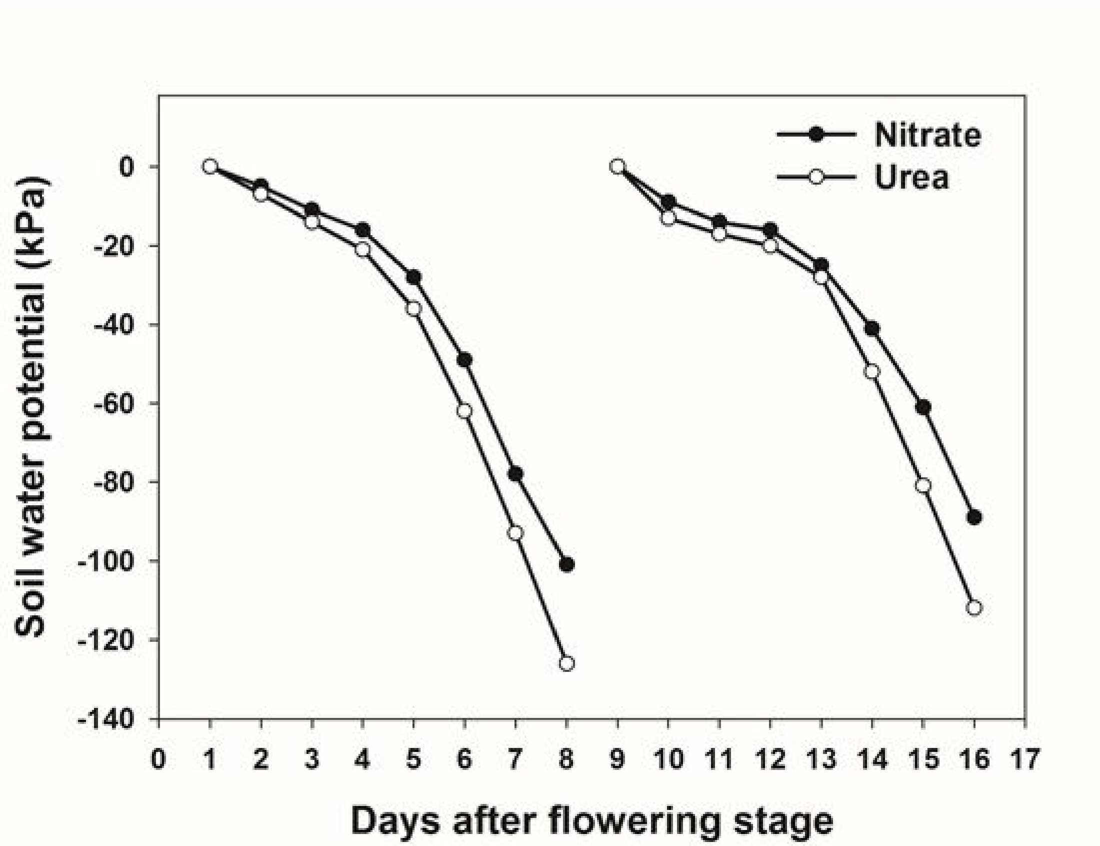

Figure 2

Daily mean soil water potential of drought treatment.

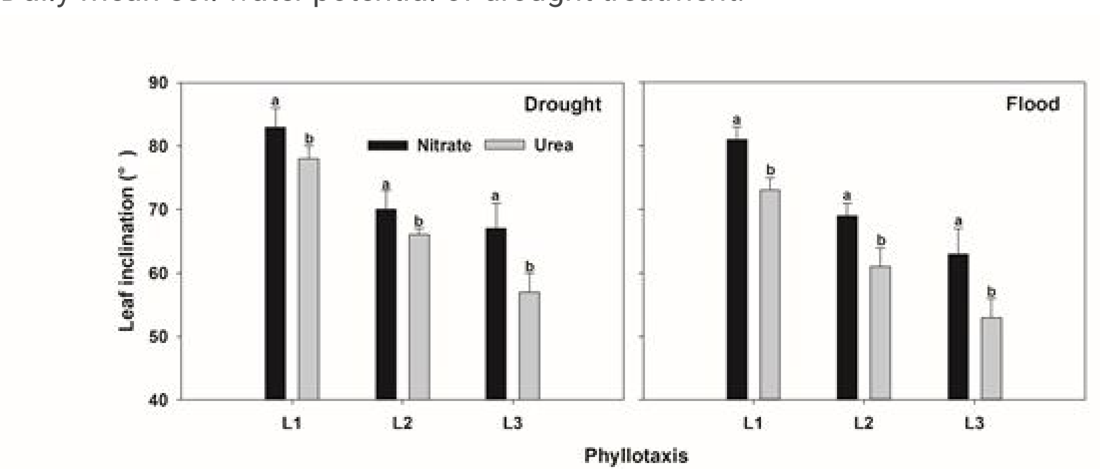

Figure 3

Leaf inclination for nitrate application and urea application under different water treatments. Lowercase letters indicate LSD (α=0.05) grouping of means across N sources within the same phyllotaxis. Column with the different letter is significantly different. The vertical bars indicate standard deviations. L1, the first leaf from the top; L2, the second leaf from the top; L3, the third leaf from the top.

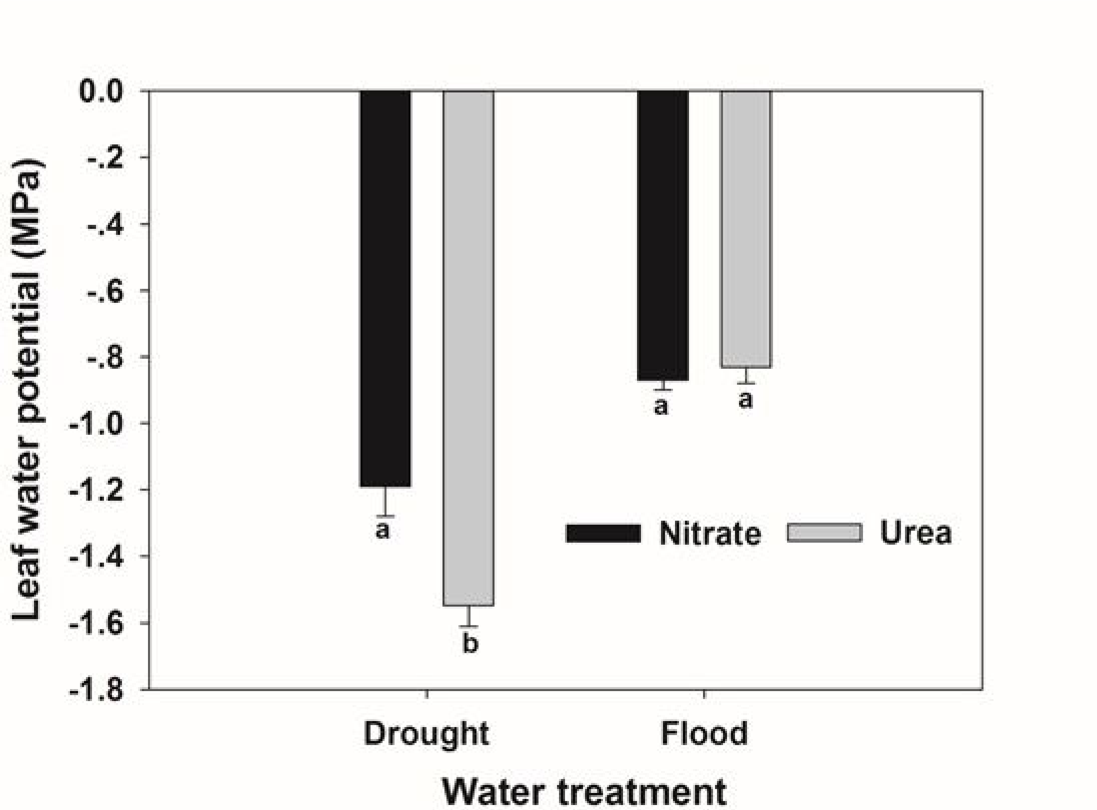

Figure 4

Leaf water potential for nitrate application and urea application under different water treatments. Lowercase letters indicate LSD (α=0.05) grouping of means across N sources within the same water treatment. Column with the different letter is significantly different. The vertical bars indicate standard deviations.

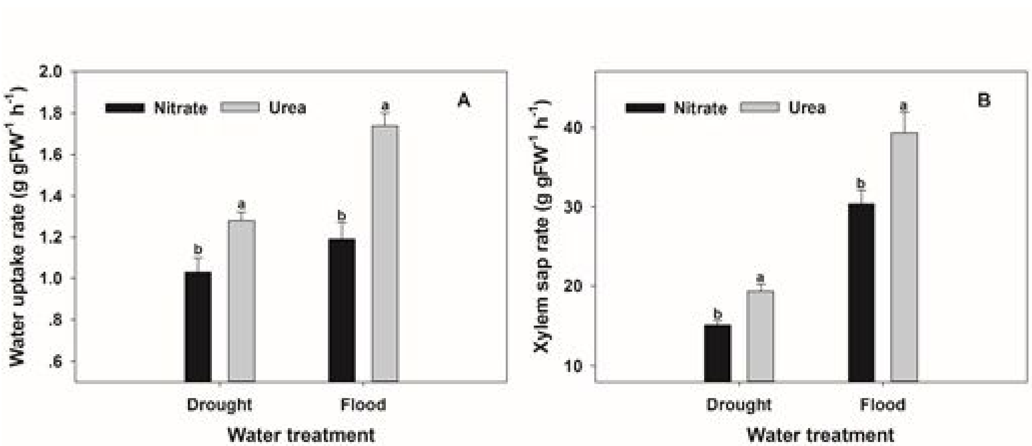

Figure 5

Water uptake rate (A) and xylem sap rate (B) for nitrate application and urea application under different water treatments. Lowercase letters indicate LSD (α=0.05) grouping of means across N sources within the same water treatment. Column with the different letter is significantly different. The vertical bars indicate standard deviations.

Supplementary Files

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- FigureS1.jpg