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Effects of soil water and nitrogen availability on photosynthesis and water use efficiency of *Robinia pseudoacacia* seedlings

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Abstract

The efficient use of water and nitrogen (N) to promote growth and increase yield of fruit trees and crops is well studied. However, little is known about their effects on woody plants growing in arid and semiarid areas with limited water and N availability. To examine the effects of water and N supply on early growth and water use efficiency (WUE) of trees on dry soils, one-year-old seedlings of *Robinia pseudoacacia* were exposed to three soil water contents (non-limiting, medium drought, and severe drought) as well as to low and high N levels, for four months. Photosynthetic parameters, leaf instantaneous WUE (WUE_i) and whole tree WUE (WUE_b) were determined. Results showed that, independent of N levels, increasing soil water content enhanced the tree transpiration rate (T_r), stomatal conductance (G_s), intercellular CO_2 concentration (C_i), maximum net assimilation rate (A_{max}), apparent quantum yield (AQY), the range of photosynthetically active radiation (PAR) due to both reduced light compensation point and enhanced light saturation point, and dark respiration rate (R_d), resulting in a higher net photosynthetic rate (P_n) and a significantly increased whole tree biomass. Consequently, WUE_i and WUE_b were reduced at low N, whereas WUE_i was enhanced at high N levels. Irrespective of soil water availability, N supply enhanced P_n in association with an increase of G_s and C_i and a decrease of the stomatal limitation value (L_s), while T_r remained unchanged. Biomass and WUE_i increased under non-limiting water conditions and medium drought, as well as WUE_b under all water conditions; but under severe drought, WUE_i and biomass were not affected by N application. In conclusion, increasing soil water availability improves photosynthetic capacity and biomass accumulation under low and high N levels, but its effects on WUE vary with soil N levels. N supply increased P_n and WUE, but under severe drought, N supply did not enhance WUE_i and biomass.

Key words: drought; nitrogen; photosynthesis; water use efficiency; *Robinia pseudoacacia*

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Introduction

Drought is the main abiotic factor, along with nutrient deficient soils, limiting plant growth and ecological restoration in arid and semiarid areas. Plants growing outside arid and semiarid regions are also often subjected to periods of soil and atmospheric water deficit during their life cycle (Chaves et al., 2002; Rennenberg et al., 2006; Nahm et al., 2007). Photosynthesis, as a sensitive physiological parameter of plant metabolism and development, can rapidly reflect plant response to changes in environmental factors. Hence, the effect of water availability on plant photosynthesis is still a crucial area of study. Under drought stress, loss of leaf turgor and stomatal closure to prevent desiccation reduces photosynthetic carbon (C) uptake and

assimilation (Comstock and Mencuccini, 1998; Flexas et al., 1999; Chaves et al., 2002, 2009; Cornic and Fresneau, 2002; McDowell et al., 2005, 2008; Breda et al., 2006; Galmés et al., 2007). Continued demand for carbohydrates to maintain metabolism under drought stress will deplete carbohydrate reserves, leading to carbon starvation and, under prolonged conditions, plant death (Katul et al., 2003; McDowell et al., 2008). Plants adapted to maintaining hydraulic regulation and photosynthesis during drought and on nutrition-poor sites exhibit high water use efficiency (WUE), leading to greater survival and performance (Sage, 2004; Flexas et al., 2006; Zhang et al., 2009; Gong et al., 2011).

Because most leaf nitrogen (N) is present in the chloroplasts, e.g., in the photosynthetic machinery (Evans and Seemann, 1989), photosynthesis is closely linked to N

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availability (Field and Mooney, 1986; Evans, 1989). Concurrently in severely dry environments, however, soil water deficits are often associated with low nutrition availability (Li et al., 1997; Li, 2002). Drought-mediated reduction in environmental N availability, due to (1) decreased biomass input into soil, (2) decreased soil nutrition turnover, (3) wind erosion, and (4) decreased movement of soil N sources to the root surface, amplifies drought impact on photosynthesis and subsequent plant growth and reductions in productivity (Arora et al., 2001; Breda et al., 2006; Drake et al., 2010; Cairns et al., 2011). In return, reduced photosynthetic capacity in response to drought stress leads to decreased nitrate reductase activity in leaves, and subsequently, N assimilation and internal availability of whole plants (Field et al., 1983; Kaiser and Foerster, 1989; Kaiser and Brendle-Behnisch, 1991; Pinheiro et al., 2001; Fresneau et al., 2007). Therefore, drought-mediated reduction of photosynthesis is often coupled with low N metabolism. While more N can increase plant photosynthesis and growth, severe soil water deficiency can negate benefits from more available N (Li et al., 1997; Li, 2002). Hence, plants building root symbiosis with N_2 fixing bacteria exhibit a higher potential to survive and grow during drought and on nutrition-poor sites (Ferrari and Wall, 2007).

In previous studies, plant WUE was expressed on different scales, e.g., photosynthetic WUE reflecting instantaneous relation of leaf P_n to T_r ; biomass WUE defined as the weight ratio of assimilated C to transpired water during a period of growth; yield WUE reflecting the relation of agricultural economic yield to water consumption; or WUE using C isotope discrimination (Smith, 1980; Polley, 2002; Zhang and Shan, 2002; Brueck and Senbayram, 2009; Zhang et al., 2009). Irrespective of expression form, plant WUE differs among species and genotypes and is strongly affected by the amount of unproductive transpiration, which is closely linked to environmental water and N availability (Field et al., 1983; Condon et al., 2002; Brueck and Senbayram, 2009).

In dry environments, more water enhances not only photosynthesis, by increasing stomatal aperture and activity of photosynthetic enzymes, but also the transpirational water loss (Maroco et al., 2000; Sage, 2004; Gong et al., 2011), resulting in uncertain effects on instantaneous and/or long-term WUE. In low N soils, an increase of N availability promotes crop rooting and soil N uptake and subsequently enhances leaf chlorophyll content and photosynthesis as well as plant tree WUE. Consequently, the effects of N supply on WUE have mostly been positive (Li et al., 1997; Raven et al., 2004; Brueck, 2008). However, constant WUE and negative effects on WUE in response to N supply have also been observed (Hubick, 1990; Van den Boogaard et al., 1995; Górný and Garczynski, 2002; Brueck, 2008). The inconsistency of N effects on WUE may be due to species differences, which somewhat limits

their interpretation for practical application in managed plant systems. In previous studies, the interactive effects of water and N availability on photosynthesis and WUE have been extensively studied in crops and fruit trees (Heitholt, 1989; Li et al., 1997; Prasertsak and Fukai, 1997; Stoneman et al., 1997; Arora et al., 2001; Sadras, 2005; Warren and Adams, 2006; Zhou et al., 2006; Waraich et al., 2011). Interactive water and N impact has not been widely studied in non-agricultural woody plants (Ripullone et al., 2004; Brueck, 2008; He et al., 2009; Han and Zhao, 2010; Forrester et al., 2012), especially those growing in arid and semiarid areas.

Robinia pseudoacacia (black locust) is a N_2 -fixing leguminous tree native to the hardwood forests of the eastern U.S., and is used worldwide for protection against soil erosion. Based on its relatively high resistance to drought and relatively fast growth on alkali soil, black locust is also used for ecological restoration in marginal soils with low water and N availability, especially on the Loess Plateau and other arid regions of northwest China. However, it does not survive and grow well when it is transplanted into N poor and drought suffering sites (Ferri and Wall, 2007; He et al., 2009; Han and Zhao, 2010). In this study, we aimed to examine whether increasing water and N availability can improve the survival and growth in the early phase of development of *R. pseudoacacia* in low water and N soils.

1 Materials and methods

1.1 Materials and treatments

One-year-old seedlings of *R. pseudoacacia* were planted individually in pots (0.50 m high, diameter 0.35 m, volume 48 L) filled with a mixture of loess from local soil down to 150 cm depth and vermiculite (4:1, V/V), on March 15, 2010. The N contents of total N, NH_4^+ -N and NO_3^- -N of the mixed substrate were 0.039%, 11.18 mg/kg and 13.55 mg/kg, respectively, on a dry weight basis, similar to that in the Loess Plateau (Dang et al., 2007). Half of the pots were fertilized using ammonium nitrate (NH_4NO_3) (Paini Chemical Reagents Company, Zhengzhou, China) at 0.44 g/kg dry weight (dw) soil (154 mg N/kg dw soil equivalently). To simulate a nutrition-poor soil condition, no other nutrients were supplied during the course of the experiment. After planting, the seedlings were well watered and shoots of the seedlings were cut off 3–5 cm above the soil surface. This pruning technique is often used in afforestation of dry areas to promote seedling survival and growth in the early phase of development. The plants were grown outside under full sun conditions (Han and Zhao, 2010). Meteorological conditions during the course of the experiment are shown in **Table 1**. From late May, seedlings were exposed to three soil water treatments: non-limiting soil water content, medium drought, and severe drought, corresponding to soil water contents

Table 1 Day and night temperature, average daily duration of sunshine, and maximum of irradiation during the course of the experiment

	Highest temperature at day (°C)	Lowest temperature at night (°C)	Average daily duration of sunshine (hr)	Maximum of daily irradiation ($\mu\text{mol photons}/(\text{m}^2\cdot\text{sec})$)
May	18.4–31.1	9.5–18.6	4.3	790–1750
June	24.1–36.2	13.1–23.7	5.1	820–2030
July	24.9–37.5	19.0–26.6	2.4	760–1790
August	22.4–33.7	16.7–25.5	2.3	770–1860

between 70%–75%, 50%–55% and 30%–35% of field water capacity ($n = 6$ for each treatment), respectively. Soil water contents were maintained by weighing the pots and then replacing water lost by transpiration at dusk every day by the addition of the equivalent volume of tap water. The weight of the pots, seedlings and soil, and the calculated weights of pots (including seedling and soil and pot self-weight) were known at each soil water treatment range, so we restored water back to this weight at dusk every day. A rainout shelter was used to avoid rainfall confounding soil water content during rainfall. Plants were harvested on September 2, 2010, and whole tree biomass was determined by weighing shoot and roots of seedlings.

1.2 Measurement of diurnal variations of photosynthesis parameters

On July 21, a cloudless day, diurnal variation of leaf net photosynthesis rate (P_n), stomatal conductance (G_s), intercellular CO_2 concentration (C_i), transpiration rate (T_r), as well as ambient CO_2 concentration (C_a), air temperature (T_a), air relative humidity (RH) and photosynthetic active radiation (PAR), were measured every two hours from 07:00 to 19:00 using a LI-COR 6400XT portable photosynthesis system (Li-COR Biosciences, Inc., Lincoln, Nebraska, USA). The measurements were conducted on one fully expanded third compound leaf from 6 individual plants from all treatments. The stomatal limitation value (L_s) was calculated using the formula: $L_s = 1 - C_i/C_a$ (Yin et al., 2006).

A light response curve was measured using an artificial light source built into the LI-COR 6400 at radiation intensities of 0, 20, 50, 100, 200, 500, 800, 1000, 1200, 1500, 2000, 2500 $\mu\text{mol}/(\text{m}^2\cdot\text{sec})$. The response curve of P_n to PAR was then plotted. Based on response curves of P_n as functions of PAR, a non-rectangular hyperbola model was configured using the statistics program SPSS 17.0 (SPSS Inc., Chicago, USA) (Cannell and Thornley, 1998; Endo et al., 2001):

$$P_n = \frac{\text{PAR} \times \text{AQY} + A_{\text{max}} - \sqrt{(\text{PAR} \times \text{AQY} + A_{\text{max}})^2 - 4\text{AQY} \times \text{PAR} \times A_{\text{max}}}}{2k} - R_d$$

where, k is the curvature (convexity) of the light-photosynthesis relationship.

The maximum net assimilation rate (A_{max}), dark respiration rate (R_d), and apparent quantum yield (AQY) were calculated from this response function (Liu et al., 2005).

The light compensation point (LCP) and light saturation point (LSP) were estimated using a regression equation of light and P_n in the range of radiation intensity from 0 to 200 $\mu\text{mol}/(\text{m}^2\cdot\text{sec})$ at $P_n = 0$ and $P_n = A_{\text{max}}$, respectively (Liu et al., 2005).

1.3 Determination of WUE

In this experiment under controlled conditions, WUE was studied at the levels of both leaf instantaneous ratio of P_n to T_r (WUE_i) (Polley, 2002) and biomass to water use (WUE_b). WUE_b was calculated as the ratio of whole tree biomass (g dw) to the difference of compensated water weight (kg) subtracting evaporative water loss of soil from pots without seedlings ($n = 3$). The difference was assumed to be transpired water loss at the different levels of water application (Oweis et al., 2000; Abbate et al., 2004).

1.4 Statistical analysis

Significant differences in observed parameters at a measuring point among water or N treatments ($n = 6$) were analyzed with the one-way ANOVA test using the SPSS 16.0 for Windows (Chicago, USA). The main effects of water and N availability and their interactions on transpirational water loss, biomass, and WUE_b were determined by two-way analysis of variances (ANOVA). The differences were considered significant at $P < 0.05$.

2 Results

2.1 Diurnal variation of environmental factors

On the measurement day, the PAR increased steeply from 07:00 to 09:00 and remained at high levels until 15:00, then decreased sharply (Fig. 1a). Under the impacts of PAR diurnal variation, C_a (Fig. 1a) and RH (Fig. 1b) showed high levels in early morning, decreased sharply and remained at relatively low levels during midday, then began to increase again from 17:00, whereas T_a exhibited a trend of diurnal variation similar to PAR (Fig. 1b).

2.2 Water and N availability effects on diurnal variation of photosynthetic parameters

2.2.1 Diurnal variation of T_r

Transpirational water loss was compensated for at dusk every day. Hence, based on diurnal variation of the main environmental factors affecting transpiration (Fig. 1), leaf T_r maintained a relatively high level during 09:00–13:00, and after that, decreased significantly and continuously,

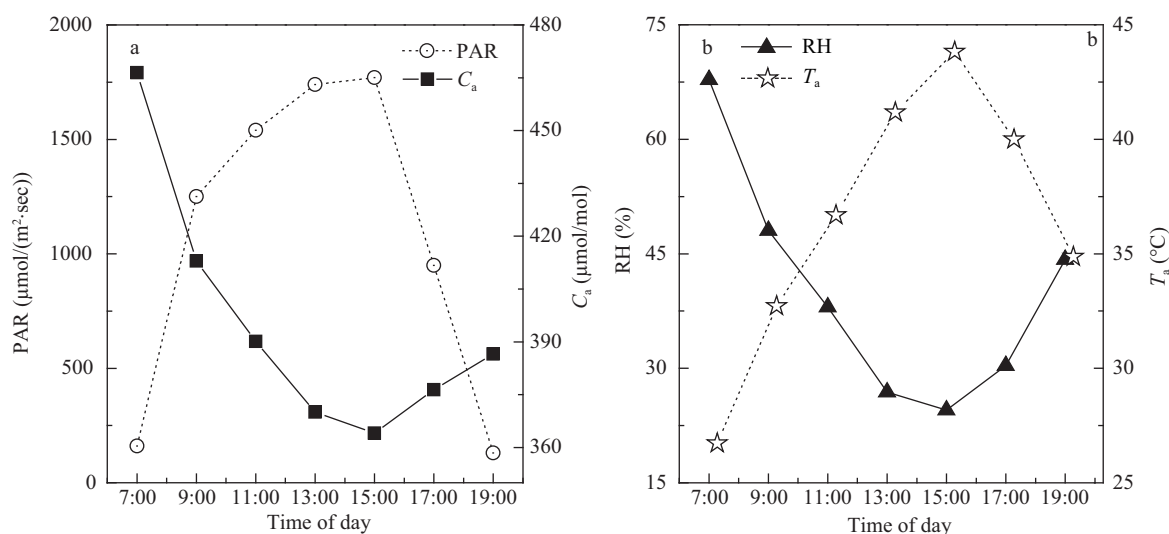


Fig. 1 Diurnal variations of environmental photosynthetic active radiation (PAR) and ambient CO₂ concentration (C_a) (a); air temperature (T_a) and air relative humidity (RH) (b) from 07:00 to 19:00 on the measuring day.

reaching the lowest value of the day at 19:00 (**Fig. 2a**). The daytime pattern of T_r was similar across all treatments. Irrespective of N levels, T_r decreased with decreasing soil water availability at each time point of the day. Comparing T_r between different N levels but under the same water contents, N supply did not have significant effects on T_r .

2.2.2 Diurnal variation of G_s

Stomata are the main portal for carbon dioxide (CO₂) and vapor water exchange between plant leaves and the atmosphere, thus G_s directly controls photosynthesis and transpiration. Diurnal variation of G_s under all water and N treatments showed similar trends (**Fig. 2b**). From 07:00 to 09:00, G_s maintained at relatively high levels, due to compensation for transpirational water loss being performed at dusk the day before. Then, G_s decreased significantly until dusk. Irrespective of N levels, G_s was reduced with decreasing soil water contents. At comparable soil water contents, the G_s of trees receiving the high N treatment was consistently higher than that of the low N trees. In afternoon, the effect of N supply on G_s under non-limiting water conditions and medium drought, but not severe drought, was statistically significant (**Table 2**).

2.2.3 Diurnal variation of C_i and L_s

In general, C_i is dependent on G_s and the ability of mesophyll cells to assimilate intracellular CO₂. At 07:00, C_i was high (**Fig. 2c**) consistent with high C_a , associated with low PAR and high G_s . During the period from mid morning to early evening (09:00–17:00), C_i reached a constant low floor due to high PAR and depletion of C_a in the plant canopy, and high G_s , allowing C_a depletion (**Fig. 1a**), then returned to early morning levels as light and G_s decreased. Increasing soil water content did not change the trend of diurnal C_i variation, leading only to a weak increase of C_i under both low and high N levels over the day.

Table 2 Statistical tests of low and high nitrogen effects on G_s , C_i , L_s , P_n , and WUE_i of *Robinia pseudoacacia* seedlings at the same measuring time points and the same soil water availability

Treatment	07:00	09:00	11:00	13:00	15:00	17:00	19:00
Effects of nitrogen availability on G_s							
70%–75%	*	–	*	*	*	*	*
50%–55%	*	–	–	*	*	*	*
30%–35%	–	–	–	–	–	–	–
Effects of nitrogen availability on C_i							
70%–75%	–	–	–	–	–	–	*
50%–55%	–	–	–	–	–	–	*
30%–35%	–	–	*	–	–	–	*
Effects of nitrogen availability on L_s							
70%–75%	–	–	*	–	*	*	–
50%–55%	–	*	*	–	–	–	–
30%–35%	–	–	–	–	–	–	–
Effects of nitrogen availability on P_n							
70%–75%	*	*	*	*	*	*	–
50%–55%	*	–	*	–	–	*	–
30%–35%	–	–	–	–	–	–	–
Effects of nitrogen availability on WUE_i							
70%–75%	*	–	*	–	–	*	*
50%–55%	*	–	*	–	–	*	–
30%–35%	–	–	–	–	–	–	–

The seedlings were exposed to three soil water conditions (non-limiting soil water content, medium drought, and severe drought, corresponding to soil water contents between 70%–75%, 50%–55% and 30%–35% of field water capacity, respectively) and two nitrogen levels (low and high nitrogen; $n = 6$ for each treatment).

* Indicates significant difference between N treatments at a specific time of day under the same soil water content (ANOVA, $P < 0.05$), – indicates no significant difference.

Compared to low N treatments (**Fig. 2c1**), C_i of high N treatments (**Fig. 2c2**) was higher over the middle of the day, but significantly low in late afternoon under all soil water treatments (**Table 2**). This could be explained through the N supply enhancing CO₂ assimilation of mesophyll cells under weak light by increasing G_s , since PAR, but not C_i , was the key factor limiting C assimilation in the early morning.

Independent of N levels, L_s was continuously high over the middle of the day and lower in the early morning and early evening (**Fig. 2d**). At both low and high N

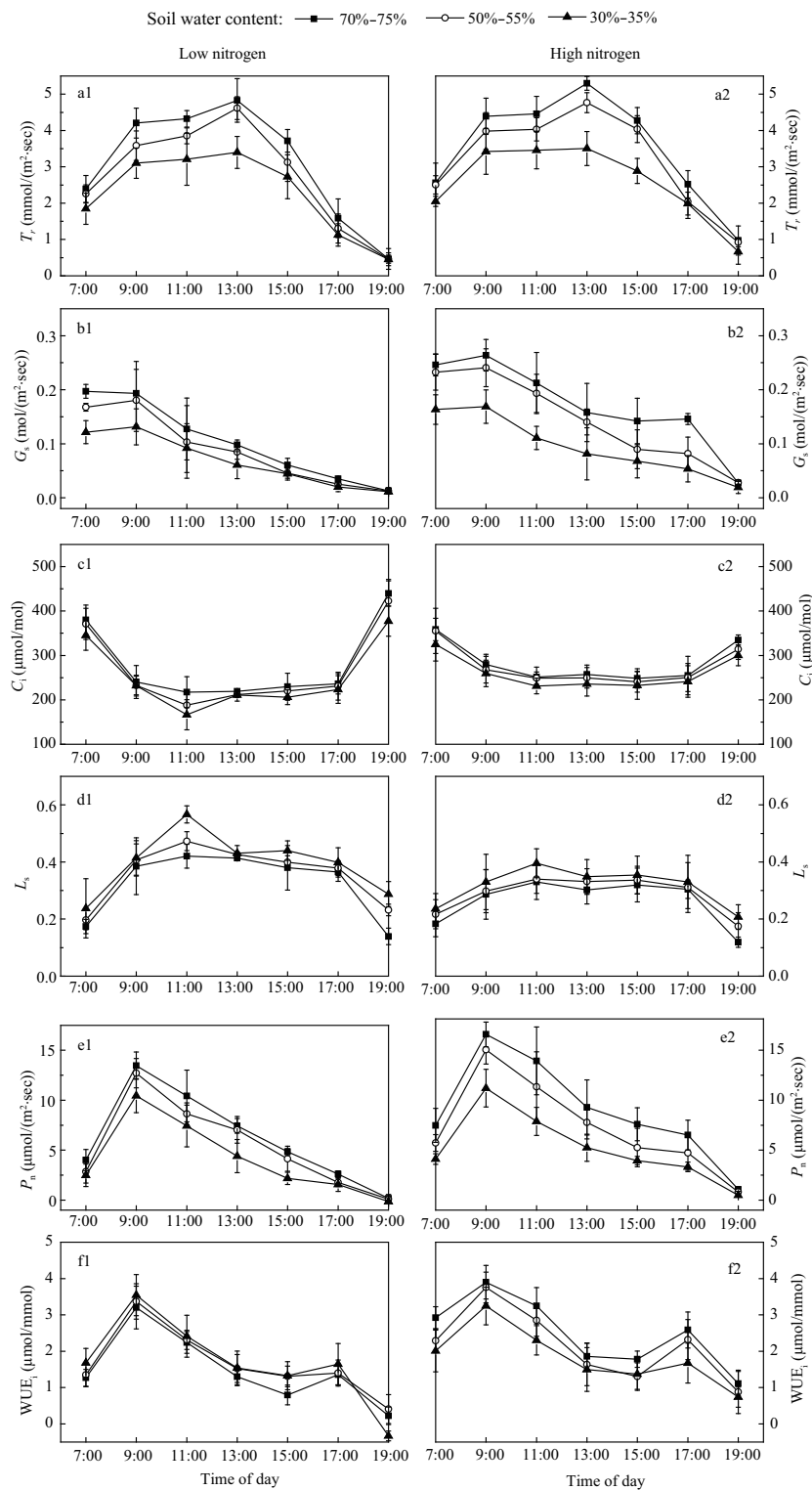


Fig. 2 Diurnal variations in leaf transpiration (T_r) (a), stomata conduction (G_s) (b), intercellular CO_2 concentration (C_i) (c), stomatal limitation values (L_s) (d), net photosynthetic rate (P_n) (e), and leaf instantaneous water use efficiency (WUE_i) (f) of *Robinia pseudoacacia* exposed to three soil water conditions and two nitrogen levels, $n = 6-8$).

levels, L_s tended to decrease with increasing soil water contents. Compared to low N treatment (**Fig. 2d1**), the high N treatment (**Fig. 2d2**) reduced stomatal limitations over the day under all water treatments and at 19:00 in

drought treatments, suggesting that N supply modified stomata limitation of CO_2 diffusion for most of the day, especially in seedlings grown under non-limiting soil water conditions (**Table 2**).

2.2.4 Diurnal variation of P_n

Diurnal variations of P_n are shown in **Fig. 2e**. Just after sunrise at 07:00, P_n was apparently light-limited due to low PAR, as G_s and C_i were at high levels. Overall, the pattern of P_n mirrored G_s . P_n and G_s maxima were at 09:00 as PAR and G_s increased, even though C_i was reduced. Subsequently P_n steadily declined under all water and N treatments until early evening minima at 19:00, similar to G_s . Hence, G_s was the main factor limiting photosynthesis of mesophyll cells during this time of day. At 19:00, P_n was at the lowest level of the day due to low PAR and G_s , despite high C_i .

Water and N availability did not affect the trend of diurnal variation of P_n (**Fig. 2e**). Independent of soil N availability, increasing soil water availability resulted in increased P_n . Under all soil water contents, P_n of the high N treatment was higher than that of low N treatments. The N effects under non-limiting water conditions and medium drought at each measurement over the day were significantly different (**Table 2**). The results indicated that N supply enhanced P_n , including the ability to use weak light.

2.2.5 Diurnal variation of WUE_i

Similar to the trend of diurnal variation of P_n , WUE_i (**Fig. 2f**) was low in early morning, concurrent with low PAR (**Fig. 1a**) and P_n (**Fig. 2e**), reaching the maximum level of the day later in the morning at 09:00 due to high P_n and PAR. Through the rest of the day, WUE_i declined as T_a rose and RH (**Fig. 1b**) and P_n fell, while T_r remained at relatively high levels (**Fig. 2a**). Decreasing soil water content led to an increasing WUE_i when plants were grown under low N levels (**Fig. 2f1**), but to a decreasing WUE_i if plants were grown under high N levels (**Fig. 2f2**). Comparing seedlings grown under low and high N levels, increasing N availability enhanced seedling WUE_i (**Table 2**).

2.3 P_n response to PAR

To test the effects of water and N availability on the photosynthetic capacity of mesophyll cells, P_n response to different PAR intensities was measured using an artificial

light source to create a light response curve (**Fig. 3**). Although under different water and N treatments the response curves of P_n to PAR show a similar trend, enhancing soil water contents significantly increased the response of P_n to PAR when PAR > 180 $\mu\text{mol}/(\text{m}^2\cdot\text{sec})$ within a N level. High N treatments increased the response of P_n to PAR and highlighted the difference in the water-mediated response of P_n to PAR.

Results expressed using a non-rectangular hyperbola model showed that decreasing soil water content significantly decreased leaf A_{max} and R_d , irrespective of soil N content (**Table 3**). Comparing the two N levels, N supply significantly increased A_{max} and R_d under non-limiting water conditions and medium drought, as well as R_d under severe drought. AQY was reduced with decreasing water content under both N treatments. Under non-limiting water conditions, high N enhanced leaf AQY. Irrespective of soil N levels, decreasing water availability increased LCP gradually, but significantly reduced LSP, resulting in a narrower range of PAR (difference of LSP and LCP) within which plants could photosynthesize. N supply did not have significant effects on LCP under any soil water treatment, but significantly increased LSP under non-limiting water conditions, leading to an increased of PAR range.

2.4 Effects of water and N availability on transpirational water loss, biomass and WUE_b

Under controlled conditions in the experiment, seedling transpirational water loss – calculated from applied water and increased biomass – decreased significantly with decreasing water supply under both low and high N levels (**Fig. 4a**). Under the low N level, seedling biomass was not impacted by medium drought, but was reduced significantly under severe drought (**Fig. 4b**). Under the high N level, biomass was continuously significantly reduced with decreasing soil water content. Hence, independent of N levels, water availability had significant effects on transpirational water loss and biomass accumulation. Transpired water loss between the two N levels was not different; biomass increased significantly on application of N under non-limiting water conditions, but not under limiting water conditions. The combination of high water and high N lev-

Table 3 Effects of water and nitrogen availability on the maximum net assimilation rate (A_{max}), apparent quantum yield (AQY), dark respiration rate (R_d), light compensation point (LCP), and light saturation point (LSP)*

Treatment	A_{max} ($\mu\text{mol}/(\text{m}^2\cdot\text{sec})$)	R_d ($\mu\text{mol}/(\text{m}^2\cdot\text{sec})$)	AQY ($\mu\text{mol}/\mu\text{mol}$)	LCP ($\mu\text{mol}/(\text{m}^2\cdot\text{sec})$)	LSP ($\mu\text{mol}/(\text{m}^2\cdot\text{sec})$)
W1/LN	16.37 ± 0.43 c	1.56 ± 0.03 b	0.058 ± 0.005 b	17.23 ± 1.42 a	477.9 ± 15.2 b
W2/LN	10.06 ± 1.40 b	1.25 ± 0.07 a	0.039 ± 0.004 ab	64.10 ± 2.50 b	453.6 ± 17.2 ab
W3/LN	6.59 ± 0.54 a	1.14 ± 0.10 a	0.026 ± 0.005 a	106.39 ± 6.86 c	420.3 ± 12.6 a
W1/HN	19.22 ± 1.53 d	3.09 ± 0.09 d	0.069 ± 0.005 c	19.49 ± 1.17 a	546.4 ± 16.2 c
W2/HN	15.35 ± 1.04 c	2.19 ± 0.09 c	0.043 ± 0.005 b	60.58 ± 1.53 b	454.2 ± 16.9 ab
W3/HN	7.62 ± 1.07 a	2.09 ± 0.10 c	0.032 ± 0.002 a	88.90 ± 2.72 c	433.7 ± 14.0 a

* Photosynthetic parameters were simulated using a non-rectangular hyperbola model based on response curves of P_n to PAR (means ± SE, $n = 6$). W1, W2, W3, corresponding to soil water contents between 70%–75%, 50%–55% and 30%–35% of field water capacity, respectively; LN: low nitrogen, HN: high nitrogen. Different letters among treatments indicate significant differences at $P < 0.05$ (ANOVA).

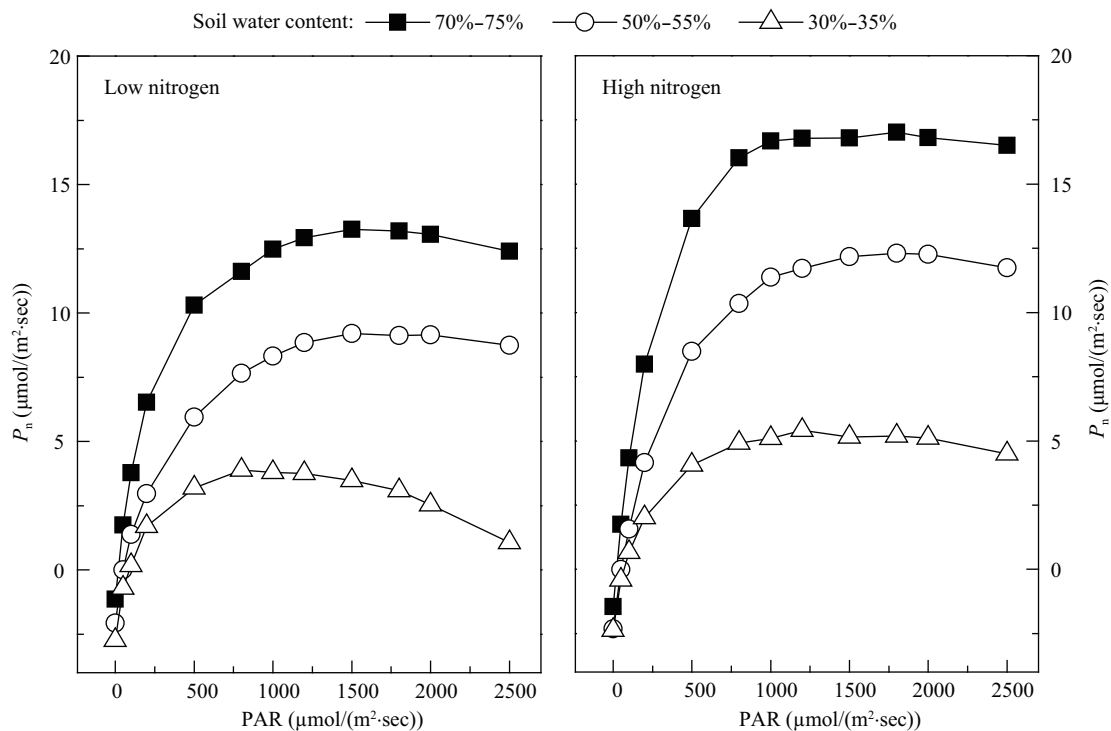


Fig. 3 Response curve of P_n to PAR of *Robinia pseudoacacia* growing under different soil water contents and nitrogen availabilities.

els significantly enhanced biomass. However, interactive effects of water and N on the two parameters were not statistically significant.

At low N levels, decreasing soil water availability enhanced WUE_b (Fig. 4c) due to both reduced biomass and water consumption from transpiration under drought (Fig. 4a, b). However, a positive effect on WUE_b was not observed at high N levels (Fig. 4c). Under non-limiting soil water and medium drought, N supply significantly enhanced WUE_b of *R. pseudoacacia*. The interactions of water and N availability did not have significant effects on WUE_b .

3 Discussion

In previous studies, drought-induced loss of leaf turgor and reduction of stomatal aperture was found to limit photosynthetic CO_2 uptake, internal conductance, and assimilation ability (Comstock and Mencuccini, 1998; Flexas et al., 1999; Chaves et al., 2002, 2009; Cornic and Fresneau, 2002; DaMatta et al., 2002; McDowell et al., 2008, 2005; Breda et al., 2006; Yin et al., 2006; Galmés et al., 2007; Cramer et al., 2008; Dordas and Sioulas, 2008; Wu et al., 2008). Long-term severe drought could lead to C starvation and plant death (Katul et al., 2003; McDowell et al., 2008). Studies of diurnal variations in photosynthetic parameters in this experiment under controlled conditions demonstrated that decreasing soil water content led to a decrease in G_s and an increase in L_s , subsequently reducing T_r and C_i , and ultimately decreasing P_n and biomass of *R. pseudoacacia* seedlings. Here, drought-induced reduction

of internal conductance to CO_2 transfer could play a key role (Cowan and Troughton, 1971; Flexas and Medrano, 2002; Warren, 2004, 2008). The negative effects of low soil water availability on the photosynthetic ability of leaves, as photosynthetic machinery, were reflected in a decrease in A_{max} , AQY, and the range of PAR (He et al., 2009; Han and Zhao, 2010). Primarily, the impacts of water availability were independent of soil N availability. However, decreasing soil water content enhanced WUE_i and WUE_b at low N levels, but reduced the WUE_i at high N levels. The discrepancy between low and high N effects on WUE_i was not reported in previous studies, and possible reasons cannot be interpreted here. Differences in G_s , P_n , WUE_i , and biomass in response to different soil water contents was amplified by N supply (Warren, 2004), showing an increased drought susceptibility to decreasing soil water content (Forrester et al., 2012).

Most studies have reported positive effects of N supply on plant photosynthesis and WUE (Bruck et al., 2001; Raven et al., 2004; Brueck, 2008), although a constant WUE and negative effects on WUE in response to N supply have been observed in some experiments (Hubick, 1990; Van den Boogaard et al., 1995; Górný and Garczyński, 2002; Brueck, 2008). In this study, increasing soil N availability did not alter the trend of diurnal variations of photosynthetic parameters measured in response to soil water availability. However, compared to plants grown under the same water conditions, N supply generally increased G_s and C_i , diminished L_s , and enhanced A_{max} , R_d , AQY, and LSP, resulting in an increase of P_n . Increased G_s and improved CO_2 assimilation in response to N supply

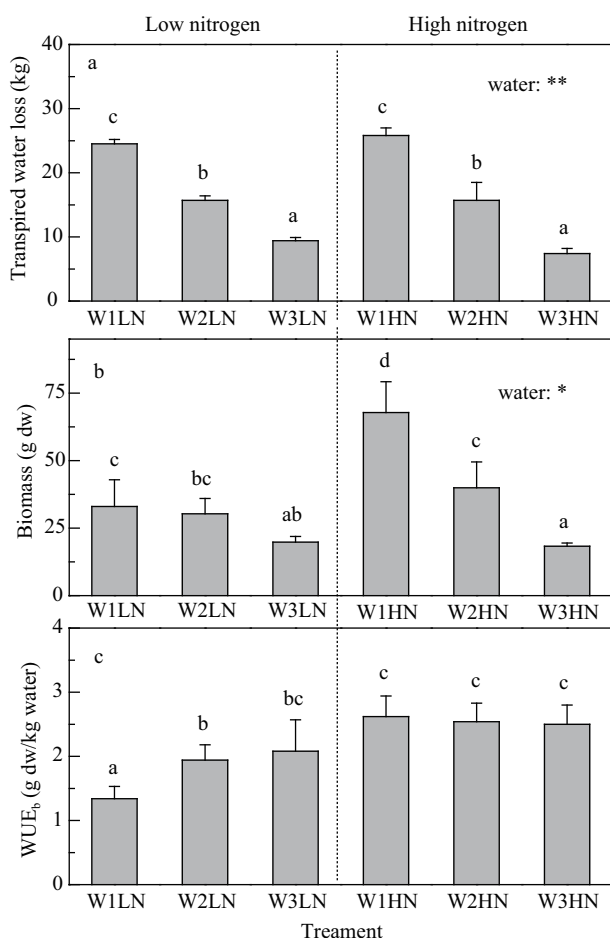


Fig. 4 Effects of soil water and nitrogen availability on transpirational water loss (a), biomass (b) and water use efficiency based on dry matter biomass (WUE_b) (c) of *Robinia pseudoacacia*. Different letters among treatment combinations indicate significant differences at $P < 0.05$ (two-way ANOVA). Water: * and ** show the main effects of water treatments corresponding to $P < 0.05$ and $P < 0.01$, respectively.

was not associated with an increase of T_r and transpired water loss, showing a proportionally lower rate of water vapor loss relative to C assimilation rate, possibly due to a reduction in leaf internal resistance to CO₂ assimilation and/or an elevation of CO₂ conductance and assimilation capacity. Hence, N supply enhanced biomass and WUE_i and WUE_b under non-limiting water conditions and medium drought. The results are consistent with previous studies (Heitholt, 1989; Stitt and Schulze, 1994; Guehl et al., 1995; Virgona and Farquhar, 1996; Pan et al., 2011), but contrary to the conclusions of Yin et al. (2006). Under severe drought, increasing N availability did not enhance WUE_i as T_r and P_n were not affected by N supply; however, N supply enhanced WUE_b because of decreased transpirative water loss though biomass accumulation of *R. pseudoacacia* seedlings remained at the same levels under the two N levels. The positive effects of N supply on biomass accumulation and growth observed under non-limiting water conditions and medium drought were counteracted by severe drought, possibly due to a signif-

icant increase of R_d (e.g., increased C consumption) and the limitation of lower water content to soil N utilization in response to drought stress (Shangguan et al., 2000; Fageria and Baligar, 2005; Dordas and Sioulas, 2008). Hence, the interactions of water and N availability did not have significant effects on transpirative water loss, biomass, and WUE_b. The results indicate that N supply can effectively improve growth in the early phase of development of *R. pseudoacacia* seedlings if soil water is not limited. Under limited soil water availability, especially under severe drought, the positive effect of N supply is clearly reduced. Generally, increasing soil water availability is more effective than an increase of N availability to improve the growth of *R. pseudoacacia* seedlings. Although differences between pot study and field experiment conditions often limit the practical application of pot experimental results, this study provides useful data for management in the early phase of *R. pseudoacacia* seedlings.

In conclusion, increasing soil water availability enhanced photosynthetic capacity and biomass of *R. pseudoacacia* seedlings under low and high N levels, but its effect on WUE varied with soil N levels. An increase of N availability did not alter the diurnal pattern of photosynthetic parameters and biomass accumulation in response to soil water availability, but increased G_s and C_i while T_r was not affected, and hence, improved photosynthetic capacity and WUE; under severe drought, N supply did not increase WUE_i and biomass accumulation of *R. pseudoacacia* seedlings, but enhanced WUE_b by reducing transpirative water loss.

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