DOI: 10.1007/s11099-013-0033-2 PHOTOSYNTHETICA 51 (3): 359-369, 2013

The responses of photosynthetic rate and stomatal conductance of *Fraxinus rhynchophylla* to differences in CO_2 concentration and soil moisture

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Abstract

The photosynthetic parameters in leaves of three-year-old seedlings of *Fraxinus rhynchophylla* L. were studied under different soil water conditions and CO_2 concentrations ($[CO_2]$) with a *LI-COR 6400* portable photosynthesis system. The objective was to investigate the response of photosynthesis and stomatal conductance (g_s) to various $[CO_2]$ and soil water conditions, and to understand the adaptability of *F. rhynchophylla* to such conditions. The results showed that the soil water content (RWC) required to maintain high photosynthetic productivity in *F. rhynchophylla* was 49.5–84.3%; in this range, net photosynthetic rate (P_N) rose with $[CO_2]$ increasing from 500 to 1,400 µmol mol^{-1}. Outside this RWC range, P_N decreased significantly. The apparent maximum photosynthetic rate ($P_{max,c}$) and carboxylation velocity (V_c) increased with increasing RWC and remained relatively high, when RWC was between 49.5 and 96.2%. CO_2 compensation points and photorespiration rate exhibited a trend opposite to that of $P_{max,c}$ and V_c, indicating that moderate water stress was beneficial for increasing plant assimilation, decreasing photorespiration, and increasing production of photosynthates. g_s declined significantly with increasing $[CO_2]$ under different water supplies, but the RWC range maintaining high g_s increased. g_s reached its maximum, when RWC was approximately 73% and then decreased with declining RWC. The maximal g_s was found with increasing RWC. Thus, based on photosynthetic characteristics in artificial, vegetation construction in semiarid loess hill and gully area, *F. rhynchophylla* could be planted in habitats of low soil water content.

Additional key words: CO_2 response; net photosynthetic rate; photorespiration; relative water content; soil moisture.

Introduction

Atmospheric $[CO_2]$, soil moisture, and photosynthetic radiation are the major factors that limit plant productivity in large areas of the world. They affect the growth of both agricultural and forest species and influence the distribution and composition of vegetation (Smith *et al.* 2000, Boucher *et al.* 2001, Pozo *et al.* 2005, Pérez *et al.* 2007, Hernández-Santana *et al.* 2008). The ongoing increase in atmospheric $[CO_2]$ might eventually lead to higher temperatures and greater evaporative demands; droughts will be more frequent, intense, and erratic and may affect regions not currently subjected to drought (Tuchman *et al.* 2003, Kettunen *et al.* 2006, Jarvis *et al.* 2008, Geissler *et al.* 2009, Ciais *et al.* 2010). This raises important issues, such as how photosynthesis in elevated $[CO_2]$ is affected by evaporative demand, water supply, and drought, and whether increased photosynthetic efficiency in elevated $[CO_2]$ could be offset by the adverse influences of drought on the soil-plant-atmosphere continuum. Therefore, research on the changes in photosynthetic rate and stomatal conductance to differences in $[CO_2]$ and soil moisture is crucial for investigating the carbon and water cycles of ecological

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Received 30 October 2011, *accepted* 12 December 2012.
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Abbreviations: C_a – air CO_2 concentration; C_i – intercellular CO_2 concentration; C_{s0} – constant; $[CO_2]$ – CO_2 concentration(s); FC – field capacity; g_s – stomatal conductance; g_{smax} – maximum stomatal conductance; $P_{max,c}$ – apparent maximum photosynthetic rate; P_N – net photosynthetic rate; P_{Nmax} – maximum net photosynthetic rate; PPFD – photosynthetic photon flux density; RH – relative humidity; R_D – dark respiration rate; R_p – photorespiration rate; RWC – relative soil water content; R^2 – correlation coefficient; SWC – soil water content; T_a – atmospheric temperature; V_c – carboxylation velocity; Γ – CO_2 compensation points.
Acknowledgements: The work was financed by Major State Basic Research Development Program (No. 2012CB416904/zgc) and the National Natural Science Foundation of China (No. 31100468 and No. 31100196).

systems and it has important practical significance both in food safety and in ecological environment construction and improvement during global climate changes.

Semiarid, hilly loess areas are fragile areas in China, where water deficiency is a particularly serious issue (Sun *et al.* 2001, Fang *et al.* 2008, Xu *et al.* 2009). Therefore, the question, how plants adapt to drought, light stress, and increasing atmospheric [CO_2], is a problem that requires attention. Most previous studies have demonstrated that C_4 photosynthesis is nearly at saturation (Ludlow and Wilson 1971, von Caemmerer *et al.* 1977), but elevated CO_2 has been reported to increase net assimilation rate in well watered C_4 plants (Ziska *et al.* 1999, Hui *et al.* 2002, Pfanz et *al.* 2007). Ghannoum *et al.* (2000) reported that any improvement in the net assimilation rate and growth in C_4 plants under elevated CO_2 will most likely occur because of an improvement in water conditions (stomatal limitation) rather than alterations in biochemical factors (non-stomatal limitation). In C_3 plants, the rise in atmospheric CO_2 may promote photosynthesis and therefore the growth and yield (Morison and Lawlor 1999). Partial stomata closure induced by elevated CO_2 suppresses transpiration per unit of the leaf area and slows the depletion of the available soil moisture in water-limited environments (Baker *et al.* 1997, Allen *et al.* 1998). Increases in the net assimilation and dry matter production of about 20–30% are often recorded under elevated CO_2 (Allen *et al.* 1998, Mulholland *et al.* 1998, Turner *et al.* 2002, Špunda *et al.* 2005, Fleisher *et al.* 2008). These beneficial effects may increase the yields obtained in areas, where drought currently causes a crop failure, provided that the reduction in g_s under elevated CO_2 is not outweighed by concurrent increases in a leaf area and water loss (Kruijt *et al.* 1999). Because the moisture is a key factor limiting the plant growth in the Loess Plateau, studies on the response and adaptation of plants to [CO_2] and soil moisture are necessary.

Researchers worldwide have conducted a great deal of research on the changes in photosynthesis and g_s to differences in [CO_2] (Niklaus *et al.* 2001, Wang *et al.* 2005, Flexas *et al.* 2006, Ainsworth and Rogers 2007). Some studies have found that elevated [CO_2] frequently lead to decreases in g_s in C_3 plants (Eamus and Jarvis 1989, Jarvis 1989, Drake *et al.* 1997). Mott (1990) noted that stomata respond to the intercellular CO_2 concentration (C_i) to adjust the diffusive limitations to the assimilation rate, thereby improving instantaneous transpiration efficiency. Thus, if all the other factors are equal, elevated C_i results in decreased g_s. However, there has been a debate over the relevance of such studies (Whitfield *et al.* 1996, Ray and Sinclair 1998). For example, Bunce (1992) did not find a decrease in g_s in response to elevated CO_2 in *Malus domestica* and *Quercus prinus*. Seedlings of *F. sylvatica* grown under elevated CO_2 increased rate of soil drying, resulting from a combination of increased g_s with unchanged leaf area under low nutrient supplies and unchanged g_s with increased leaf area under high nutrient supplies (Heath and Kerstiens 1997). However, most previous studies have concentrated on a simple increase in [CO_2] under natural light conditions or only considered the effect of several water levels with increasing [CO_2]. Research on the responses of ecophysiological characteristics, such as P_N, transpiration, and g_s, to continuous changes in soil moisture and [CO_2] is lacking. Therefore, this study used *F. rhynchophylla*, one of the main drought-resistant trees in semiarid, hilly loess areas, as a study material to investigate the responses of photosynthetic characteristics to changes in the soil moisture and [CO_2]. These results could therefore provide a foundation for restoring natural vegetation, protecting and improving the ecological environment, and promoting the sustainable utilization of water resources.

Materials and methods

Study area: The experimental site is located in the Chemingyu forest station, Zhongyang County, Shanxi province, China, which is a part of the gully hilly area of the Loess Plateau in the middle reaches of the Yellow River. It lies at latitude 37°03′14″N and longitude 110°04′15″E and it is in a warm temperature zone with a dry and obviously continental monsoon climate. The average annual precipitation is 525 mm, of which the precipitation from June to September makes more than 70%. The annual potential evaporation is 1,019.7 mm. The average temperature is approximately 6°C, and the highest and the lowest recorded temperatures were 35.6°C (June 16, 1994) and –24.3°C (January 30, 1980), respectively. The frostless season is approximately 135 d, and the annual accumulated temperature over 10°C is 2,750°C. The soil is classified as brown and cinnamon soil, with inferior development and severe water and soil erosion. The vegetation types are forest-steppe and shrub zones with a few shrub species, and the most of the woodland is open forest with low stability.

Study material and treatment: Three-year-old *Fraxinus rhynchophylla* plants, which were growing in full sun, were selected from a nursery and potted in cinnamonic soil in March 2008 (the pots were buried in the soil to keep them at the same temperature). Every tree was inspected and selected before transplanting to ensure consistent seedling height, a diameter at breast height, and growing conditions. The average height was 98.6 ± 4.3 cm and the average diameter at the breast height was 1.83 ± 0.31 cm. Before transplanting, the roots of *F. rhynchophylla* were rinsed with water, and excess water was absorbed by blotting. The seedling fresh mass was measured using electronic scales. During the experiment, the cultivation substrate maintained natural fertility with no added fertilizer. Each treatment was repeated 3 times with a total of 21 pots. The pot was 0.6 m in diameter and 1.2 m deep with drainage holes at the bottom. The shape of the pot was cylindrical and the volume per pot was 0.34 m^3.

When the experiment was finished, the soil around the plant root was digged by ring sampling, and each pot was measured three times. The average field capacity and bulk density of the pots measured by ring sampling were 25.3 ± 1.3% and 1.26 ± 0.13 g cm^{-3}, respectively. A 1-m-long aluminum tube from a *LNW-50A* neutron probe (*CAS*, Nanjing, Jiangsu, CHN) was buried approximately 0.2 m away from each tree. The soil water content (SWC) in 0.3 cm of the root zone was measured and the average value was calculated. The soil water gradient was obtained by irrigation and natural water consumption**.** The detailed method was as follows: the pots were irrigated to field capacity if the plants were alive. According to the D-optimum law (Kiefer and Wolfowitz 1952), continuous soil water stress was produced by evapotranspiration on the 1st, 3rd, 5th, 8th, 11th, 15th, and 20th d. SWC was measured with a *LNW-50A* neutron probe in three groups (average of three trees). For the comparability with other tree species over the literature, RWCs were used and calculated by ring sampling; they were 96.2 ± 0.2%, 84.3 ± 0.4%, 72.7 ± 0.2%, 60.1 ± 0.3%, 49.5 ± 0.5%, 35 ± 0.3%, and 24.4 ± 0.5. Every treatment had a steady soil water gradient maintained by the natural evaporation and supplemental irrigation, and the soil surface was covered by small dinar.

Measurement methods: Three fully developed, mature leaves were selected from the center of each crown and denoted carefully; nine leaves were measured for every treatment, and each leaf was measured three times. A portable photosynthesis system (*LI-COR 6400*, *LI-COR Inc*., Lincoln, NE, USA) was used to measure the photosynthetic parameters. To reduce the effect of light fluctuations, all measurements were collected between 09:00 and 11:00 h of the local time on sunny days. During the measurements, twelve [CO_2] (1,400; 1,200; 1,000; 800, 600, 400, 250, 200, 150, 100, 50, and 20 μmol mol^{-1}) were supplied *via* the *LI-COR* CO_2 injection system (*LI-COR Inc*., Lincoln, NE, USA), and photosynthetic photon flux density (PPFD) was maintained at 1,000 μmol m^{-2} s^{-1} with the *LI-COR* LED (*LI-COR Inc*., Lincoln, NE, USA) irradiation source. The air temperature of the leaf chamber was maintained at approximately 30ºC, the relative humidity was maintained at 36.3 ± 2.7%, and the air flow rate in the leaf cuvette was 200 μmol m^{-2}. The physiological parameters P_N, g_s, and intercellular CO_2 concentration (C_i), as well as the environmental factors of atmospheric temperature (T_a) and relative humidity (RH), were recorded automatically. Before the data were recorded, the measured leaves were kept in the leaf chamber for at least 5 min to reach a steady state of photosynthesis.

In this paper, SWC was the mass soil water content, and RWC was the ratio of SWC to the field capacity (FC).

Data processing: *The Statistical Program for the Social Sciences* (*SPSS*, Chicago, IL, USA) software and *Excel 2003* for *Windows* were used for statistical evaluations and regression analyses. The P_N-C_i curves were simulated according to the Michaelis-Menten equation (Thomley 1983) to calculate $P_{max,c}$. The equation was as follows:

$$P_N = \frac{\eta C_i P_{max,c}}{\eta C_i + P_{max,c}} - R_D ,$$

where $P_{max,c}$ is the apparent maximum net photosynthetic rate, when the CO_2 concentration reaches saturation at a certain light intensity; η is the apparent carboxylation velocity; and R_D is the dark respiration rate.

According to Farquhar *et al.* (1980), in the low C_i range (< 200 μmol mol^{-1}) of the P_N-C_i response curves, P_N is mainly restricted by the activity and quantity of Rubisco.

$$P_N = V_c \times C_i - R_p ,$$

where V_c is the carboxylation velocity and R_p represents the photorespiration rate.

Results

The response of net photosynthetic rate to CO_2 concentration: The changes in P_N in response to [CO_2] under different water conditions are shown in Fig. 1. The response of P_N was basically similar in low [CO_2]. Namely, at low [CO_2], P_N increased with increasing [CO_2], indicating that [CO_2] was a major limiting factor for photosynthesis. As [CO_2] increased to more than 350 μmol mol^{-1}, the response of P_N exhibited a different trend. First, when RWC was greater than 72.7%, P_N increased with increasing [CO_2]; when [CO_2] reached a certain value (about 1,000 μmol mol^{-1}), P_N reached saturation and decreased slowly but remained high. When RWC was in the range of 24.4–72.7%, P_N increased with increasing [CO_2]. After [CO_2] reached saturation, P_N decreased, indicating that the leaves could not absorb and utilize high [CO_2]; under these conditions, the enzymatic reactions of CO_2 assimilation lagged (Xu 2001). When RWC was in the range of 24.4–72.7%, there was a considerable difference in the decreases of P_N among different water conditions: with increasing RWC, the decrease in P_N gradually declined. For example, when RWC was 49.5 and 72.7%, the decrease in P_N was

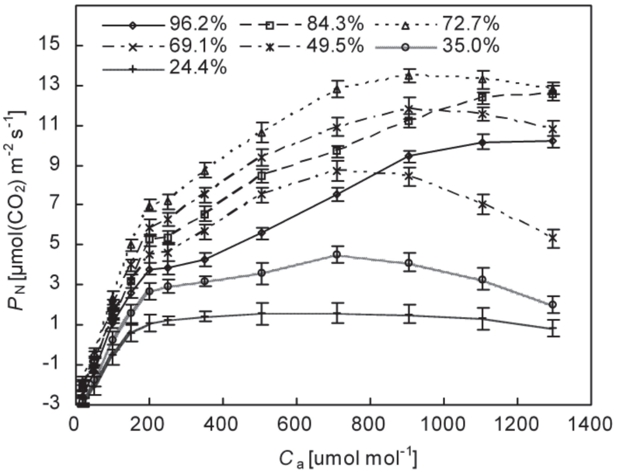

Fig. 1. Response of the net photosynthetic rate (P_N) to air CO$_2$ concentrations (C_a) under different relative soil water content (RWC). Points are the mean of at least 27 replicates P_N responses for each C_a. Error bars represent ± 1 SE of the mean. Lines are fitted to the response of P_N to C_a.

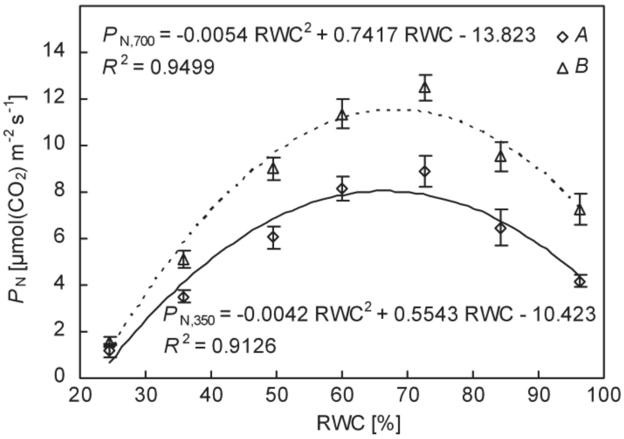

Fig. 2. The threshold value of net photosynthetic rate (P_N) in response to relative soil water content (RWC) under (*A*) the normal CO$_2$ concentration (350 μmol mol^{-1}) and (*B*) twice the normal CO$_2$ concentration (700 μmol mol^{-1}). Each point represents the mean of at least three plants with 27 replicates of P_N for each RWC. Regression lines were fitted using a polynomial expression. Error bars represent ± 1 SE of the mean.

38.7 and 3.9%, respectively. When RWC was less than 35.0%, particularly when it reached 24.4%, P_N decreased severely and remained low, indicating that soil moisture was a major limiting factor for photosynthesis under sufficient [CO$_2$]. Overall, when RWC was less than 72.2%, P_N increased with increasing RWC, but when RWC was greater than 72.2%, P_N decreased with increasing RWC, so RWC of 72.2% could be the turning point for P_N variations.

These analyses showed that under different [CO$_2$], there would be suitable coupling of soil moisture conditions to improve the photosynthetic productivity of *F. rhynchophylla*. The proper moisture level to maintain the high photosynthetic productivity was in the range of 49.5–84.3%, and in this range, the appropriate [CO$_2$] was in the range of 300–1,400 μmol mol^{-1}. P_N was the highest when RWC was about 72.7% and [CO$_2$] was 500–1,400 μmol mol^{-1}. Under slightly deficient soil moisture conditions or mild water stress, the moderate photosynthetic productivity was obtained, but when RWC was less than 35.0%, P_N decreased significantly, and the normal growth of *F. rhynchophylla* was restricted.

The soil moisture threshold of net photosynthetic rate: To reveal the critical point of soil moisture at which the P_N of *F. rhynchophylla* changed, the values of P_N were measured with [CO$_2$] of 350 μmol mol^{-1} and 700 μmol mol^{-1}. The results were consistent with the quadratic equation (Fig. 2). The maximum P_N values calculated by the quadratic equation were 7.9 and 11.6 μmol m^{-2} s^{-1}, respectively, and the soil moisture values, which maintained the maximum P_N, were 66.0 and 68.7%, respectively. When the [CO$_2$] was 350 μmol mol^{-1} and P_N was zero, the corresponding soil moisture values were 22.7 and 109.3%, respectively, and when [CO$_2$] was 700 μmol mol^{-1} and P_N was zero, the corresponding soil moisture values were 46.3 and 91%, respectively. According to the integration of the regression equations:

$$\overline{P_{N350}} = \frac{1}{95.2-23.8}\int_{23.8}^{95.2}\left(\frac{-0.0042}{3}x^3+\frac{0.5543}{2}x^2-10.423\,x\right)dx$$

$$\overline{P_{N700}} = \frac{1}{95.2-23.8}\int_{23.8}^{95.2}\left(\frac{-0.0054}{3}x^3+\frac{0.7417}{2}x^2-13.823\,x\right)dx$$

the average values of P_N in the measured range of 23.8–95.2% were calculated and found to be 5.9 and 8.9 μmol m^{-2} s^{-1}, respectively. When the [CO$_2$] was 350 μmol mol^{-1}, RWC was 44.5 and 87.5%, respectively, and when the [CO$_2$] was 700 μmol mol^{-1}, RWC was 46.3 and 91.0%, respectively. Therefore, the range of RWC, which maintained higher P_N values in *F. rhynchophylla*, was 44.5–87.5% under normal [CO$_2$], and the most suitable RWC was 66.0%. With increasing [CO$_2$], the average value of P_N would obviously ascend and increased by approximately 51%, but the range of soil moisture and the most suitable soil moisture increased by only 2%, indicating that [CO$_2$] was the main limiting factor for photosynthesis under optimal water conditions.

The response of photosynthetic parameters to soil moisture: $P_{max,c}$ and carboxylase efficiency (V_c) increased in a similar way rapidly with increasing RWC (Fig. 3). For example, when RWC increased from 49.5 to 60.1%, $P_{max,c}$ and V_c increased by 33.3 and 27.2%, respectively, and when RWC increased to a certain critical value (about 73%), both $P_{max,c}$ and V_c reached their highest levels of 20.6 and 0.05 μmol m^{-2} s^{-1}, respectively (Table 1). As RWC continued to increase, $P_{max,c}$ and V_c declined significantly, indicating that both excessive and deficient RWC led to decreases in $P_{max,c}$ and V_c.

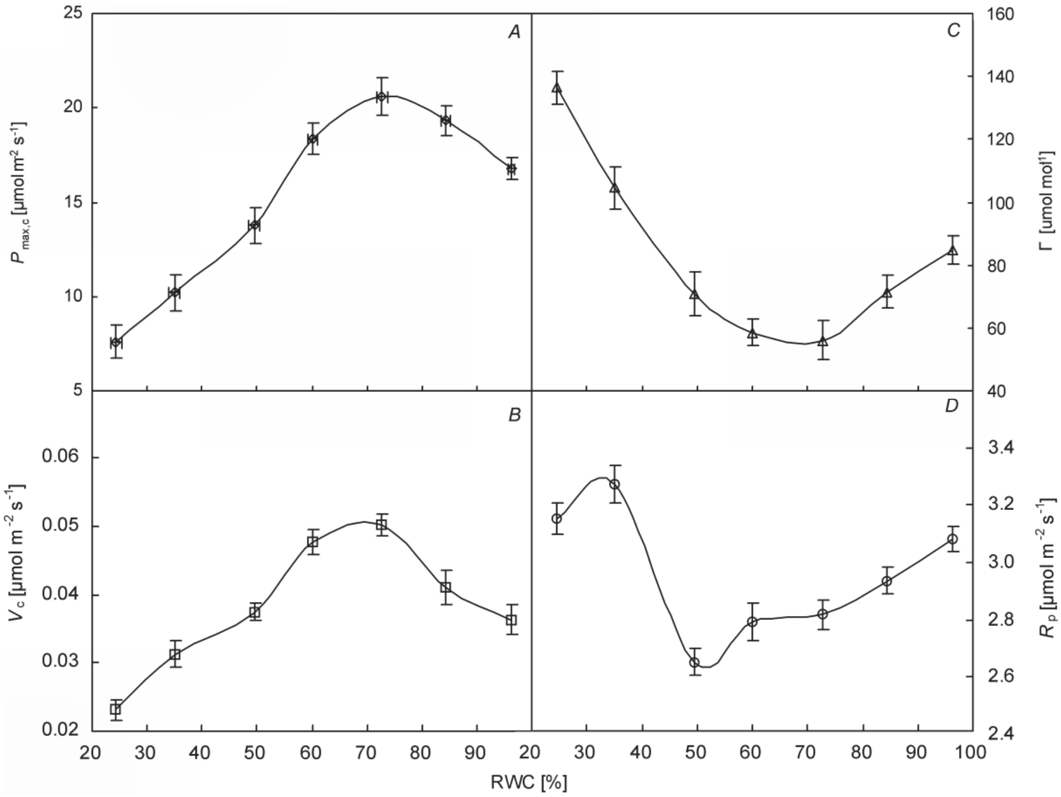

Fig. 3. The responses of (*A*) apparent maximum net photosynthetic rate ($P_{max,c}$); (*B*) carboxylation velocity (V_c); (*C*) CO_2 compensation point (Γ); and (*D*) photorespiration rate (R_p) to relative soil water content (RWC). Each point represents the mean of at least 3 plants for each RWC. Error bars represent ± 1 SE of the mean. Lines are fitted to the response of $P_{max,c}$, V_c, Γ, and R_p to RWC.

Table 1. Photosynthetic parameters – carboxylation velocity (V_c), photorespiration rate (R_p); CO_2 compensation point (Γ), and correlation coefficient (R^2) of net photosynthetic rate (P_N) in response to intercellular CO_2 concentrations (C_i) under different relative soil water contents (RWC). Mean, $n = 27$.

RWC [%]	Simulated equations	V_c [µmol m^{-2} s^{-1}]	R_p [µmol m^{-2} s^{-1}]	Γ [µmol mol^{-1}]	R^2
96.2	$P_N = 0.0363 \times C_i - 3.0823$	0.0363	3.0823	84.9	0.9816
84.3	$P_N = 0.0411 \times C_i - 2.9359$	0.0411	2.9359	71.4	0.9986
72.7	$P_N = 0.0502 \times C_i - 2.8175$	0.0502	2.8175	56.1	0.9975
60.1	$P_N = 0.0447 \times C_i - 2.8283$	0.0477	2.7930	58.6	0.9948
49.5	$P_N = 0.0375 \times C_i - 2.6532$	0.0375	2.6532	70.8	0.9886
35.0	$P_N = 0.0313 \times C_i - 3.2711$	0.0313	3.2711	104.5	0.9886
24.4	$P_N = 0.0231 \times C_i - 3.1571$	0.0231	3.1517	136.4	0.9690

The response of the CO_2 compensation point (Γ) to RWC (Fig. 3) was the opposite of that of $P_{max,c}$ and V_c. When RWC was approximately 73%, Γ reached its minimum (56.1 µmol mol^{-1}) (Table 1). Variance analysis showed that there was no significant change in Γ when the RWC was in the range of 49.5–84.3%. Γ increased significantly with increasing or decreasing RWC.

R_p had an obvious threshold response to changing RWC (Fig. 3). When RWC was 49.5%, R_p reached its minimum (2.6532 µmol m^{-2} s^{-1}) (Table 1) and increased slowly with increasing RWC. For example, when RWC was 60.1%, R_p increased by approximately 5%. However, R_p increased significantly with decreasing RWC; *e.g.*, when RWC was 35.0%, R_p was 23.3% higher, indicating that moderate water stress induced a decrease in oxygen consumption, which could improve photosynthetic production.

The response of g_s to [CO_2]:. Under different water supplies, g_s decreased with increasing [CO_2], indicating that higher [CO_2] limited the stomata opening. Under different [CO_2], g_s increased gradually with increasing RWC. When RWC was 72.7%, g_s reached its maximum and then began to decrease but remained high. When the RWC was greater than 72.7%, g_s decreased slowly, and when the RWC was less than 72.7%, g_s decreased rapidly

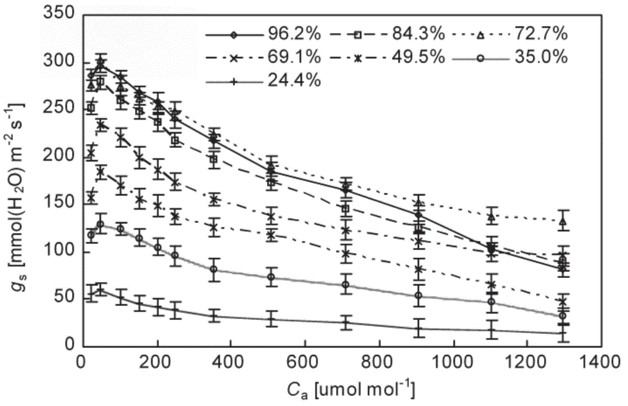

Fig. 4. Response of the stomatal conductance (g_s) to air CO_2 concentrations (C_a) under different relative soil water content (RWC). Points are the mean of at least 3 plants with 27 replicates of g_s responses for each C_a. Error bars represent ± 1 SE of the mean. Lines are fitted to the response of g_s to C_a.

Table 2. Photosynthetic parameters – maximal stomatal conductance (g_{smax}), constant (C_{s0}), and correlation coefficient (R^2) of stomatal conductance (g_s) in response to intercellular CO_2 concentrations (C_i) under different relative soil water contents (RWC) ($n = 324$).

RWC [%]	g_{smax} [mmol m^{-2} s^{-1}]	C_{s0}	R^2
96.2	318.71	673.64	0.965
84.3	300.00	727.92	0.968
72.7	275.00	969.17	0.980
60.1	231.79	823.21	0.960
49.5	184.80	718.55	0.939
35.7	112.00	600.42	0.959
24.4	44.00	429.31	0.983

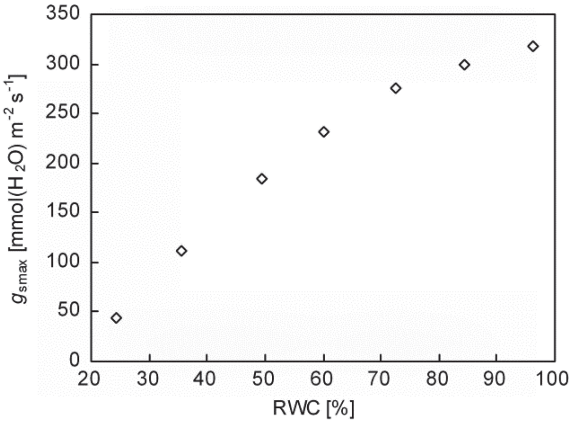

Fig. 5. Response of the maximal stomatal conductance (g_{smax}) to relative soil water content (RWC). Each point represents the mean of at least 3 plants for each RWC. Error bars represent ± 1 SE of the mean.

at [CO_2] higher than 350 µmol mol^{-1}. Under severe water stress (RWC of 24.4%), g_s was very low and did not change, indicating that the stomata were almost closed, and normal plant growth was significantly influenced (Fig. 4).

Though there has been a great deal of research on simulating the responses of stomata to atmospheric CO_2 concentration (C_a) or C_i using different equations (Cannon and Roberts 1995, Royer 2001, Lambreva *et al.* 2005, Laurin *et al.* 2006, de Beeck *et al.* 2010), no consensus on the response of stomata to [CO_2] has been reached because of its complex nature. Jarvis (1976) suggested use of a discontinuous function to represent the relationship between (C_a) and g_s, but the limit of the independent variable was uncertain for various plants and growth conditions, so the utilization of this function in practice was not convenient. In this study, we adopted the following hyperbolic function (Wang *et al.* 2005) to describe the response of g_s to C_a, and the simulated stomatal conductance parameters are shown in Table 2.

$$g_s = \frac{g_{smax}}{1 + C_a / C_{s0}},$$

where C_{s0} is constant.

The correlation coefficient (R^2) of this equation was significant under different water-supply conditions (Table 2), indicating that the curves could describe the relationship between g_s and C_a. The maximum stomatal conductance (g_{smax}) increased with increasing water supply (Fig. 5).

The soil moisture threshold of g_s: To reveal the critical point of soil moisture at which the g_s of *F. rhynchophylla* obviously changed, the g_s values were measured under [CO_2] of 350 and 700 µmol mol^{-1}, and the results were consistent with the quadratic equation (Fig. 2). The coefficient of determination (R^2) of the equation exceeded

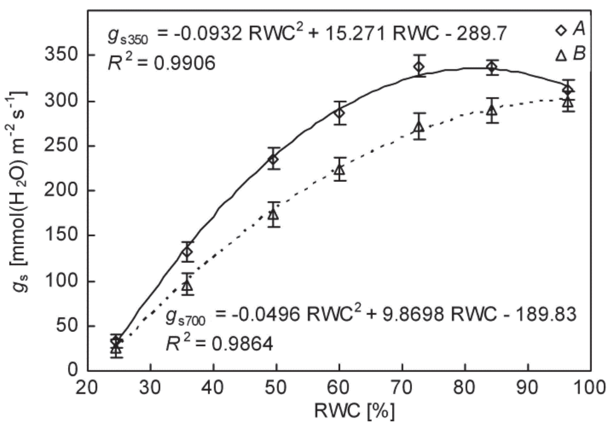

Fig. 6. The threshold value of the stomatal conductance (g_s) in response to relative soil water content (RWC) under (*A*) the normal CO_2 concentration (350 µmol mol^{-1}) and (*B*) twice the normal CO_2 concentration (700 µmol mol^{-1}). Each point represents the mean of at least 3 plants with 27 replicate g_s for each RWC. Regression lines were fit using a polynomial expression. Error bars represent ± 1 SE of the mean.

0.98, indicating that the relationship between g_s and RWC could be simulated well by quadratic equations. g_s gradually increased with increasing RWC, when the [CO_2] was 350 µmol mol^{-1}; g_s reached its maximum when RWC was approximately 84.3%, and then decreased slowly, similarly to the changes in g_s and [CO_2] under different soil moisture conditions (Fig. 6). g_s did not decrease but increased slowly, and the average value decreased significantly, when the [CO_2] was 700 µmol mol^{-1}. Using the method described above, the means of g_s in the range of 23.8–95.2% were 252 mmol and 204 mmol m^{-2} s^{-1}, respectively.

When [CO_2] was 350 µmol mol^{-1}, g_s remained high, while the RWC was between 52.0 and 111.9%, and when [CO_2] was 700 µmol mol^{-1}, RWC was in the range of approximately 55.2–143.2%, indicating that increasing [CO_2] was not beneficial for stomata opening, but it could improve the adaptability of plants to high water contents.

Discussion

Responses of P_N and g_s: P_N, g_s, and V_c are very sensitive to changes in the C_a and respond very quickly to CO_2 changes (Royer 2001, Lambreva *et al.* 2005, Avola *et al.* 2008). Research has shown that the increase of [CO_2] in the short term will promote photosynthesis, increase stomatal resistance, and reduce transpiration (Niklaus *et al.* 2001, Paoletti *et al.* 2005, Kosugi *et al.* 2006, Xia *et al.* 2009). The results in this study also supported this point. P_N of *F. rhynchophylla* gradually increased with increasing [CO_2]. The positive effects of increasing [CO_2] on P_N reduced the adverse effects of drought and improved tolerance to drought stress. This effect was quite clear under the moderate water stress. With increasing severity of water stress, the response of the CO_2 saturation point of P_N changed from a slow decrease under mild water stress to a linear decrease. The increase in P_N was small under more water-deficient conditions; therefore, as the [CO_2] increase in the future, increasing irrigation will be necessary to fully exploit the positive effects of increasing [CO_2] on P_N. Overall, whether under conditions of sufficient water or drought stress, increasing atmospheric [CO_2] could significantly improve P_N.

Stomata are the main channel through which plants carry out CO_2 and water vapor exchange, and g_s is a very important physiological index that reflects the exchange capacity, thus the effect of increasing [CO_2] on g_s is particularly important (Matsumoto *et al.* 2005, Paoletti *et al.* 2005, Laurin *et al.* 2006, Reiter *et al.* 2008). Although most studies have shown that g_s decreases with increasing [CO_2], some studies showed that different plant species responded differently to increasing [CO_2]. To explain the decline in g_s, some studies suggested lowered stomata density (Peschel *et al.* 2003, Irmak *et al.* 2008, Zaharah and Razi 2009), but other studies suggested that the increased C_i in leaves led to the partial closure of stomata (Mott and Buckley 2000, Paoletti *et al.* 2005, Kosugi *et al.* 2006). Because the stomata density was relatively constant in the short term, the primary cause of the decreasing g_s was the partial closure of stomata. Many studies have shown that stomata are an important factor in restricting photosynthesis with increasing [CO_2] (Xia *et al.* 2009), but the magnitude of g_s was not sufficient to explain the limit of the photosynthetic rate. Some studies have shown that Rubisco is a very important non-stomatal limiting factor (Niklaus *et al.* 2001). This study was restricted to the instantaneous or short-term response of g_s to increasing [CO_2], and g_s gradually decreased with increasing [CO_2]; this was consistent with most previous studies (*e.g.* Morison and Lawlor 1999). Because of the limitations of the experimental conditions, the influence of long-term [CO_2] elevation was not investigated on leaves; however, some researchers have considered this extremely necessary (Pozo *et al.* 2005, Kosugi *et al.* 2006, Xia *et al.* 2009). Most long-term experiments were not able to repeat the results of short-term experiments. The adaptability of different plant species to increasing [CO_2] indicate that plant responses to [CO_2] are much more complex and require further research.

Soil moisture adaptability of photosynthesis: Research has shown that plants have different adaptability and resistance to soil moisture deficits, and various physiological processes are active under a moderate moisture deficit (Xu 2001). This moisture range varies by plant species and physiological process. This study showed that in different ranges of [CO_2], RWC, which produced high P_N in *F. rhynchophylla*, was in the range of 35.0–84.3%, and the most suitable RWC was 72.7% (Fig. 3). This moisture range not only guaranteed a higher level of photosynthesis and the normal growth and development for *F. rhynchophylla* but also prevented the loss of a great deal of water by transpiration, which maintained the high water-use efficiency (data not shown).

To a certain extent, $P_{max,c}$ reflects the potential maximum photosynthetic rate if the [CO_2] reaches saturation in the short term. This study showed that the $P_{max,c}$ of *F. rhynchophylla* had a clear threshold value for the soil moisture; reached its maximum under moderate water stress, and the increase or decrease in water content significantly reduced $P_{max,c}$. This could be explained if soil water stress had a beneficial effect on carbon assimilation rate; namely, soil water stress increased the competition of CO_2 for Rubisco binding sites, improving V_c and P_N by inhibiting photorespiration.

Plant photosynthetic capacity is an important physiological index for evaluating different plants or crop varieties. Under optimal conditions, P_{Nmax} indicates the highest possible photosynthetic capacity (Larcher 1980, Tartachnyk and Blanke 2004). The responses of different plants to high [CO_2] differ; for example, P_{Nmax} was 41.2 µmol m^{-2} s^{-1} in *Myrica rubra* (Zhang *et al.* 2006), that of *Phragmites australis* (Liang *et al.* 2006) was 51.8 µmol m^{-2} s^{-1}, and 26.7 µmol m^{-2} s^{-1} in *Populus euphratica* olive (Zhou *et al.* 2009). This study showed that P_{Nmax} of *F. rhynchophylla* was 20.6 µmol m^{-2} s^{-1}, which was significantly lower than those of the above-mentioned plants. The maximal photosynthetic capacities of the plants were different, indicating that the plants expressed different photosynthetic responses to high [CO_2] (Cure and Acock 1986, Rowland-Bamford *et al.* 1991). Rowland-Bamford *et al.* (1991) found that P_N and increases in P_N of the same rice materials differed with different high [CO_2] and temperatures, which might be due to differences in the plant variety, its modes of photosynthesis, and possibly its relationship with surrounding conditions.

In most short-term experiments, plant photosynthetic capacity increased with increasing [CO_2] in plants with different modes of photosynthesis. Most research on C_4 plants (Cure and Acock 1986, Kimball *et al.* 2002, Farazdaghi 2011) showed that increases in [CO_2] had little influence on the rate of photosynthesis and the growth. Fewer studies have investigated plants that perform crassulacean acid metabolism (CAM) photosynthesis, and the results were not consistent (Kimball *et al.* 2002, Jeon *et al.* 2006, Croonenborghs *et al.* 2009, Weiss *et al.* 2010). Cure and Acock (1986) and Kimball *et al.* (2002) calculated that the net photosynthetic rate of C_4 plants increased by only 4%, while that of C_3 plants improved by 66% under increased [CO_2]. This study found that under increased [CO_2], P_{Nmax} of *F. rhynchophylla* increased by more than 40%, except under severe water stress. When RWC was 96.2%, P_{Nmax} increased by 75%, which was generally consistent with the research of Cure and Acock (1986) and Kimball *et al.* (2002).

Adaptability of photosynthesis-CO_2 response parameters to soil moisture: V_c can reflect the status of C_i and it can also reflect the CO_2 assimilation capability of plants under given conditions. The higher V_c, the more efficient use of CO_2. V_c depends mainly on the activity of Rubisco, and photosynthesis under high [CO_2] is limited by the regeneration rate of ribulose-1,5-bisphosphate. The results of this study showed that V_c of *F. rhynchophylla* had a threshold response to RWC; when RWC was in the range of 60.1–72.7%, V_c reached a relatively high value (the average was 0.049 µmol m^{-2} s^{-1}), and if RWC was higher or lower, V_c decreased significantly. The decline of V_c under higher water contents was much lower than that under low water contents, indicating that severe water stress reduced the CO_2 assimilation capacity of seedlings. In other studies, the V_c of *Phragmites australis* (Liang *et al.* 2006) was 0.089 µmol m^{-2} s^{-1}, that of *Quercus pannosa* (Zhu *et al.* 2006) was 0.035 µmol m^{-2} s^{-1}, and that of *Corydalis saxicola* (Wei *et al.* 2006) was 0.031 µmol m^{-2} s^{-1}. Fewer studies have been performed on V_c of C_4 plants, which were higher due to their different mode of photosynthesis. For example, V_c values of *Axonopus compressus* and *Pennisetum alopecuroides* (Jian and Zou 2003, Ju *et al.* 2005) were 0.254 and 0.235 µmol m^{-2} s^{-1}, respectively; the V_c of *Spartina alterniflora* (Liang *et al.* 2006) was 0.317 µmol m^{-2} s^{-1}, and that of *Oryza sativa* var. *japonica* (Wang *et al.* 2005) was 0.148 µmol m^{-2} s^{-1}. In this study, the V_c of *F. rhynchophylla* was closer to those of *Quercus pannosa* and *Corydalis saxicola* and significantly lower than those of C_4 plants. This indicated that different plants have different capacities to assimilate CO_2, which might be due to the plant characteristics or to the growth environment.

The CO_2 compensation point (Γ) is an important physiological index for comprehension and evaluating the relationship between photosynthesis and respiration. Most research found that C_3 plants have clear responses to CO_2, and Γ changed significantly in various stages of development and in different environments (Roussel *et al.* 2007, Reiter *et al.* 2008, Farazdaghi 2011). Within a certain temperature range, Γ increased with increasing temperatures and decreased with decreasing [CO_2] (Pfanz *et al.* 2007, Avola *et al.* 2008). Meanwhile, Γ values of various plants are different; for example, the Γ of *Q. pannosa* is 86 µmol mol^{-1} (Zhu *et al.* 2006), that of *C. saxicola* is 69 µmol mol^{-1} (Wei *et al.* 2006), and that of *M. rubra* is 87 µmol mol^{-1} (Zhang *et al.* 2006). The results of this study showed that when RWC was in the range of 49.5–83.4%, there was no obvious difference among the Γ values, which ranged from 56.1–71.4 µmol mol^{-1}. Γ increased significantly with increasing water stress and reached 136.4 µmol mol^{-1} under severe water stress, indicating that *F. rhynchophylla* expressed a certain flexibility with respect to [CO_2] under different water conditions. There were significant differences among Γ values of various plants, possibly due to the experimental time, environmental conditions, and the biological characteristics of the plant species.

Photorespiration is the process by which the green parts of plants absorb O_2 and release CO_2 in response to light, and it has been long considered one of the main factors affecting the yield. Experiments have been performed to improve the economic yield by inhibiting photorespiration (Zelitch 1974, 1982). Photorespiration was once considered to be a waste of light energy and unfavorable to dry matter accumulation (Zelitch 1974). However, further research has shown that photorespiration is very important to ensure normal photosynthesis (Jiang *et al.* 2006, Massacci *et al.* 2008, Wilhelm and Selmar 2011). There has been controversy regarding the light-protective function of photorespiration. Kozaki and Takeba (1996) demonstrated a light-protective function of photorespiration with mutants; Wingler *et al.* (1999) also showed the increase of R_p under drought conditions with an immunosorbent method. Nogués and Alegre (2002) found that under drought conditions, a decrease in the carboxylase activity of Rubisco accompanied decreases in its oxygenation activity. The results of this study showed that when RWC was in the range of 49.5–72.7%, R_p remained at a low value, improving the biological yield, which was favorable for dry matter accumulation. With increasing water stress, R_p increased sharply to ensure the normal operation of photosynthetic apparatus in excess light, which was consistent with the results of Kozaki and Takeba (1999) and Wingler *et al.* (1999); those studies indicated that photorespiration was probably a means of consuming surplus light energy to protect the photosynthetic apparatus from strong sunlight (Jiang *et al*. 2006, Massacci *et al*. 2008).

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