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Experimental and simulated light responses of photosynthesis in leaves of three tree species under different soil water conditions

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Abstract

Water deficit is one of the major limiting factors in vegetation recovery and restoration in loess, hilly-gully regions of China. The light responses of photosynthesis in leaves of two-year old *Prunus sibirica* L., *Hippophae rhamnoides* L., and *Pinus tabulaeformis* Carr. under various soil water contents were studied using the *CIRAS-2* portable photosynthesis system. Light-response curves and photosynthetic parameters were analyzed and fitted using the rectangular hyperbola model, the exponential model, the nonrectangular hyperbola model, and the modified rectangular hyperbola model. Under high light, photosynthetic rate (P_N) and stomatal conductance (g_s) were steady and photoinhibition was not significant, when the relative soil water content (RWC) varied from 56.3–80.9%, 47.9–82.9%, and 33.4–92.6% for *P. sibirica*, *H. rhamnoides*, and *P. tabulaeformis*, respectively. The light-response curves of P_N, the light compensation point (LCP), and the dark respiration rate (R_D) were well fitted using the above four models. The nonrectangular hyperbola was the best model in fitting the data; the modified rectangular hyperbola model was the second, and the rectangular hyperbola model was the poorest one. When RWC was higher or lower than the optimal range, the obvious photoinhibition and significant decrease in P_N with increasing photosynthetic photon flux density (PPFD) were observed in all three species under high light. The light saturation point (LSP) and apparent quantum yield also decreased significantly, when the upper limit of PPFD was 200 µmol m^{-2} s^{-1}. Under these circumstances, only the modified rectangular hyperbola model was able to fit well the curves of the light response, LCP, LSP, R_D, and light-saturated P_N.

Additional key words: drought-resistant tree species; light-response model; photoinhibition; photosynthetic rate; quantum yield; relative soil water content.

Introduction

Oxygenic photosynthesis is a process by which plants, algae, and cyanobacteria use energy from sunlight to produce sugar and to release oxygen (Blankenship 2002, Govindjee and Krogmann 2004). It is critical for support of life systems on the Earth and it is influenced by many factors, including temperature, carbon dioxide concentration, light intensity, soil nutrient levels, and water content. Each plant species has its own optimal light intensity range, soil conditions, and other environmental needs for photosynthesis. Water is a crucial factor. Water stress, especially drought stress, is the main restriction of plant growth and development (Hu *et al.* 2004). Studies of the light response of plant photosynthesis under different soil water conditions can help to understand the

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Abbreviations: FC – field capacity; g_s – stomatal conductance; GWC – gravitational water content; LCP – light compensation point; LSP – light saturation point; MAE – mean absolute error; MSE – mean square error; P_N – net photosynthetic rate; P_{Nmax} – light-saturated net photosynthetic rate; PPFD – photosynthetic photon flux density; R_D – dark respiration rate; RWC – relative water content; SWC – soil water content; VWC – volumetric water content; Φ – apparent quantum yield; Φ_c – quantum yield at the light compensation point; Φ_{c0} – absolute value of the slope of the photosynthetic rate–light-response curve between zero irradiance and LCP; Φ_0 – quantum yield at zero irradiance; $\Phi_{PPFD\leq120}$ – apparent quantum yield by the upper limit of PPFD of 120 µmol m^{-2} s^{-1}; $\Phi_{PPFD\leq160}$ – apparent quantum yield by the upper limit of PPFD of 160 µmol m^{-2} s^{-1}; $\Phi_{PPFD\leq200}$ – apparent quantum yield by the upper limit of PPFD of 200 µmol m^{-2} s^{-1}.
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photo-physiological characteristics of different plants, reveal quantitative relationships between these characteristics and soil water content (SWC), and give guidance in plant production processes, such as selection of good quality seeds and suitable cultivation conditions.

Light- and CO_2-response models are essential for studying responses of photosynthesis. Light-response models investigate the relationship between P_N and PPFD, and they are very important for understanding photochemical efficiency in plant photochemical processes (Robert *et al.* 1984). In addition, the main photosynthetic parameters, such as light saturation point (LSP), light-saturated net photosynthetic rate (P_{Nmax}), light compensation point (LCP), dark respiration rate (R_D), and apparent quantum yield (Φ) can be estimated by drawing light response curves of photosynthesis (Ye 2010).

Since 1980, many light-response models of photosynthesis have been constructed (Miko and Graham 1987, Thornley 1998). The rectangular hyperbola model, the exponential model, and the nonrectangular hyperbola model have been commonly used (Prioul and Chartier 1977, Levernz and Jarvis 1979, Farquhar *et al*. 1980, Marshall and Biscoe 1980). Research has shown, however, that using the above models, the fitted LSP is much smaller than the measured value, and the fitted P_{Nmax} is much larger than the measured value (Steel 1962, Ye 2007, Ye and Yu 2007, Ye and Wang 2009, Chen 2011). More recently, a new model has been constructed based on the rectangular hyperbola model (Ye 2007, Ye and Gao 2008, Ye and Yu 2008); it is known as the modified rectangular hyperbola model. There is evidence that the new model may overcome disadvantages of the three former models and fit light-response curves and main parameters of photosynthesis more accurately (Ye and Gao 2008). However, the new model has been applied so far mainly to crops and herbaceous plants under different temperatures or different carbon dioxide concentrations (Ye 2007, Ye and Gao 2008, Ye and Wang 2009, Ye and Yu 2008). It is not clear if its advantages still hold when applied to woody plants under different soil water conditions.

In recent years, much research has been done to investigate the effects of soil water stress on the photosynthesis of plants (Xiao *et al.* 2005, Subrahmanyam *et al.* 2006, Rouhi *et al.* 2007, Du *et al.* 2010, Alexandros and Angelos 2012). In most of these experiments, only a few water levels have been studied, representing mild, moderate, and severe water stress. However, it is necessary to obtain a sufficient amount of experimental data under multi-level SWC to accurately characterize the quantitative relationship between photosynthesis and SWC. In this research, we used two-year-old potted seedlings of *P. sibirica*, *H. rhamnoides*, and *P. tabulaeformis* to examine the light responses of P_N under various SWC. We analyzed the photosynthetic curves and main parameters and fitted them using the rectangular hyperbola model, the exponential model, the non-rectangular hyperbola model, and the modified rectangular hyperbola model. Our objectives were to characterize the relationship between photosynthesis and SWC, to study the ability of these models to simulate the light response of photosynthesis under different soil water conditions, and to gain further understanding of the photo-physiological characteristics of these tree species under water stress. Our results could also provide guidance for the cultivation of *P. sibirica*, *H. rhamnoides*, and *P. tabulaeformis* in loess hilly-gully regions and for the selection of optimal light response models for trees under different soil water conditions.

Materials and methods

Study area: Our experimental site was located in the Tuqiaogou watershed, Yukou Town, Fangshan County, Shanxi Province, China, a hilly-gully area of the Loess Plateau in the middle reaches of the Yellow River (37°36′58″ N and 110°02′55″ E). The average altitude is 1,200 m with a maximum of 1,446 m. The average annual precipitation is 416 mm, with more than 70% precipitation falling from June to September. The annual potential evaporation is 1,858 mm, and the greatest evaporation occurs from April to June. The average relative humidity is 50%. The soil is classified as a medium loess soil. The average soil bulk density is 1.2 g cm^{-3}, and the average field capacity (FC) is roughly 21.0%. The vegetation consists mainly of trees, shrubs, lianas, subshrubs, and annual, biennial, and perennial herbs.

Experimental seedling selection: Two-year-old *P. sibirica*, *H. rhamnoides*, and *P. tabulaeformis* were selected for experiments. In April 2010, we selected six healthy seedlings with relatively uniform plant height and basal diameter for each species from the local nursery. Each seedling was planted in a pot (1 m deep with a radius of 0.3 m) in the greenhouse under the temperature of 28–32ºC, the air humidity of 41–55%, and the CO_2 concentration of 365–395 ppm. Two months later, we selected three seedlings of similar growth. Thus, we had a total of nine experimental seedlings. The average plant heights of the three seedlings of *P. sibirica*, *H. rhamnoides*, and *P. tabulaeformis* were 1.2, 1.3, and 0.9 m, respectively, and the average basal diameters were 21, 23, and 15 mm, respectively.

Soil water content (SWC): Variations in SWC were achieved by using the artificial water supply and the plant natural water consumption during June 2010. Two days before the measurement of the photosynthetic efficiency, we provided sufficient water supply to each seedling to saturate the soil, and then monitored the change in volumetric water content (VWC) using a soil moisture meter (*Delta-T*, Cambridge, England). Two days later, the gravitational water content (GWC) of the soil was measured using the convective oven-drying method (Evett *et al*. 2008, Heyam 2012). For each seedling, five records were taken at 20 cm depth intervals in a 0–100 cm soil layer; the average of GWC was then found. As SWC decreased continuously by evapotranspiration, we measured SWC and the photosynthetic efficiency every two days, until the seedling withered. RWC is the ratio of GWC to FC. Data points were obtained under eight different SWC for each tree species.

Measurement of photosynthesis: P_N and g_s were measured using a portable photosynthesis system (*CIRAS-2*, *PPS Co. Ltd*., England) on the same days as GWC. After each SWC measurement, three fully developed, mature leaves from the center of each seedling crown were carefully selected and marked. P_N was measured three times for each selected leaf, so that nine measurements were made for each seedling. Measurements were made between 8:30–11:00 h on a sunny day. During each measurement, CO_2 concentration was maintained at 375 ± 6.0 ppm, air temperature at 24–26ºC, and relative humidity at 60 ± 4.0%, by the *CIRAS-2* portable photosynthesis system. For every observation, PPFD was controlled at 1,800; 1,600; 1,400; 1,200; 1,000; 800, 600, 400, 200, 150, 100, 50, 20, and 0 μmol m^{-2} s^{-1} by a *CIRAS-2* LED irradiation source. For each level of PPFD, the selected leaf was kept in the leaf chamber for at least 120 s to reach a steady photosynthetic state before measuring P_N and g_s.

We analyzed the data, including RWC and photosynthetic parameters under different soil water conditions. By drawing the photosynthetic light response curves (P_N-PPFD curves) for three tree species using *Microsoft Excel 2007*, LSP, P_{Nmax} (Chen *et al.* 2008, Xia *et al.* 2009), LCP (PPFD when P_N = 0), and R_D (P_N when PPFD = 0) were obtained. At the same time, the apparent quantum yield was calculated using the linear regression method of the P_N-PPFD curve under PPFD ≤ 200 μmol m^{-2} s^{-1} ($\Phi_{PPFD\leq200}$) (Xia *et al.* 2009, Xu 2002). These photosynthetic parameters were considered the measured values and they were used to compare with the fitted values obtained using the following models.

Nonlinear fitting of light-response models: Using the *SPSS 18.0* for *Windows* (*SPSS*, Chicago, USA), light-response curves and photosynthetic parameters were analyzed statistically and fitted nonlinearly using four models: the rectangular hyperbola model, the nonrectangular hyperbola model, the exponential model, and the modified rectangular hyperbola model. The initial values used in the models were: (*1*) α = 0.05, R_D = 1.0 for both rectangular and exponential model; (*2*) α = 0.05, R_D = 1.0, k = 0.7 for the nonrectangular model; (*3*) α = 0.05, β = 0.0001, γ = 0.001, I_c = 20 for the modified rectangular model (Ye 2007, 2010, Ye and Yu 2007, 2008, Ye and Gao 2008, Ye and Wang 2009). For all models, the initial value of P_{Nmax} was set to be the integral part of the measured light-saturated net photosynthetic rate.

To evaluate the accuracy of four models fitting the light response curves and parameters, the mean square error (MSE) and the mean absolute error (MAE) were calculated for each model (Chen *et al.* 2011).

Rectangular hyperbola model

The rectangular hyperbola model (Baly 1935, Thornley 1998, Lewis *et al.* 1999, Kyei-Boahen *et al.* 2003, Ye and Wang 2009) was expressed as follows:

$$P_N(I) = \frac{\alpha I P_{Nmax}}{\alpha I + P_{Nmax}} - R_D \quad (1)$$

where α was the initial quantum yield; and I was PPFD.

The quantum yield of the plants at the light compensation point was defined as Φ_c; the intrinsic quantum yield was defined as Φ_0; the absolute value of the slope of the P_N-PPFD curve between I = 0 and I = LCP was defined as Φ_{c0} (Ye 2007, Ye and Yu 2007, Ye and Wang 2009):

$$\Phi_c = \dot{P}_N(I = I_c) = \frac{\alpha {P_{Nmax}}^2}{(\alpha I_c + P_{Nmax})^2} \quad (2)$$

$$\Phi_0 = \dot{P}_N(I = 0) = \alpha \quad (3)$$

$$\Phi_{c0} = \left| \frac{R_D}{I_c} \right| \quad (4)$$

where I_c is the LCP; $\dot{P}_N(I)$ is the first derivative of $P_N(I)$.

If the experimental data can be fitted by the rectangular hyperbola model, LCP can be calculated by:

$$I_c = \frac{R_D \times P_{Nmax}}{\alpha (P_{Nmax} - R_D)} \quad (5)$$

LSP is the abscissa of the intersection of the straight line y = P_{Nmax} and linear equation, when PPFD ≤ 200 μmol m^{-2} s^{-1} (Ye and Yu 2008).

Nonrectangular hyperbola model

The nonrectangular hyperbola model is used extensively, because it includes more parameters and it can generate better results (Prioul and Chartier 1977, Leverenz and Jarvis 1979, Farquhar *et al.* 1980, Marshall and Biscoe 1980, Ögren 1993, Marschall and Proctor 2004). The formula commonly used (Takahiro *et al.* 2002, Richardson and Berlyn 2002, Ye and Wang 2009) is as follows:

$$k P^2 - P (\alpha I + P_{Nmax}) + \alpha I P_{Nmax} = 0 \quad (6)$$

where P is the total photosynthetic rate; k (0 < k < 1) is the curvilinear angle of the nonrectangular hyperbola; and α; I, and P_{Nmax} are as described above.

Φ_c, Φ_0, and Φ_{c0} were expressed by equations 7, 8, and 9, respectively (Ye 2007, Ye and Yu 2007, Ye and Wang 2009):

$$\Phi_c = \dot{P}_N(I = I_c) = = \frac{\alpha}{2k}\left[1 - \frac{(\alpha I_c + P_{Nmax}) - 2kP_{Nmax}}{\sqrt{(\alpha I_c + P_{Nmax})^2 - 4k\alpha I_c P_{Nmax}}}\right] \quad (7)$$

$$\Phi_0 = \dot{P}_N(I = 0) = \alpha \quad (8)$$

$$\Phi_{c0} = \left|\frac{R_D}{I_c}\right| \quad (9)$$

If a good fit of the data to the curve can be achieved by the non-rectangular hyperbola model, then LCP can be obtained by:

$$I_c = \frac{R_D \times P_{Nmax} - k \times R_D^2}{\alpha(P_{Nmax} - R_D)} \quad (10)$$

LSP is the abscissa value of intersection of the straight line y = P_{Nmax} and the linear equation, when PPFD ≤ 200 μmol m^{-2} s^{-1} (Richardson and Berlyn 2002, Ye and Yu 2008).

Exponential model

There are many different expressions for exponential models. One commonly used is proposed by Bassman and Zwier (1991) and it is as follows:

$$P_N(I) = P_{Nmax}\left(1 - e^{-\alpha I/P_{Nmax}}\right) - R_D \quad (11)$$

where α; I; P_{Nmax}; $P_N(I)$, and R_D were as described above.

Φ_c, Φ_0, and Φ_{c0} were expressed by equations 12, 13, and 14, respectively (Ye 2007, Ye and Wang 2009):

$$\Phi_c = \dot{P}_N(I = I_c) = \alpha e^{-\alpha I_c/P_{Nmax}} \quad (12)$$

$$\Phi_0 = \dot{P}_N(I = 0) = \alpha \quad (13)$$

$$\Phi_{c0} = \left|\frac{R_D}{I_c}\right| \quad (14)$$

LSP was estimated as the light intensity corresponding to the photosynthetic rate that was 90% of P_{Nmax} (Huang *et al.* 2009).

The modified rectangular hyperbola model

The modified rectangular hyperbola model (Ye 2007) was expressed by:

$$P_N(I) = \alpha\frac{1 - \beta I}{1 + \gamma I}(I - I_c) \quad (15)$$

$$R_D = -\alpha I_c \quad (16)$$

$$I_m = \frac{\sqrt{(\beta + \gamma)(1 + \gamma I_c)/\beta} - 1}{\gamma} \quad (17)$$

$$P_{Nmax} = P_N(I_m) = \alpha\frac{1 - \beta I_m}{1 + \gamma I_m}(I_m - I_c) \quad (18)$$

where α, β, and γ were coefficients that were independent of I (Ye 2007), I_m was LSP. All the other parameters were as described above.

Φ_c, Φ_0, and Φ_{c0} were expressed by 19, 20, and 21, respectively (Ye 2007):

$$\Phi_c = \dot{P}_N(I = I_c) = \alpha\frac{1 + (\gamma - \beta)I_c - \beta\gamma I_c^2}{(1 + \gamma I_c)^2} \quad (19)$$

$$\Phi_0 = \dot{P}_N(I = 0) = \alpha[1 + (\beta + \gamma)I_c] \quad (20)$$

$$\Phi_{c0} = \left|\frac{R_D}{I_c}\right| = \alpha \quad (21)$$

Results

Light response of P_N and g_s: The light response of P_N to PPFD could be divided into three stages, among which the first two stages showed similar patterns of the response regardless of SWC for all three tree species (Fig. 1). In the first stage, where PPFD ≤ 200 μmol m^{-2} s^{-1}, P_N increased linearly as PPFD increased, indicating that PPFD was the key factor influencing photosynthesis in this PPFD range. With the further increase of PPFD, the response entered the second stage and the increase of P_N slowed down because of possible influence by several other factors, such as temperature, CO_2 concentration, and leaf characteristics. The light response in the third stage was quite diverse under different SWC. P_N of all three species stabilized at high levels and it did not significantly increase with increasing PPFD, when RWC for *P. sibirica*, *H. rhamnoides*, and *P. tabulaeformis* was 56.3–80.9%, 47.9–82.9%, and 33.4–92.6%, respectively. The critical PPFD was LSP, at and beyond which the leaves could not absorb and use all the energy from the high light, possibly because reaction rates of enzymes in the CO_2 assimilation process could not keep up with the increasing PPFD (Xu 2002). P_N decreased with the increase of PPFD and photoinhibition occurred (P<0.05), when RWC was lower or higher than the above ranges.

A strong correlation between the light response of g_s and P_N was observed (Fig. 2). If photoinhibition did not occur, g_s stabilized at high levels, when PPFD was beyond LSP, for all three species. Otherwise, g_s either decreased under high light or remained at low levels for all PPFDs.

P_N and g_s showed distinctive threshold responses to SWC (Figs. 1,2). As RWC decreased from its highest value, P_N and g_s increased and then decreased. *P. sibirica*, *H. rhamnoides*, and *P. tabulaeformis* reached their maximal P_N when RWC was 68.2%, 71.7%, and 64.0%, respectively. No photoinhibition occurred and LSP, P_{Nmax}, and g_s were at relatively high levels when RWC was in the range of 56.3–80.9%, 47.94–82.86%, and 33.38–92.6% for *P. sibirica*, *H. rhamnoides*, and *P. tabulaeformis*, respectively. The above RWC ranges were therefore considered to be the optimal soil water conditions for the photosynthesis of these tree species.

Light-response model of photosynthetic rate: When RWC was in the range of 56.3–80.9%, 47.9–82.9%, and 33.4–92.6% for *P. sibirica*, *H. rhamnoides*, and *P. tabulaeformis*, respectively, all four models had higher determination coefficients (R^2 > 0.9), lower MSE and

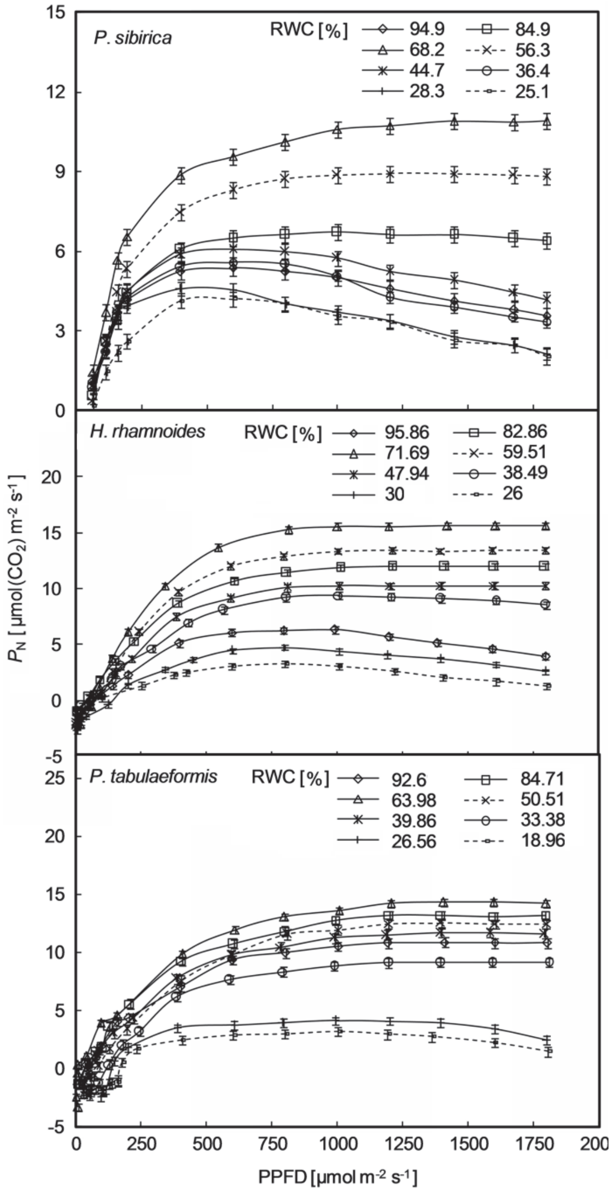

Fig. 1. Light response of photosynthetic rate (P_N) under different soil water conditions in three tree species. PPFD – photosynthetic photon flux density; RWC – relative water content. Bars indicate ± SE of the mean, *n* = 27.

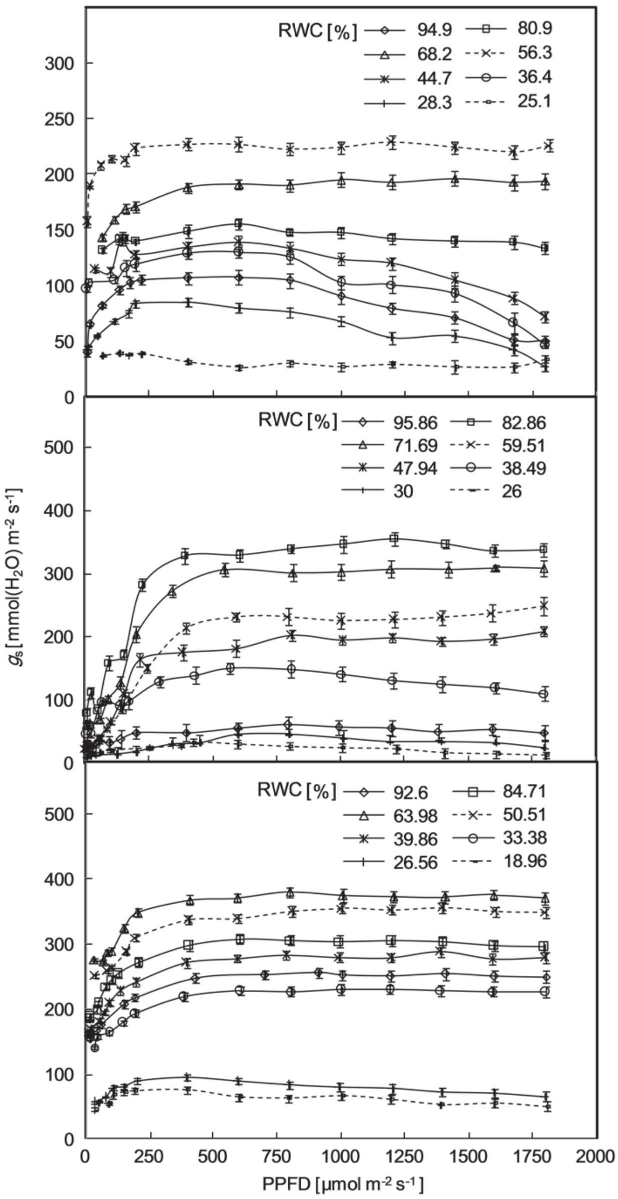

Fig. 2. Light response of stomatal conductance (g_s) under different soil water conditions in three tree species. PPFD – photosynthetic photon flux density; RWC – relative water content. Bars indicate ± SE of the mean, *n* = 27.

MAE, and fitted the light-response curves of photosynthetic rate well (Fig. 3, Tables 1S–3S, *see* the supplementary material online). The modified rectangular hyperbola model (R^2 = 0.99) fitted the curves in the best way. In the same RWC ranges, the simulated values of LCP and R_D indicated by four models showed no significant differences from the measured values (P>0.05). The data were fitted best by the nonrectangular hyperbola model; the modified rectangular hyperbola model was the second one; and the rectangular hyperbola model was the worst. The fitted P_{Nmax} of the rectangular hyperbola model, the exponential model, and the nonrectangular hyperbola model were far larger than the measured values, while the fitted LSP of each of three models was far smaller than the measured values (P<0.05). When RWC was higher or lower than the optimal ranges, P_N decreased significantly with increasing PPFD and $\Phi_{PPFD\leq200}$ and LSP also decreased significantly under high light (Fig. 1, Tables 1S–3S), indicating photoinhibition (P<0.05). Under such circumstances, only the modified rectangular hyperbola model was able to fit reasonably the light response curves, LCP, LSP, R_D, and P_{Nmax}.

Discussion

If the light energy absorbed by a plant exceeds the plant need, the excessive excitation energy can cause photoinhibition and reduce photosynthetic efficiency (Li *et al.* 2004). High light, together with water stress, breaks the balance between CO_2 fixation and light absorption within chloroplasts during photosynthesis, resulting in further accumulation of excessive light energy and intensifying photoinhibition (Sun *et al.* 2006). In addition, serious photoinhibition can even destroy the photosynthetic apparatus (D'Ambrosio *et al.* 2006). We found the degree of photoinhibition significantly related to SWC in our three tree species. High photosynthesis was maintained and no photoinhibition occurred in the leaves of *P. sibirica*, *H. rhamnoides*, and *P. tabulaeformis*, when RWC was 56.3–80.9%, 47.9–82.9%, and 33.4–92.6%, respectively. In contrast, photoinhibition occurred in all

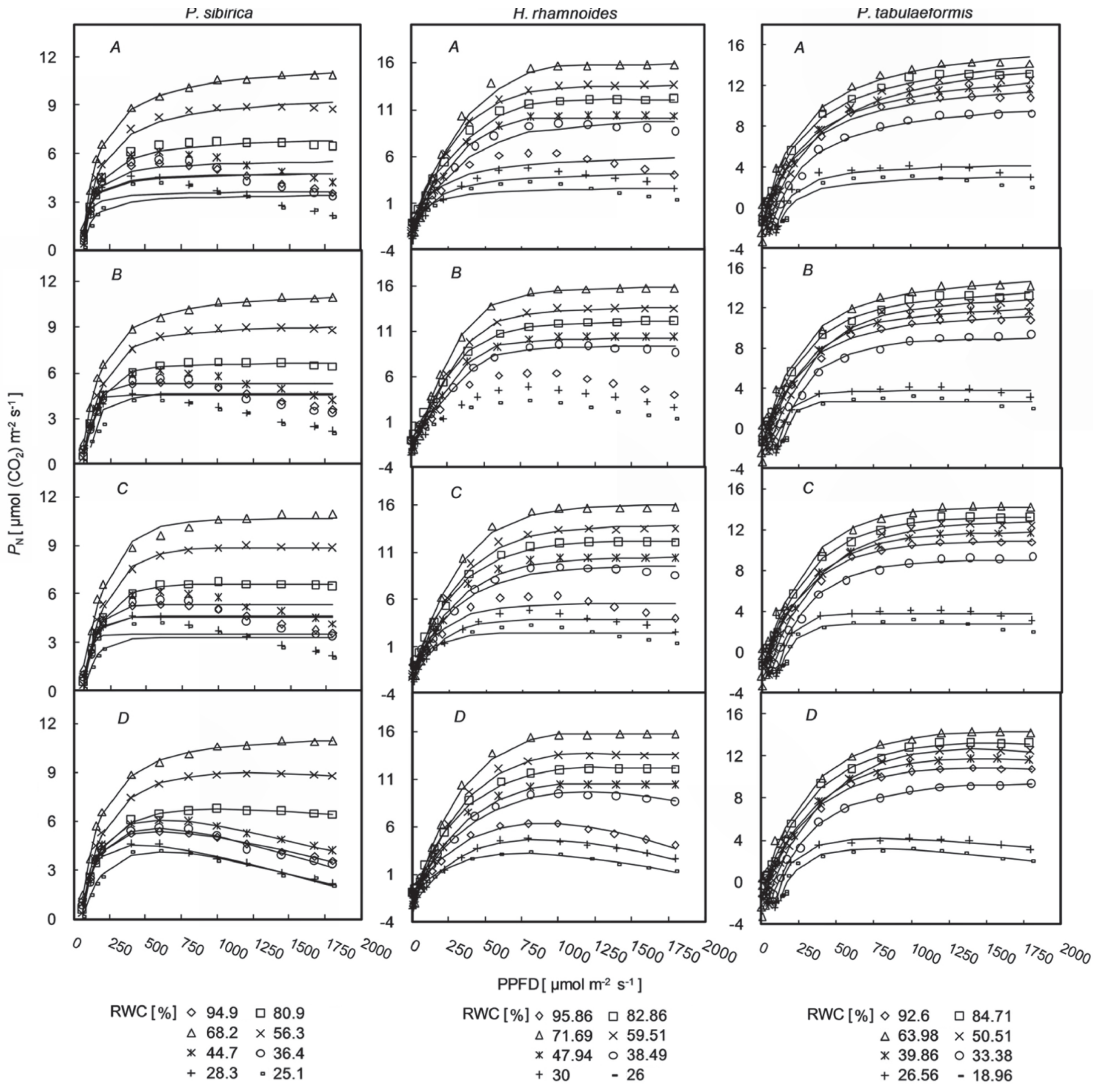

Fig. 3. Simulation of P_N/PPFD curves of the three tree species by (*A*) the rectangular hyperbola model; (*B*) the nonrectangular hyperbola model; (*C*) the exponential model; and (*D*) the modified rectangular hyperbola model. P_N – net photosynthetic rate; PPFD – photosynthetic photon flux density; RWC – relative water content.

three species, when RWC was lower or higher than the above optimal ranges. Photoinhibition reduced photosynthetic productivity in *P. sibirica* and *H. rhamnoides*, when RWC was either too high or too low under high light. In *P. tabulaeformis*, photosynthetic productivity was reduced by photoinhibition only when the SWC was too low, because photoinhibition could be restricted through enhancing photorespiration and heat dissipation under high SWC. Φ is an important indicator of light utilization efficiency by plants. The common method of calculating Φ is to use the slope of the light-response curve of photosynthetic rate, when PPFD ≤ 200 μmol m^{-2} s^{-1}. Results based on this method have shown that the range of Φ is from 0.03 to 0.05 in common plants under optimal conditions (Li 2002). Φ of *Tamarix chinensis* Lour. and *Ziziphus jujuba* var. *spinosa* Hu., *e.g.*, are about 0.0374 and 0.0361 (Xia *et al.* 2009), and of *Nongkouzaojiao* (*Capsicum annuum*) and *Zhengjiao* No. 13 (*Capsicum annuum*) are 0.036 and 0.038 (Hu *et al.* 2008). In *Campsis radicans*, it is in the range of 0.033–0.049 (Xia *et al.* 2008), and in *Parthenocissus thomsoni* it is in the range of 0.030–0.035 (Zhang *et al.* 2006). Yet Φ of some plants is lower than 0.03 even under optimal conditions. For example in peanut, Φ is about 0.0269 (Zhang *et al.* 2009), in *Aralia elata* is lower than 0.029 (Chen *et al.* 2008), and in *Wisteria sinensis* is lower than 0.022 (Xia *et al.* 2007). SWC is an important factor affecting plant Φ. However, the exact quantitative relationship between SWC and Φ is not clear. We found that the $Φ_{PPFD≤200}$ of three tree species under different soil water conditions was in the range of 0.015–0.05. *P. sibirica*, *H. rhamnoides*, and *P. tabulaeformis* showed the maximum $Φ_{PPFD≤200}$ of 0.0403, 0.0443, and 0.0466, respectively, under the respective RWC of 68.2%, 71.69%, and 63.98%. Their $Φ_{PPFD≤200}$ was above 0.03, when RWC were in their above mentioned optimal ranges. This indicated that under low light and optimal soil water conditions, the light utilization efficiencies of all three species were at the common light utilization efficiency level of most plants.

Recent research has shown that Φ calculated by the traditional linear fitting method has different values due to different PPFD ranges or different numbers of data points. Φ of winter wheat, for example, was 0.049, 0.052, and 0.055, when PPFD upper limits were 200, 160, and 120 μmol m^{-2} s^{-1}, respectively (Ye and Gao 2008). We found that Φ of all three tree species increased as the PPFD upper limit decreased. When RWC was 68.2%, *e.g.*, Φ of *P. sibirica* was 0.0412, 0.045, and 0.046 with the PPFD upper limits being 200, 160, and 120 μmol m^{-2} s^{-1}, respectively. Therefore, the apparent quantum efficiency determined by the traditional linear fitting method would give some differences as the calculation is somewhat subjective; this is related to the light-response curve of photosynthetic rate not being exactly linear under low light conditions (Xu 2002).

In theory, the rectangular hyperbola model, the exponential model, and the nonrectangular hyperbola model could calculate Φ of any point on the light-response curve (the slope of the tangent of the point) under low light intensity, including $Φ_c$, $Φ_0$, and $Φ_{c0}$. However, the application and the fitting accuracy of the above traditional models are largely limited, as each model is an asymptotically saturating curve without a clear maximum within the range of the data (Ye and Gao 2008, Ye and Yu 2008, Ye and Wang 2009). We found that all three models had difficulty in fitting the light-response curves and parameters of three tree species under soil water stress. Furthermore, there were significant discrepancies between the fitted values and the measured values of P_{Nmax} and LSP, even when there was no photoinhibition (Fig. 3, Tables 1S–3S). The modified rectangular hyperbola model was able to overcome the disadvantages of those three traditional models to some extent, and to analyze the light-response data more accurately under conditions of photoinhibition (Ye 2007, Ye and Yu 2008, Chen *et al.* 2011). However, when RWC was in their optimal range, the nonrectangular hyperbola model fitted the LCP and R_D of three tree species better than the modified rectangular hyperbola model. This was not consistent with the research on winter wheat, rice, and *Salvia miltiorrhiza*, in which the modified rectangular hyperbola model has shown the best fit (Ye and Yu 2008, Ye and Gao 2008, Ye and Wang 2009). Therefore, the fitting effects of the modified rectangular hyperbola model to LCP and R_D might be related to plant type, and there might be differences among crops, herbaceous, and woody plants.

Conclusion: Our experiment conducted to study the light response of photosynthesis in *P. sibirica*, *H. rhamnoides*, and *P. tabulaeformis* under multilevel SWC revealed that the thresholds required to reach the light-saturated net photosynthetic rate varied significantly among these three plant species. Photoinhibition was observed in *P. sibirica*, when RWC was lower than 56.3% or higher than 80.9%, in *H. rhamnoides*, when it was lower than 47.9% or higher than 82.9%, and in *P. tabulaeformis* only when it was lower than 33.4%.

Our results showed that the light response curve of photosynthetic rate was not exactly linear under low light conditions. This was a reason why different PPFD upper limits used in the traditional linear fitting method could generate quite different values of Φ. Φ was found to be highly related to RWC, and RWC required to reach the maximum Φ was consistent with that required to achieve the highest P_N in all three species. These findings were also taken into account in the nonlinear fitting of the light response models discussed in this study.

The optimal ranges of RWC for normal photosynthesis were found to be 56.3–80.9%, 47.9–82.9%, and 33.4–92.6%, in *P. sibirica*, *H. rhamnoides*, and *P. tabulaeformis*, respectively; in these ranges no photoinhibition occurred and LSP and P_{Nmax} were at relatively high levels. Although the modified rectangular hyperbola model did not generate the best fit for LCP and R_D under the optimal RWC, it did provide the best fit for LSP and P_{Nmax}, when compared with the other three models (the rectangular hyperbola model, the exponential model, and the nonrectangular hyperbola model). Moreover, among four models discussed, only the modified rectangular hyperbola model could successfully fit the light-response curves of photosynthesis and all parameters (LCP, LSP, R_D, P_{Nmax}) under all the tested soil water conditions, especially, when photoinhibition occurred.

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