Experimental and simulated CO$_2$ responses of photosynthesis in leaves of *Hippophae rhamnoides* L. under different soil water conditions

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Abstract

CO₂ concentrations and soil moisture conditions seriously affect tree growth and physiological mechanisms. CO₂ responses of photosynthesis are an important part of plant physiology and ecology research. This study investigated the photosynthetic CO₂ responses in the leaves of two-year-old Hippophae rhamnoides L. under eight soil water conditions in a semi-arid loess hilly region, and discussed the quantitative relationship between CO₂ responses and soil moisture. CO₂ response curves and parameters were fitted using a rectangular hyperbola model, non-rectangular hyperbola model, exponential equation, and modified rectangular hyperbola model. Results revealed that the relative soil water content (RWC) required to maintain a high photosynthetic rate (Pₙ) and carboxylation efficiency (CE) ranged from 42.8% to 83.2%. When RWC fell outside these ranges, the photosynthetic capacity (Pₙmax), CE, and CO₂ saturation point (CSP) decreased. CO₂ response curves and three parameters, CE, CO₂ compensation point (Γ), and photorespiration rate (Rₚ), were well fitted by the four models when RWC was appropriate. When RWC exceeded the optimal range, only the modified rectangular hyperbola model fitted the CO₂ response curves and photosynthetic parameters better.

Introduction

Photosynthesis is a complex process affected by many factors in plants, including CO₂ and water, which have important effects[1,2]. CO₂ is the substrate of photosynthesis, and its atmospheric concentration is predicted to reach ~550 μmol·mol⁻¹ by 2050[3,4]. Global water shortages are aggravated by changes due to increasing CO₂ concentrations and the warming climate[5,6]. The increase in CO₂ can cause global climate change and directly affect the metabolism and growth of plants[7,8]. Drought affects plant growth and development severely [9,10], as well as limits photosynthesis through carbon metabolism by restricting CO₂ diffusion[11,12]. However, plants display adaptability and resistance to water deficits[13,14]. Moreover, photosynthetic efficiency is higher within a certain water range, which varies according to the plant species and photosynthetic mechanism[15,16]. CO₂ responses are an important part of plant physiology and ecology research, the measurement and simulation of which are the main approaches for studying photosynthesis[17,18]. The photosynthesis CO₂ response model has played an important role in increasing our understanding of photosynthetic carbon uptake, which has thereby improved our understanding and predictions of plant photosynthetic physiology and its response to environmental changes and biogeochemical systems[19,20]. CO₂ response curves reflect the quantitative relationship between plant net photosynthetic rate (Pₙ) and CO₂ concentration and can be used to estimate photosynthetic parameters, including the CO₂ saturation point (CSP), photosynthetic capacity (Pₙmax), compensation point (Γ), carboxylation efficiency (CE), and photorespiration rate (Rₚ)[21,22].

CO₂ responses have been fitted using biochemical models[23], empirical models[24,25], and optimized models[26,27], which are based on biochemical models. Biochemical models calculate two key model parameters, the maximum rate of carboxylation (Vₑ₅₉₅ₐₓ) and the maximum electron
transport rate \((J_{\text{max}})\)[28,29]. Empirical models include the Michaelis-Menten model [30], rectangular hyperbola model[31], non-rectangular hyperbola model [32], and exponential equation [33], which have been applied in most crops[34,35]and some woody species[36,37]. Ye [38]thought the Michaelis-Menten and rectangular hyperbolic models were essentially the same. In recent years, some studies have proposed an improved rectangular hyperbolic model, namely, the modified rectangular hyperbola model[39,40]. This model has been applied to some plants, including some gramineous plants[41,42], herbs[43,44], and woody plants[45,46]. Results revealed that this new model could overcome the limitations of traditional models and accurately fit the CO\(_2\) response curve and its characteristic parameters. Previous studies on photosynthesis CO\(_2\) response models have focused on the estimation and optimization of key parameters in field crops[47,48]. However, the applicability of different models simulating the CO\(_2\) response data of woody plants under adverse conditions, such as continuous drought, has rarely been reported.

**Hippophae rhamnoides** L. is a common afforestation species found in the arid and semi-arid regions of Northern China, which has a high economic value and plays an important role in ecological restoration and soil and water conservation. *H. rhamnoides* L. is a non-leguminous and nitrogen-fixing species, deciduous shrubs, and is resistant to barren and dry conditions. In recent years, studies have focused on its growth[49], water consumption[50,51], and photosynthetic light response characteristics[52,53]. These studies have been conducted under water stress, while only a few studies related to the physiological characteristics of drought stress have been conducted[54,55]. However, continuous observations and the examination of photosynthesis CO\(_2\) response in leaves of *H. rhamnoides* L. at many soil moisture gradients during the accelerated soil drought process have not been addressed. Therefore, the quantitative relationship between the photosynthetic CO\(_2\) response process and soil moisture remains unclear.

In this study using potted seedlings of *H. rhamnoides* L., CO\(_2\) response curves and parameters were evaluated and fitted with the rectangular hyperbola model, non-rectangular hyperbola model, exponential equation, and modified rectangular hyperbola model under different soil moisture conditions. The goals of this study were to define the quantitative relationship between photosynthetic CO\(_2\) response processes and soil moisture, as well as explore the applicability of different CO\(_2\) response models to fit CO\(_2\) response processes and parameters. The findings of this study will provide an in-depth understanding of the photosynthetic physiology-ecological characteristics and cultivation of *H. rhamnoides* L. in the loess hilly-gully region of Northern China. Furthermore, the applicability of different CO\(_2\) response models can be evaluated from these findings and used in future studies.

**Material and methods**

**Study area**

The experimental site was located in the Tuqiaogou watersheds (37°36′58″N, 110°02′55″E) of Yukou Town, Fangshan County, Shanxi Province, China, a portion of the gully-hilly area of the Loess Plateau in the middle reaches of the Yellow River. This area has a sub-arid, warm temperate, continental monsoon climate. The average annual precipitation is 525.0 mm with more than 70% of
the precipitation concentrated between July and September. The annual potential evaporation is 1839.7 mm with the greatest amount of evaporation occurring between April and June. The annual frost-free period lasts 140 d. The soil is classified as medium loessial soil, and the soil texture is uniform with a pH value ranging from 8.0 to 8.4. Vegetation consists mainly of trees, shrubs, lianas, and subshrubs. Tree species are predominantly *Robinia pseudoacacia*, *Ulmus pumila*, *Platycladus orientalis*, and *Syringa oblata*. Shrubs are mainly *Rosa xanthina* and *Ulmus macrocarpa*. Herbs consist of *Compositae* and *Gramineae*, of which the *Compositae* belong to the *Artemisia* genus. Most of the forest land consists of sparse woodland with poor stand stability.

**Materials and water treatments**

Two-year-old *H. rhamnoides* L. were used as the experimental materials and were selected carefully to ensure consistency in their height, diameter, and growth. Plants were investigated and marked one by one before transplantation. In March 2018, seedlings were transplanted in containers (50 cm in height, 35 cm in diameter) that had drainage holes in the bottom. A total of six basins with one plant in each pot were used. The relative soil water content (*RWC*) and photosynthetic CO$_2$ responses in the leaves of *H. rhamnoides* L. were determined in August. Three strong plants were selected and watered to saturation, and the initial *RWC* was obtained; the first CO$_2$ response was also determined. Then, soil moisture gradients were obtained every two days through the natural water consumption method after artificially supplying water. The soil mass water content (*MWC*, %) was measured by the stoving method. The *RWC* was considered as the ratio of *MWC* to the field water capacity (*FC*, %). The potting soil *FC* was 24.3%, according to the cutting ring method, and the soil bulk density was 1.26 ± 0.13 g·cm$^{-3}$. Eight *RWC* gradients were obtained and found to be 91.7%, 83.2%, 71.5%, 54.6%, 42.8%, 31.9%, 26.1%, and 21.4%. The experiment was monitored under a canopy with a plastic film covering the top on rainy days to prevent rain from interfering with the *RWC*.

**CO$_2$ response determination**

Three strong, mature leaves were selected and marked in a central test plant. CO$_2$ responses under different soil moisture conditions were measured using a CIRAS-2 (PP Systems, Hitehin, UK) portable photosynthesis system. The light saturation point for *H. rhamnoides* L. was 1400 μmol·m$^{-2}$·s$^{-1}$[52,54]. Measurements were obtained under each soil moisture condition on separate days. The time of measurements occurred from 08:30 to 11:00 h in completely clear weather to reduce the effects of outside light fluctuations. Measurements were obtained three times for each leaf, and the average value was calculated and used for the analyses. The atmospheric temperature ranged from 24°C to 26°C, and the relative humidity was approximately 60% ± 4.0%. The CO$_2$ concentration in the leaf chamber was controlled and regulated from 0 to 1400 μmol·mol$^{-1}$ by a small cylinder with high CO$_2$ concentrations. The CO$_2$ concentration gradients were 1400, 1200, 1000, 800, 600, 400, 200, 180, 150, 120, 90, 60, 30, and 0 μmol·mol$^{-1}$. The duration of the measurement lasted 120 s at each CO$_2$ concentration, and the apparatus automatically recorded the photosynthetic physiological parameters, including the $P_n$ (μmol·m$^{-2}$·s$^{-1}$) and intercellular CO$_2$ concentration ($C_i$, μmol·mol$^{-1}$).
Data analysis

CO₂ response curves were drawn with $C_i$ as the horizontal axis and $P_n$ as the vertical axis. According to the measured data point trends, $CSP$ ($\mu$mol·mol$^{-1}$), $P_{n\text{max}}$ ($\mu$mol·m$^{-2}$·s$^{-1}$), and $\Gamma$ ($\mu$mol·mol$^{-1}$) were estimated and regarded as measured values. $CE_\Gamma$ (mol·m$^{-2}$·s$^{-1}$) at $\Gamma$, the intrinsic carboxylation efficiency ($CE_0$, mol·m$^{-2}$·s$^{-1}$) at 0 $\Gamma$, the absolute value ($CE_{\Gamma0}$, mol·m$^{-2}$·s$^{-1}$) of the slope of the line from $C_i = 0$ to $C_i = \Gamma$ in the CO₂ response curve, and $R_p$ (µmol·m$^{-2}$·s$^{-1}$) were calculated using the traditional linear regression method and used as the measured values to compare to the fitted values of the four models.

Statistical analyses were performed using Microsoft Excel 2003 (Microsoft Corp., Redmond, Wash.). Significant differences were analyzed by a one-way ANOVA and Duncan’s post-hoc test. Nonlinear regression was analyzed using SPSS v18.0 (SPSS Inc., Chicago, Illinois). Data were expressed as the mean ± standard deviation (S.D.), and significance was interpreted as $p < 0.05$.

The CO₂ response curve was fitted using the rectangular hyperbola model, non-rectangular hyperbola model, exponential equation, and modified rectangular hyperbola model (described below).

Rectangular hyperbolic model

The rectangular hyperbolic model is expressed as follows[31]:

$$P_n(C_i) = \frac{aP_{n\text{max}} C_i}{aC_i + P_{n\text{max}}} - R_p$$

(1)

where $P_n$ is the net photosynthesis rate, $C_i$ is the intercellular CO₂ concentration, $\alpha$ is the slope of the CO₂ response curve when $C_i = 0$ (namely, the initial slope of the CO₂ response curve and the initial $CE$), $P_{n\text{max}}$ is the photosynthetic capacity, and $R_p$ is the photorespiration rate.

$CE_\Gamma$, $CE_0$, and $CE_{\Gamma0}$ are expressed as follows:

$$CE_\Gamma = P_n'(C_i = \Gamma) = \frac{aP_{n\text{max}}^2}{(a\Gamma + P_{n\text{max}})^2}$$

(2)

$$CE_0 = P_n(C_i = 0) = \alpha$$

(3)

$$CE_{\Gamma0} = \left| \frac{R_p}{\Gamma} \right|$$

(4)

$\Gamma$ is expressed as follows:

$$\Gamma = \frac{R_p \cdot P_{n\text{max}}}{\alpha(P_{n\text{max}} - R_p)}$$

(5)

where the line $y = P_{n\text{max}}$ intersects the linear equation when $C_i$ is below 200 µmol·mol$^{-1}$, and the value of the intersected point on the x-axis is $CSP$[56].

Non-rectangular hyperbola model

The non-rectangular hyperbola model is expressed as follows [32]:
\[ P_n(C) = \frac{\alpha C_i + P_{\text{max}}}{\sqrt{(\alpha C_i + P_{\text{max}})^2 - 4\alpha C_i P_{\text{max}}} - R_p} \quad (6) \]

where \( k \) is the curved angle of the non-rectangular hyperbola; the definitions of other parameters are the same as above.

\[ CE_\Gamma, CE_0, \text{ and } CE_{\Gamma0} \text{ are expressed as follows:} \]

\[ CE_\Gamma = P'_n(C_i = 0) = \alpha \quad (7) \]
\[ CE_0 = P'_n(C_i = 0) = \alpha \quad (8) \]
\[ CE_{\Gamma0} = \frac{R_p}{\Gamma} \quad (9) \]

\( \Gamma \) is expressed as follows:

\[ \Gamma = \frac{R_p P_{\text{max}} - k R_p^2}{\alpha(P_{\text{max}} - R_p)} \quad (10) \]

where the line \( y = P_{\text{max}} \) intersects the linear equation when \( C_i \) is below \( 200 \, \mu\text{mol} \cdot \text{mol}^{-1} \), and the value of the intersected point on the x-axis is \( \text{CSP}[38] \).

**Exponential equation**

The exponential equation is expressed as follows [33]:

\[ P_n(C_i) = P_{\text{max}} \left(1 - e^{-\alpha C_i/P_{\text{max}}} \right) - R_p \quad (11) \]

where the definitions of \( P_n, C_i, P_{\text{max}}, \alpha, \) and \( R_p \) are the same as above.

\[ CE_\Gamma, CE_0, \text{ and } CE_{\Gamma0} \text{ are expressed as follows:} \]

\[ CE_\Gamma = P'_n(C_i = \Gamma) = \alpha e^{-\alpha C_i/P_{\text{max}}} \quad (12) \]
\[ CE_0 = P'_n(C_i = 0) = \alpha \quad (13) \]
\[ CE_{\Gamma0} = \frac{R_p}{\Gamma} \quad (14) \]

\( \Gamma \) is expressed as follows:

\[ \Gamma = \frac{P_{\text{max}} \ln P_{\text{max}} - R_p}{P_{\text{max}}} \quad (15) \]

where the line \( y = P_{\text{max}} \) intersects with the linear equation at \( C_i \leq 200 \, \mu\text{mol} \cdot \text{mol}^{-1} \), and the value of the intersected point on the x-axis is \( \text{CSP}[57] \).

**Modified rectangular hyperbola model**

The modified rectangular hyperbola model is expressed as follows [39]:

\[ P_n(C_i) = \frac{1 - b C_i}{1 + c C_i} C_i - R_p \quad (16) \]

where \( b \) and \( c \) are coefficients; the definitions of other parameters are the same as above.

\[ CE_\Gamma, CE_0, \text{ and } CE_{\Gamma0} \text{ are expressed as follows:} \]

\[ CE_\Gamma = P'_n(C_i = \Gamma) = \alpha \frac{1 + (c-b) C_i - b c C_i^2}{(1 + c C_i)^2} \quad (17) \]
\[ CE_0 = P'_n(C_i = 0) = \alpha \quad (18) \]
\[ CE_{\Gamma0} = \frac{R_p}{\Gamma} \quad (19) \]
CSP and $P_{\text{max}}$ are expressed as follows:

$$CSP = \frac{\sqrt{b+c} - b}{c}$$ (20)

$$P_{\text{max}} = a \left( \frac{\sqrt{b+c} - \sqrt{b}}{c} \right)^2$$ (21)

Results

Photosynthetic CO2 response

Fig 1. This is the Fig 1 Title. Photosynthetic CO$_2$ response curves in the leaves of *H. rhamnoides* L. under different soil water conditions (mean ± S.D.).

This is the Fig 1 legend.

Soil moisture significantly affected the photosynthetic CO$_2$ response of *H. rhamnoides* L. (Fig. 1). Under different soil moisture conditions, $P_n$ increased rapidly as $C_i$ increased, when $C_i$ was below ~200 μmol·mol$^{-1}$. $P_n$ increased slowly as $C_i$ increased, and the maximum $P_{\text{max}}$ appeared at CSP. When $C_i$ reached CSP, the CO$_2$ response was considerably different under different soil water conditions, specifically when RWC ranged from 42.8% to 83.2%. $P_n$ of each CO$_2$ response curve changed slightly as $C_i$ increased after $C_i$ reached CSP. When RWC was out of the above ranges, $P_n$ decreased considerably after $C_i$ reached CSP, $P_n$ in each curve at the highest $C_i$ was significantly smaller than its $P_{\text{max}}$ under the same soil moisture conditions ($p < 0.05$) (Table 1) Clearly, CO$_2$-saturated inhibition had occurred. Furthermore, the CO$_2$ responses to soil moisture had an obvious RWC threshold. The overall level of $P_n$ in each CO$_2$ response curve increased initially, then decreased as RWC decreased. The $P_n$ level was the highest when RWC was 71.5%; thus, an increase or decrease in RWC led to a decrease in the overall $P_n$ level. CSP and $P_{\text{max}}$ were high and $P_n$ did not decrease at high CO$_2$ concentrations when RWC ranged from 42.8% to 83.2%; thus, these RWC ranges were suitable for photosynthesis in the leaves of *H. rhamnoides* L.

| CO$_2$ response parameter | Relative soil water content (RWC, %) |
|--------------------------|-------------------------------------|
|                          | 91.7  | 83.2  | 71.5  | 54.6  | 42.8  | 31.9  | 26.1   | 21.4   |
| $C_i$ ($\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) | 0.0395d | 0.0539b | 0.0575a | 0.0521b | 0.0483c | 0.0378d | 0.0352e | 0.0274f |
Simulation of CO₂ response curves and characteristic parameters

Table 2. Data on the photosynthetic CO₂ response parameters of Hippophae rhamnoides L. fitted by 4 models.

| CO₂ response model               | CO₂ response parameter | Relative soil water content (RWC, %) |
|----------------------------------|------------------------|-------------------------------------|
|                                  |                        | 91.7  | 83.2  | 71.5  | 54.6  | 42.8  | 31.9  | 26.1  | 21.4  |
| Rectangular hyperbola model      | CE₀ (mol·m⁻²·s⁻¹)      | 0.0609 | 0.0575 | 0.0587 | 0.0568 | 0.0543 | 0.0561 | -     | -     |
|                                  | CEΓ (mol·m⁻²·s⁻¹)      | 0.0582 | 0.0552 | 0.0561 | 0.0537 | 0.0512 | 0.0534 | -     | -     |

Note: Different letters indicate significant differences between values in the same row (p < 0.05); the same letter indicates no significant differences.
Modified rectangular hyperbola model

Exponential equation

Non-rectangular hyperbola model

determination coefficient $R^2$

| Parameter | Value | Value | Value | Value | Value | Value | Value | Value | Value | Value | Value | Value | Value | Value |
|-----------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| $C_{eq}$ (mol m$^{-2}$ s$^{-1}$) | 0.0593 | 0.0563 | 0.0572 | 0.0552 | 0.0527 | 0.0546 |       |       |       |       |       |       |       |       |
| $CSP$ (µmol mol$^{-1}$) | 433 | 581 | 596 | 539 | 548 | 412 |       |       |       |       |       |       |       |       |
| $P_{\text{CSP}}$ (µmol m$^{-2}$ s$^{-1}$) | 26.22 | 42.57 | 45.84 | 38.4 | 35.61 | 19.29 |       |       |       |       |       |       |       |       |
| $I'$ (µmol mol$^{-1}$) | 82.78 | 73.2 | 70.07 | 74.33 | 76.09 | 85.7 |       |       |       |       |       |       |       |       |
| $R_p$ (µmol m$^{-2}$ s$^{-1}$) | 4.91 | 4.12 | 4.19 | 4.1 | 4.01 | 4.68 |       |       |       |       |       |       |       |       |
| determination coefficient $R^2$ | 0.794 | 0.991 | 0.994 | 0.994 | 0.993 | 0.801 |       |       |       |       |       |       |       |       |

Water is a major limiting factor in the recovery and restoration of vegetation found in the loess, hilly-gully regions of China. $RWC$ seriously affected light-response curves and photosynthetic parameters, which also profoundly affected CO$_2$ response curves and photosynthetic parameters in the leaves of *H. rhamnoides* L. The classical form of a $P_n$-$C_i$ curve can be summarized in three stages[58,59]. First, an approximately linear segment is observed when $C_i \leq 200$ µmol mol$^{-1}$. Thus, $P_n$ increases rapidly as $C_i$ increases, namely, during the ribulose bisphosphate (RuBP) restriction phase. The slope of the straight line is the mesophyll conductance, $CE$, which reflects the assimilative capacity of plant responses to low CO$_2$[60,61]. Second, the curved segment is observed when $C_i \approx 200$ µmol mol$^{-1}$ to $CSP$, and $P_n$ increases slowly as $C_i$ increases, gradually entering the restriction stage of RuBP regeneration[62]. Third, an almost linear segment when $C_i > CSP$, $P_n$ changes insignificantly as $C_i$ increases, moving into the restriction stage of triose-phosphate

Discussion

Effects of soil moisture on CO$_2$ response curves and photosynthetic parameters

The effects of soil moisture on CO$_2$ response curves and photosynthetic parameters were investigated in the leaves of *H. rhamnoides* L. The classical form of a $P_n$-$C_i$ curve can be summarized in three stages[58,59]. First, an approximately linear segment is observed when $C_i \leq 200$ µmol mol$^{-1}$. Thus, $P_n$ increases rapidly as $C_i$ increases, namely, during the ribulose bisphosphate (RuBP) restriction phase. The slope of the straight line is the mesophyll conductance, $CE$, which reflects the assimilative capacity of plant responses to low CO$_2$[60,61]. Second, the curved segment is observed when $C_i \approx 200$ µmol mol$^{-1}$ to $CSP$, and $P_n$ increases slowly as $C_i$ increases, gradually entering the restriction stage of RuBP regeneration[62]. Third, an almost linear segment when $C_i > CSP$, $P_n$ changes insignificantly as $C_i$ increases, moving into the restriction stage of triose-phosphate.
utilization (TPU). $P_n$ at this stage is $P_{\text{max}}$, which reflects photosynthetic electron transport and photophosphorylation activity [63].

The form of the $P_n$-$C_i$ curve changes when plants encounter stressful conditions, such as drought. Bernacchi et al. [64] considered that numerous factors would influence the curve of $P_n$-$C_i$, which included physiological changes (e.g. $V_{\text{cmax}}, J_{\text{max}}$ or $R_d$) and environmental changes (e.g. drought, temperature and/or atmospheric CO$_2$ concentration). However, the quantitative relationship between this change and soil moisture has remained unclear. This study demonstrated that the photosynthetic $P_n$-$C_i$ curve of H. rhamnoides L. exhibited a classical form, with $P_{\text{max}}$, CE, CSP, and $R_p$ being high and $\Gamma$ being low within a suitable RWC range (i.e., 42.8%–83.2%); $P_n$ levels were highest when RWC was 71.3% (Fig. 1; Table 1). Three photosynthetic parameters, $P_{\text{max}}$, CE, and CSP, declined dramatically when soil moisture was beyond this range. H. rhamnoides L. exhibited wide photosynthetic adaptability to soil moisture compared to the suitable RWC ranges of Robinia pseudoacacia L. (50.0%–81.6%), Platycladus orientalis L. (5.3%–75.0%) [65], Syringa oblata Lindl. (58.8%–76.6%) [66], and Ziziphus jujube (46.0%–80.5%) [67].

The common method for obtaining CE is the traditional linear regressive method, whereby CE is the slope of the straight line of the $P_n$-$C_i$ curve at a low CO$_2$ concentration ($C_i \leq 200 \mu$mol mol$^{-1}$) [35,68]. Many studies have shown that the CE values of different plants vary greatly [69,70]. For example, under normal growth conditions, the CE values of Rheum tanguticum, Anisodus tanguiticus, and Gentiana straminea were approximately 0.0453, 0.1116, and 0.0902 [71], those of two pepper (Capsicum annuum L.) cultivars were approximately 0.145 and 0.159 [74] (Hu et al. 2008), that of Zantedeschia aethiopica was approximately 0.074 [72] (Yiotis & Manetas 2010) and that of Sophora moorcroftiana was about 0.03 [70]. Although Hu et al. [44] showed that soil moisture greatly affects the CE values of plants, the quantitative relationship between CE and soil moisture has remained unclear. According to a previous study, the $P_n$-$C_i$ curve of photosynthesis does not have a strictly linear relationship at a low CO$_2$ concentration [43].

**CO$_2$ response curves and photosynthetic parameters fitted by different models**

The major use of different CO$_2$ response models lies in the equations used to fit the CO$_2$ response and its characteristic parameters to extract physiologically meaningful variables; these parameters are used to describe physiological responses of leaves to different treatments [64,73]. For example, $CE_1$ at the CO$_2$ compensation point, $CE_0$, and the absolute value of the slope of the line between $C_i = 0$ and $C_i = \Gamma$ on the $CE_1$ curve can be fitted, and they have clear physiological meaning and unique values. However, the applicability and simulated accuracy of the empirical models are limited by their asymptotic form with no extreme values [38,39] (Ye & Gao 2009, Ye 2010). In some studies [43,45,46], $P_{\text{max}}$ was much larger than the measured value, while CSP was far less than the measured value. In particular, the CO$_2$ response curves could not be fitted under stressful conditions. The same problem was noted in this study.

Although the modified rectangular hyperbola model proposed in recent years can fit and analyze various forms of CO$_2$ response curves more accurately [77,41], overcoming the limitations of
other models to a certain extent, there are few reports regarding its application in plants under different soil moisture conditions. This study indicated that when the soil moisture was within a suitable RWC range, the CO$_2$ response curves and characteristic parameters were well fitted by the four models ($R^2 > 0.99$, Fig. 2; Table 2), where the non-rectangular hyperbola model and modified rectangular hyperbola model fit the data better than the other two models (Fig. 2 B, D). When soil moisture was too high or too low, the modified rectangular hyperbola model was better than the other three models fitting the CO$_2$ response process and its characteristic parameters in the leaves of _H. rhamnoides_ L. (Fig. 2 D). This result is consistent with the findings of Jiao & Wei [45] and Lv et al. [46]. This study demonstrated that the simulation results of the photosynthetic-CO$_2$ response model were closely related to soil moisture content.

**Conclusions**

Research on the effects of soil moisture on the physiological mechanisms related to photosynthetic responses is garnering attention toward CO$_2$ response curves and photosynthetic parameters in trees. This study indicated that soil moisture content affected the CO$_2$ response processes in the leaves of _H. rhamnoides_ L. The photosynthetic $P_N$-$C_i$ curve exhibited a classical form, with $P_{\text{max}}$, $CE$, $CSP$, and $R_p$ being high, while $\Gamma$ was low when the RWC ranged from 42.8% to 83.2%. _H. rhamnoides_ L. exhibited high photosynthetic efficiency in this soil moisture range, and the $P_n$ levels were highest when RWC was 71.5%. Three photosynthetic parameters, $P_{\text{max}}$, $CE$, and $CSP$, declined dramatically when soil moisture was outside the aforementioned range. Thus, the suitable RWC for _P. sibirica_ L. ranged from 46.5% to 81.6%, and the most suitable RWC was ~66.8%.

The $CE$ (i.e. $CE_0$, $CE_{\Gamma}$, $CE_{\Gamma0}$) values of _H. rhamnoides_ L. were significantly different under different soil moisture conditions. For example, the _H. rhamnoides_ L. $CE_{\Gamma0}$ ranged from 0.0260 to 0.0564, with a comparatively higher level > 0.047 in the RWC range of 42.8%–83.2%; the maximum (0.0564) appeared when RWC was 71.5%. $CE$ of _H. rhamnoides_ L. decreased markedly when the soil moisture was too high or too low. When soil moisture was within the suitable RWC range, the CO$_2$ response curves and characteristic parameters were well fitted by the four models ($R^2 > 0.99$). The non-rectangular hyperbola model and modified rectangular hyperbola model fitted better than the other two models ($R^2 > 0.998$). However, when soil moisture exceeded the suitable RWC range, only the modified rectangular hyperbola model fit the CO$_2$ response curves and photosynthetic parameters well. Compared to the other three models, the modified rectangular hyperbola model demonstrated extensive applicability for fitting photosynthetic CO$_2$ responses under different soil moisture conditions.

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Appendix

Name and abbreviation

| RWC | relative soil water content | MWC | soil mass water content | FC | field water capacity |
|-----|-----------------------------|-----|-------------------------|----|----------------------|
| Pn  | net photosynthetic rate     | Ci  | intercellular CO₂ concentration | CSP | CO₂ saturation point |
| F   | CO₂ compensation points     | CE  | carboxylation efficiency | Rp | photorespiration rate |