Experimental and simulated CO₂ 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 (P_n) and carboxylation efficiency (*CE*) ranged from 42.8% to 83.2%. When *RWC* fell outside these ranges, the photosynthetic capacity (P_{nmax}), *CE*, and CO₂ saturation point (*CSP*) decreased. CO₂ response curves and three parameters, *CE*, CO₂ compensation point (*I*), and photorespiration rate (R_p), 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 (P_n) and CO₂ concentration and can be used to estimate photosynthetic parameters, including the CO₂ saturation point (*CSP*), photosynthetic capacity (P_{nmax}), compensation point (*I*), carboxylation efficiency (*CE*), and photorespiration rate (R_p)[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 (V_{cmax}) and the maximum electron

transport rate ($J_{\max}$)[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 CO₂ response curve and its characteristic parameters. Previous studies on photosynthesis CO₂ 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 CO₂ 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 CO₂ 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 CO₂ response process and soil moisture remains unclear.

In this study using potted seedlings of *H. rhamnoides* L., CO₂ 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 CO₂ response processes and soil moisture, as well as explore the applicability of different CO₂ response models to fit CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 $1.26 \pm 0.13 \text{ g}\cdot\text{cm}^{-3}$. 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*.

CO₂ response determination

Three strong, mature leaves were selected and marked in a central test plant. CO₂ responses under different soil moisture conditions were measured using a CIRAS-2 (PP Systems, Hitchin, UK) portable photosynthesis system. The light saturation point for *H. rhamnoides* L. was $1400 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ [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 $60\% \pm 4.0\%$. The CO₂ concentration in the leaf chamber was controlled and regulated from 0 to $1400 \mu\text{mol}\cdot\text{mol}^{-1}$ by a small cylinder with high CO₂ concentrations. The CO₂ concentration gradients were 1400, 1200, 1000, 800, 600, 400, 200, 180, 150, 120, 90, 60, 30, and $0 \mu\text{mol}\cdot\text{mol}^{-1}$. The duration of the measurement lasted 120 s at each CO₂ concentration, and the apparatus automatically recorded the photosynthetic physiological parameters, including the P_n ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and intercellular CO₂ concentration (C_i , $\mu\text{mol}\cdot\text{mol}^{-1}$).

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 ($\mu\text{mol}\cdot\text{mol}^{-1}$), $P_{n\max}$ ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), and Γ ($\mu\text{mol}\cdot\text{mol}^{-1}$) were estimated and regarded as measured values. CE_{Γ} ($\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) at Γ , the intrinsic carboxylation efficiency (CE_0 , $\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) at 0 Γ , the absolute value ($CE_{\Gamma 0}$, $\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) of the slope of the line from $C_i = 0$ to $C_i = \Gamma$ in the CO₂ response curve, and R_p ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) 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 $\pm$ 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]:

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

(1)

where P_n is the net photosynthesis rate, C_i is the intercellular CO₂ concentration, α 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), $P_{n\max}$ is the photosynthetic capacity, and R_p is the photorespiration rate.

CE_{Γ} , CE_0 , and $CE_{\Gamma 0}$ are expressed as follows:

$$CE_{\Gamma} = P'_n(C_i = \Gamma) = \frac{\alpha P_{n\max}^2}{(\alpha \Gamma + P_{n\max})^2} \quad (2)$$

$$CE_0 = P'_n(C_i = 0) = \alpha \quad (3)$$

$$CE_{\Gamma 0} = \left| \frac{R_p}{\Gamma} \right| \quad (4)$$

Γ is expressed as follows:

$$\Gamma = \frac{R_p \cdot P_{n\max}}{\alpha(P_{n\max} - R_p)} \quad (5)$$

where the line $y = P_{n\max}$ 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 CSP [56].

Non-rectangular hyperbola model

The non-rectangular hyperbola model is expressed as follows [32]:

$$P_n(C_i) = \frac{\alpha C_i + P_{nmax} - \sqrt{(\alpha C_i + P_{nmax})^2 - 4\alpha k C_i P_{nmax}}}{2k} - R_p \quad (6)$$

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

CE_Γ , CE_0 , and $CE_{\Gamma 0}$ are expressed as follows:

$$CE_0 = P'_n(C_i = 0) = \alpha \quad (7)$$

$$CE_0 = P'_n(C_i = 0) = \alpha \quad (8)$$

$$CE_{\Gamma 0} = \left| \frac{R_p}{\Gamma} \right| \quad (9)$$

Γ is expressed as follows:

$$\Gamma = \frac{R_p P_{nmax} - k R_p^2}{\alpha (P_{nmax} - R_p)} \quad (10)$$

where the line $y = P_{nmax}$ 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 $CSP[38]$.

Exponential equation

The exponential equation is expressed as follows [33]:

$$P_n(C_i) = P_{nmax} (1 - e^{-\alpha C_i / P_{nmax}}) - R_p \quad (11)$$

where the definitions of P_n , C_i , P_{nmax} , α , and R_p are the same as above.

CE_Γ , CE_0 , and $CE_{\Gamma 0}$ are expressed as follows:

$$CE_\Gamma = P'_n(C_i = \Gamma) = \alpha e^{-\alpha C_i / P_{nmax}} \quad (12)$$

$$CE_0 = P'_n(C_i = 0) = \alpha \quad (13)$$

$$CE_{\Gamma 0} = \left| \frac{R_p}{\Gamma} \right| \quad (14)$$

Γ is expressed as follows:

$$\Gamma = \frac{P_{nmax}}{-\alpha} \ln \frac{P_{nmax} - R_p}{P_{nmax}} \quad (15)$$

where the line $y = P_{nmax}$ 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 $CSP [57]$.

Modified rectangular hyperbola model

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

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

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

CE_Γ , CE_0 , and $CE_{\Gamma 0}$ are expressed as follows:

$$CE_\Gamma = P'_n(C_i = \Gamma) = \alpha \frac{1 + (c - b) C_i - b c C_i^2}{(1 + c C_i)^2} \quad (17)$$

$$CE_0 = P'_n(C_i = 0) = \alpha \quad (18) \square$$

$$CE_{\Gamma 0} = \left| \frac{R_p}{\Gamma} \right| \quad (19)$$

CSP and P_{nmax} are expressed as follows:

$$CSP = \frac{\sqrt{(b+c)b} - 1}{c} \quad (20)$$

$$P_{nmax} = \alpha \left(\frac{\sqrt{b+c} - \sqrt{b}}{c} \right)^2 - R_p \quad (21)$$

□

Results

Photosynthetic CO₂ response

Fig 1. This is the Fig 1 Title. Photosynthetic CO₂ 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 CO₂ 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 $\mu\text{mol} \cdot \text{mol}^{-1}$. P_n increased slowly as C_i increased, and the maximum P_{nmax} appeared at CSP . When C_i reached CSP , the CO₂ response was considerably different under different soil water conditions, specifically when RWC ranged from 42.8% to 83.2%, P_n of each CO₂ 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_{nmax} under the same soil moisture conditions ($p < 0.05$) (Table 1) Clearly, CO₂-saturated inhibition had occurred. Furthermore, the CO₂ responses to soil moisture had an obvious RWC threshold. The overall level of P_n in each CO₂ 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_{nmax} were high and P_n did not decrease at high CO₂ 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..

Table 1. Data on the photosynthetic CO₂ response parameters of *Hippophae rhamnoides* L. under different soil water conditions (mean ± S.D.).

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
$CE_{C_i \leq 120}$ ($\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	0.0395d	0.0539b	0.0575a	0.0521b	0.0483c	0.0378d	0.0352e	0.0274f

$CE_{Ci\leq 100}$ ($\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	0.0376d	0.0517b	0.0543a	0.0491b	0.0452c	0.0358d	0.0325e	0.0251f
$CE_{Ci\leq 50}$ ($\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	0.0389d	0.0523b	0.0564a	0.0503b	0.0469c	0.0369d	0.0338e	0.0260f
CSP ($\mu\text{mol}\cdot\text{mol}^{-1}$)	940c	998b	1160a	987b	950c	800d	673e	573f
$P_{n\max}$ ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	18.6e	26.1b	28.9a	24.2c	22.5d	14.1f	12.3f	10.4g
Γ ($\mu\text{mol}\cdot\text{mol}^{-1}$)	93b	75a	73a	77a	80a	95b	98c	106d
R_p ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	3.62c	3.92b	4.12a	3.87b	3.75b	3.51c	3.31d	2.76e

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

Simulation of CO₂ response curves and characteristic parameters

▲91.7% ○83.2% △71.5% □54.6% ×42.8% ●31.9% ■26.1% —21.4%

Fig 2. This is the Fig 2 Title. Photosynthetic CO₂ response curves of the leaves of *Hippophae rhamnoides* L. simulated by four models under different soil water conditions (mean $\pm$ S.D.): A) Rectangular hyperbola model; B) Non-rectangular hyperbola model; C) Exponential equation; and D) Modified rectangular hyperbola model.

This is the Fig 2 legend.

The simulated effects of the four models fitting the CO₂ response data were notably different under different soil moisture conditions (Fig. 2; Table 2). CO₂ responses curves and photosynthetic characteristic parameters (CE_0 , CE_{Γ} , CE_{Γ} , Γ , and R_p) were well simulated by the four models, and the determination coefficients were all > 0.991 when RWC ranged from 42.8% to 83.2% (Table 2). Moreover, within the above RWC range, $P_{n\max}$ and CSP fitted by the modified rectangular hyperbola model were comparable with the measured value. The $P_{n\max}$ values fit by the other three models were significantly higher than their observed values, while the fit CSP values were significantly lower than their observed values. When RWC was outside the range of 42.8%–83.2%, only the modified rectangular hyperbola model fit the CO₂ responses ($R^2 > 0.99$) and characteristic parameters well (Figure 2D; Table 2), the other three kinds of models produced large deviation to fit the CO₂ response process and its characteristic parameters (Figures 2A,B,C; Table 2).

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

CO ₂ response model	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
Rectangular hyperbola model	CE_0 ($\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	0.0609	0.0575	0.0587	0.0568	0.0543	0.0561	-	-
	CE_{Γ} ($\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	0.0582	0.0552	0.0561	0.0537	0.0512	0.0534	-	-

Non-rectangular hyperbola model	CE_{T0} ($\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	0.0593	0.0563	0.0572	0.0552	0.0527	0.0546	-	-
	CSP ($\mu\text{mol}\cdot\text{mol}^{-1}$)	433	581	596	539	548	412	-	-
	$P_{n\max}$ ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	26.22	42.57	45.84	38.4	35.61	19.29	-	-
	Γ ($\mu\text{mol}\cdot\text{mol}^{-1}$)	82.78	73.2	70.07	74.33	76.09	85.7	-	-
	R_p ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	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	-	-
	CE_0 ($\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	0.0503	0.0565	0.0581	0.0532	0.0528	0.0497	-	-
	CE_T ($\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	0.0476	0.0534	0.0537	0.0501	0.0475	0.0458	-	-
	CE_{T0} ($\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	0.0487	0.0542	0.0567	0.0512	0.0487	0.0472	-	-
	CSP ($\mu\text{mol}\cdot\text{mol}^{-1}$)	439	558	570	533	487	403	-	-
Exponential equation	$P_{n\max}$ ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	23.98	34.84	39.62	33.05	28.68	23.3	-	-
	Γ ($\mu\text{mol}\cdot\text{mol}^{-1}$)	87.18	73.96	73.19	76.79	78.29	90.32	-	-
	R_p ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	4.25	4.01	4.15	3.93	3.81	4.26	-	-
	determination coefficient R^2	0.865	0.999	0.999	0.999	0.998	0.853	-	-
	CE_0 ($\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	0.0501	0.0596	0.0596	0.0551	0.0499	0.0476	0.0471	0.0457
	CE_T ($\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	0.0451	0.0538	0.0571	0.0525	0.0463	0.0452	0.0437	0.0396
	CE_{T0} ($\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	0.0483	0.0554	0.0585	0.0539	0.0489	0.0465	0.0453	0.0403
	CSP ($\mu\text{mol}\cdot\text{mol}^{-1}$)	357	428	446	399	352	343	315	336
	$P_{n\max}$ ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	21.01	31.73	33.16	28.96	26.73	15.51	13.79	11.95
	Γ ($\mu\text{mol}\cdot\text{mol}^{-1}$)	87.09	72.69	71.28	75.86	78.91	89.79	85.03	92.39
Modified rectangular hyperbola model	R_p ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	4.21	4.03	4.17	4.09	3.86	4.18	3.85	3.72
	determination coefficient R^2	0.864	0.996	0.998	0.995	0.998	0.836	0.727	0.534
	CE_0 ($\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	0.0429	0.0559	0.0596	0.0541	0.0509	0.0422	0.0385	0.0323
	CE_T ($\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	0.0387	0.0536	0.0563	0.0503	0.0465	0.0377	0.0343	0.0281
	CE_{T0} ($\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	0.0402	0.0548	0.0578	0.0517	0.0483	0.0394	0.0364	0.0292
	CSP ($\mu\text{mol}\cdot\text{mol}^{-1}$)	936	1081	1155	1003	991	769	604	502
	$P_{n\max}$ ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	18.72	26.48	27.97	24.53	22.57	14.3	12.51	10.02
	Γ ($\mu\text{mol}\cdot\text{mol}^{-1}$)	91.55	73.91	71.39	76.66	79.33	92.89	95.31	101.77
	R_p ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	3.68	4.05	4.19	3.96	3.83	3.66	3.47	2.97
	determination coefficient R^2	0.998	0.998	0.998	0.999	0.999	0.998	0.997	0.996

Discussion

Effects of soil moisture on CO_2 response curves and photosynthetic parameters

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 $C_i \leq 200 \mu\text{mol}\cdot\text{mol}^{-1}$. Thus, P_n increases rapidly as C_i increases, namely, during the ribulose biphosphate (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 is $\sim 200 \mu\text{mol}\cdot\text{mol}^{-1}$ 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_{nmax} , 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_{cmax} , J_{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_{nmax} , CE , CSP , and R_p being high and Γ 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_{nmax} , 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 ($C_i \leq 200 \mu\text{mol mol}^{-1}$) [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 tanguticus*, 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].

CO₂ 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_Γ 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 $CE_{\Gamma 0}$ 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_{nmax} 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 CO₂ 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 CO₂ 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-CO₂ 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 CO₂ response curves and photosynthetic parameters in trees. This study indicated that soil moisture content affected the CO₂ response processes in the leaves of *H.rhamnoides* L. The photosynthetic P_n - C_i curve exhibited a classical form, with P_{nmax} , CE , CSP , and R_p being high, while Γ 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_{nmax} , 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 CO₂ 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 CO₂ response curves and photosynthetic parameters well. Compared to the other three models, the modified rectangular hyperbola model demonstrated extensive applicability for fitting photosynthetic CO₂ responses under different soil moisture conditions.

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Appendix

Name and abbreviation

<i>RWC</i> relative soil water content	<i>MWC</i> soil mass water content	<i>FC</i> field water capacity
<i>P_n</i> net photosynthetic rate	<i>C_i</i> intercellular CO ₂ concentration	<i>CSP</i> CO ₂ saturation point
<i>Γ</i> CO ₂ compensation points	<i>CE</i> carboxylation efficiency	<i>R_p</i> photorespiration rate