

The comparison of light responses among four species of *Calligonum* L. in early autumn

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Abstract. The photosynthetic characteristics of 4 species from different *Calligonum* sections were examined in autumn. Light response curves were measured in the field and fitted by the nonrectangular hyperbola model and modified rectangular hyperbola model. Modified rectangular hyperbola model was found greater when the fitting effects of two models were analyzed by relative errors. The comparison of the photosynthesis among four species revealed that *C. pumilum* had the maximum net photosynthetic rate (P_{max}) with high utilization of light. The lowest light saturation point (LSP) and apparent quantum yield (AQY) were observed in *C. Calliphysa* which seemed to be the low utilization of light. *C. densum* had the highest photo inhibition coefficient and smallest photo saturation coefficient; in contrast, *C. leucocladum* had the smallest photo inhibition coefficient and highest photo saturation coefficient. Present study revealed that there were differences of photosynthetic characteristics between four species in the genus *Calligonum*. Further studies are needed to elucidate this conclusion with more species and data collected in other season.

1. Introduction

Xinjiang lies in the northwest of China, and is a typical temperate arid zone with a high diversity of landscapes, such as glacier, alpine, basin, plain, grassland and desert. With the uplift of the Qinghai-Tibet Plateau (QTP) and the aridification originated in early Miocene [1] and the following Pleistocene aridification, large scale expansion of sandy deserts developed. The climate changes gave rise to a diversified ecosystems and desert flora. However, the amount and diversity of plant species decreased due to the enhanced aridification, thus an urgent vegetation protection and ecological restoration is required.

The genus *Calligonum* contains 35 species in the world, among which 22 were found in Xinjiang. Based on fruit morphological characteristics, *Calligonum* has been divided into four sections, including sect. *Calliphysa* (Fisch. et Mey) Borszcz, sect. *Pterococcus* (Pall.) Borszcz, sect. *Calligonum*, and sect. *Modusa* Sosk et Alexandr. According to the Flora Xinjiangensis, there is 1 species in sect. *Calliphysa*, 3 in sect. *Pterococcus*, 5 in sect. *Calligonum* and 13 in sect. *Modusa* [2]. *Calligonum* species are drought-tolerant, and mainly distributed on semi mobile or stable sand dunes and sandy lands in Xinjiang, playing an important role in wind breaking and sand fixation.



The photosynthesis is important in plants nourishment and growth. Photo response characteristics is the most important tool to study plant photosynthesis [3,4]. Several studies concerning the photosynthesis of *Calligonum* have been published, dealing mainly with the photosynthetic physiology and drought resistance of different species of *Calligonum* in different areas [5-7]. However, no studies have focused on the comparison of photosynthesis among species from different sections of *Calligonum*, and it may shed new light on our knowledge of *Calligonum* species' divergence and adaptation. In addition, some species of *Calligonum* are re-blooming in early autumn, so more attention should be paid to the photosynthesis in this season. In the present study, the light response curves of four species of *Calligonum* were measured and analyzed by the nonrectangular hyperbola model [8] and modified rectangular hyperbola model [9]. The aim of this study was to provide further knowledge of the photosynthetic physiological characteristics of *Calligonum* and make a contribution to their protection and restoration.

2. Materials and methods

2.1. Plant materials

The study area was in Turpan desert botanical garden of Chinese Academy of Sciences Institute of Xinjiang Ecology and Geography (Turpan, 42°91'N, 89°19'E). 4 species from 4 *Calligonum* sections were examined, (1) *C. leucocladum* from sect. *Pterococcus*; (2) *C. pumilum* from sect. *Modusa*; (3) *C. calliphysa* from sect. *Calliphysa*; (4) *C. densusum* from sect. *Calligonum*. Three individuals were chosen to represent the average growth of each species, and fully developed, mature, and healthy shoots were selected and carefully tested.

2.2. Photosynthetic analysis and Light response measurements

The measurements were taken under continuous cloudless weather at 11:00 to 13:00. The photosynthetic active radiation (PAR) gradient was set at 0, 25, 50, 100, 150, 200, 300, 500, 800, 1000, 1200, 1500, 1800 and 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$. The physiological parameters were automatically recorded by LI-6400 portable photosynthesis system.

Light response curves were created with two models, nonrectangular hyperbola model [8] and modified rectangular hyperbola model [9].

2.3. Data analysis

Statistical analyses were carried out using the Statistical Product and Service Solutions (SPSS19.0) software. Figures were drawn with Origin 9.0.

3. Results

As shown in figure 1, net photosynthetic rates (P_n) of the 4 species exhibiting similar S-shape. The P_n values increased along with increase of PAR in low light intensities and reached a plateau (maximum net photosynthetic rate, P_{max}) when PAR reached 1200–1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$. All the 4 species have similar light saturation point (LSP). When PAR was higher than LSP, 4 species maintain a high level of P_n , with significant differences ($p < 0.01$).

The physiological parameters, such as light compensation point (LCP), light saturation point (LSP), maximum net photosynthetic rate (P_{max}) and dark respiration rate (R_d) were obtained by the nonrectangular hyperbola model and modified rectangular hyperbola model. These parameters provide a basis to evaluate the photosynthesis systems, and study the photosynthesis ability and light adaptability of plants. Table 1 shows the parameters measured and fitted by two models, and the apparent quantum yield (AQY) were estimated by applying linear regression under low-light intensities (0-150 $\mu\text{mol m}^{-2} \text{s}^{-1}$). The light response curves measured and predicted by the two models were shown in figure 2.

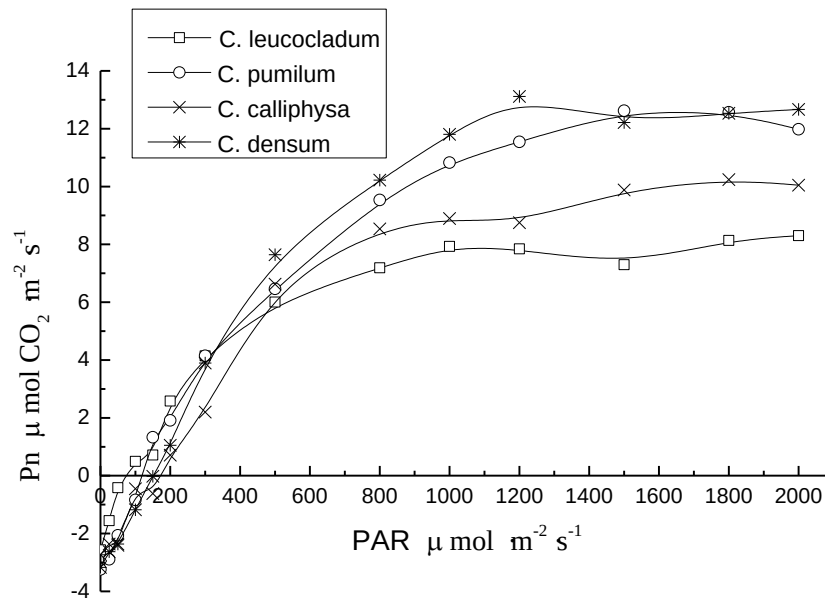


Figure 1. The photosynthesis light response curves of 4 species (4 sections).

PAR: photosynthetic active radiation; Pn: net photosynthetic rate.

Table 1. The photosynthetic parameters of 4 species (four sections) measured and fitted by two models.

Groups	Species	Model	Pmax	LSP	LCP	Rd	AQY/ α	Adjusted R^2
Sect. <i>Pterococcus</i>	<i>C. leuocladum</i>	Measured	8.3	1600	80	2.56	0.022	
		Model I	10.736		89	2.209	0.026	0.993
		Model II	8.09	1588	80	2.476	0.037	0.995
Sect. <i>Modusa</i>	<i>C. pumilum</i>	Measured	12.62	1700	120	3.24	0.03	
		Model I	17.974		122	3.405	0.03	0.996
		Model II	12.39	1755	120	2.268	0.033	0.999
Sect. <i>Calliphysa</i>	<i>C. calliphysa</i>	Measured	10.05	1600	140	2.73	0.017	
		Model I	13.254		153	3.02	0.02	0.993
		Model II	10.13	1643	141	3.237	0.026	0.994
Sect. <i>Calligonum</i>	<i>C. densum</i>	Measured	13.12	1500	130	3.17	0.021	
		Model I	16.689		144	3.403	0.024	0.997
		Model II	13.04	1525	133	3.664	0.03	0.998

Model I : the nonrectangular hyperbola model; Model II : modified rectangular hyperbola model; Pmax ($\mu\text{mol CO}_2\text{ m}^{-2}\text{ s}^{-1}$): light-saturated net photosynthetic rate; LSP ($\mu\text{mol m}^{-2}\text{ s}^{-1}$): the light saturation point; LCP ($\mu\text{mol m}^{-2}\text{ s}^{-1}$): light compensation point; Rd ($\mu\text{mol m}^{-2}\text{ s}^{-1}$): dark respiration rate; AQY: apparent quantum yield estimated by applying linear regression; α : initial quantum efficiency or intrinsic quantum yield estimated by two models; Adjusted R^2 : the conformity coefficient of models.

Though both models had high determination coefficients ($R^2 > 0.99$), the fitting effects presented significant differences between two models (figure 2), the fitting results of Pmax with the nonrectangular hyperbola model were significantly higher than the measured values ($p < 0.01$), the relative errors (RE) between the measured and fitted values was 27%-42%. However, modified rectangular hyperbola model fitted the light response curves of *Calligonum* well and the RE is 1%-

2.5%. The fitting results for LCP with two models were largely identical to the measured values ($p > 0.05$), the RE of the nonrectangular hyperbola model and modified rectangular hyperbola model was 2%-11% and 0-8%, respectively. The rectangular hyperbolic model is unable to estimate LSP on account of the model is an asymptotically saturating curve without a clear maximum within the range of the data [10-12], while the fitting values of LSP were the most similar to the measured values by modified rectangular hyperbola model (RE is 0-6%).

Pmax fitted by modified rectangular hyperbola model was that *C. pumilum* and *C. densum* was significant higher than other two species ($p < 0.01$), *C. leucocladum* is the lowest and show significant differences ($p < 0.05$). The comparison of LSP values was that *C. pumilum* > *C. leucocladum* > *C. densum* > *C. calliphysa*. The values of LCP were that *C. calliphysa* > *C. densum* > *C. pumilum* > *C. leucocladum*. The β values by modified rectangular hyperbola model were *C. densum* > *C. calliphysa* > *C. pumilum* > *C. leucocladum*. The γ values were that *C. leucocladum* is significantly higher than other species ($p < 0.01$), and others show no significant differences ($p > 0.05$). The AQY values showed that *C. pumilum* > *C. Densum* > *C. leucocladum* > *C. Calliphysa* ($p < 0.01$).

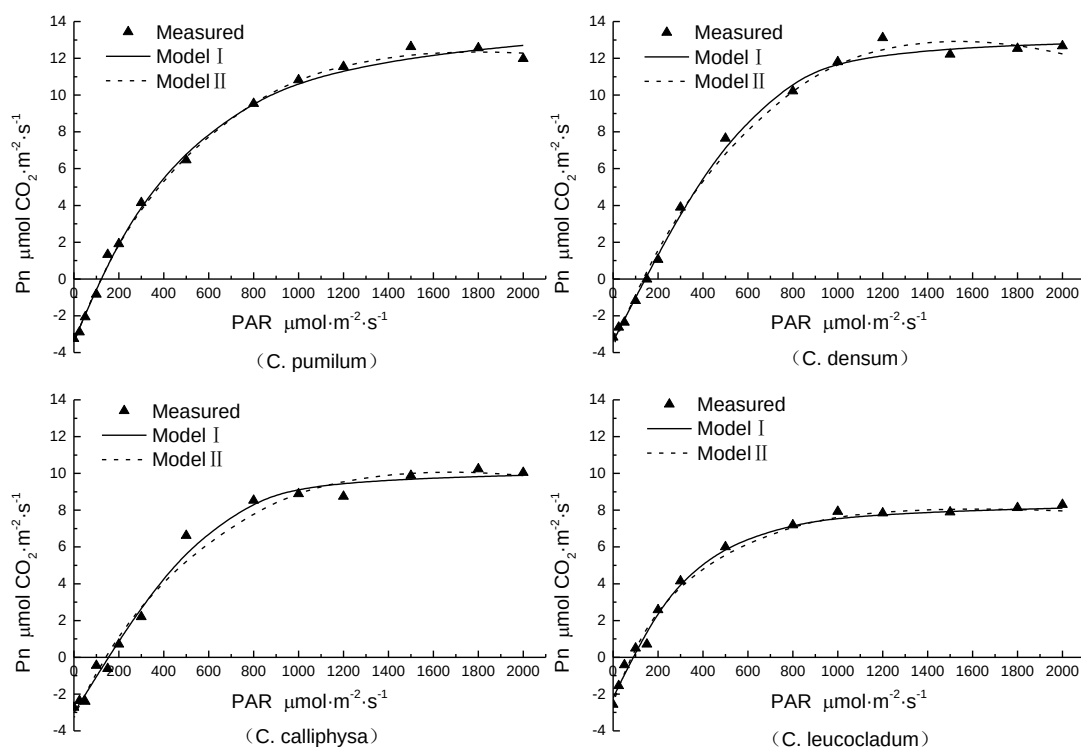


Figure 2. The light response curves of 4 species(4 sections) measured and predicted by two models. PAR: photosynthetic active radiation; Pn: net photosynthetic rate; Model I : the nonrectangular hyperbola model; Model II: modified rectangular hyperbola model.

4. Discussion

4.1. The comparison and fitting of two models

Light response curve models were widely used in plant photosynthetic physiological studies, among which nonrectangular hyperbola and modified rectangular hyperbola model were the most commonly adopted models. The fitting effects of light-response models were variable among different plants, environments and seasons [13, 14]. The nonrectangular hyperbola model was also an asymptote same to the rectangular hyperbola model, which couldn't estimate the values of LSP accurately [15]. Several studies indicated that the nonrectangular hyperbola model couldn't fit photo inhibition plants because

this model had not extreme values and usually overestimated P_{max} when the P_n was declining after LSP [12]. Modified rectangular hyperbola model introduced the photo-inhibition term β and the photo-saturation term γ , which could estimate the value of LSP accurately because it wasn't an asymptotically saturating curve. This model also had high accuracy and applicability in fitting the process that curve is declining or remaining consistent after LSP.

The present research is again proves that the nonrectangular hyperbola model significantly overestimates the values of P_{max} and modified rectangular hyperbola model is mostly consistent with measurements. Although both models had higher determination coefficients ($R^2 > 0.99$), R^2 didn't indicate that the model is consistent to the actual measurement. RE (relative errors) should be a new parameter for the quantitative evaluation of the fitting effect of light response models [16], the less the value of RE is, the more perfect of the model is. The comparison of the RE between two models show that modified rectangular hyperbola model is the most suitable light-response model for *Calligonum*. However, it's hard to say that modified rectangular hyperbola model is the best model for *Calligonum* under any conditions. It is difficult to compare the parameters because they were of different meanings in two models. The value of AQY resulted in linear regression were not precise due to the different ranges of light intensity or different numbers of data points. In addition, the fitting effects of modified rectangular hyperbola model might be related to plant type, different temperatures or different carbon dioxide and soil water conditions [12,14,17]. Thus, further researches are needed to demonstrate the fitting effects of *Calligonum* by modified rectangular hyperbola model.

4.2. The differences among 4 sections of *Calligonum*

Photosynthesis plays an important role in plants growth because it provides organic matters for their development. Plants adjust their ecological strategy to improve the efficiency of photosynthesis under different habitats, for example, allocating more biomass into above ground part and changing root/shoot ration to compete for light resource [18], and controlling the stomata conductance to adapt to drought stress [19]. *Calligonum* species with higher ability of photosynthetic efficiency are superior to other species for accumulating organic materials. Furthermore, high ability of photosynthesis contributes to high resistance and adaptability to variety of environments. The lower the AQY or the lower the LCP, the stronger ability of the plants to use weak light, it means the organic matter of plants start positive growth under very low PAR. What's more, these plants have high light use efficiency under the light limited conditions, thus increasing the accumulation of organic material. Light ecological amplitude to plants is the range between LCP and LSP, and it indicates the ability of plants to different illumination intensity. A higher value of LSP and P_{max} shows a high utilization efficiency of high PAR. In this study, the photosynthetic parameters of four *Calligonum* species in the same habitat were analyzed by linear regression and modified rectangular hyperbola model.

We found that *C. pumilum* had the most widely light ecological amplitude, the highest light-saturated net photosynthetic rate (P_{max}) and light utilization efficiency; *C. pumilum* had not only strong drought resistance but also favorable adaptability to high light quantum flux density that may be why they are widely distributed and usually the dominant or primary constructive species in their ecological communities. Several species in sect. *Modusa* are endemic that evolved in the severely arid environment in Xinjiang, such as *C. taklimakanense*, *C. roborovskii*, *C. kurlaense*, *C. yengisaricum*, and *C. juochiangense* [2]. *C. calliphysa* have narrow light ecological amplitude and the lowest light utilization efficiency. As a result, the habitats of *C. calliphysa* is poor under natural conditions, and they are usually prostrate on the ground seems to be dying. *C. calliphysa* seldom is the dominant species or constructive species. The significant differences between *C. pumilum* and *C. calliphysa* may due to the physiological adaptability and resistance of different sections. Li [20] suggested that the fruit of *Calligonum* grows to be shallow trench and multi-spine density to adapt to the complex and harsh environment. Lv [21] suggested that *C. calliphysa* is the oldest section and *C. pumilum* is the youngest section after genetic variation and population evolution. The theory of evolution and survival of the fittest all prove that *C. calliphysa* has the weakest photosynthetic capacity while *C. pumilum* has the strongest photosynthetic capacity.

In modified rectangular hyperbola model, β is the correction factor and considered as photo-inhibition term, γ is the coefficient and considered as photo-saturation term, their biological significances are the product of cross section of photosynthetic pigment in PS II for quantum absorption and average life of photosynthetic pigment in the excited state [22]. The significance suggests that the plants are easily photo-inhibited if the value of β is large, while plants are easily photo-saturated if the value of γ is large. The light use efficiency of plants depends on the comprehensive of β and γ , the higher the β and γ , the low use efficiency of plants. In this study, specie of *C. densum* has the highest value of β and the lowest value of γ , it may reveal that *C. densum* is most easily affected by photo inhibition while most hardly reaching photo saturation, while *C. leucocladum* behaves like a shade plant and is most hardly affected by photo inhibition and most easily reaching photo saturation. In fact, we didn't find the similar trend in the light response curves, and this is because of the neutralization combination of the two parameters. The lower the β and γ is, high utilization of light of the plants is. This confirms the theory that *C. densum* and *C. leucocladum* are the transition stage of evolutionary development and have the medium utilization of light. *Calligonum* as an important windbreak and sand-fixing shrub is usually introduced in shelter forest construction and ecological restoration. *C. densum* and *C. leucocladum* may both not suitable for introducing as dominant or constructive species in saline, extreme drought conditions, because they are easily affected by environmental factors. Furthermore, the photo inhibition, photo saturation and low values of P_{max} lead to decline of light utilization rates and photosynthetic rates, which resulting in low amount of organic accumulation and poor growth under severe interferences.

Although it was advocated that photosynthesis of plants is not as good as that of in summer [19], the present study still provides some meaningful implications that photosynthesis differences are existing among the four species and each of them have their own characteristics. Studies have illustrated that the various phenology of *Calligonum* show different responses of plants to the same environment associated with seeds morphology [23]. Kang [24] indicated that the intersection differences of *Calligonum* under same habit decided by the heredity of fruit differences. Our study showed the different *Calligonum* sections have different microenvironments, and their various physiological adaptability and resistance lead to different utilization degrees of illumination. However, further evidences to confirm the differences of light responses among *Calligonum* sections are needed. Next year, the photosynthesis of more *Calligonum* species from four sections will be studied. Moreover, anatomy and carbon isotope will also be included in our future research to gain a deeper insight of the divergence among *Calligonum* species, as well as the evolution and adaption of the genus in arid environment.

Acknowledgments

This research was supported by National Science Foundation of China "Studies on kinship, geographical replacement law and evolution reason of *Calligonum* plants in Xinjiang" (NSF-41271069) and the Province Science Foundation of Xinjiang (Y55315100).

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