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The photosynthetic eco-physiological adaptability of the endangered plant *Tetracentron sinense* to different habitats and altitudes

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Abstract

Tetracentron sinense Oliv, the only tall deciduous tree in the family *Tetracentraceae*, is listed as a national second-grade key protected plant in China. To reveal the effect of associated species, irradiance, and altitudes on photosynthetic capacity of *T. sinense*, photosynthetic physiological characteristics of *T. sinense* and its associated species *Acer pictum* and *Pterocarya stenoptera* were measured by a *Li-6400* portable photosynthetic meter. The light saturation point (LSP), the maximum net photosynthetic rate of the P_N-PAR (P_{Nmax}), carboxylation efficiency (CE), the maximum net photosynthetic rate of the P_N-CO_2 (P^*_{Nmax}), carbon dioxide compensation point (CCP) and light respiration rate (R_p) of *T. sinense* in forest gap (FG) were higher than those in forest edge (FE) and understory (US). In FE, the net photosynthetic rate (P_N), light compensation point (LCP), LSP, P^*_{Nmax} of *T. sinense* were lower than those of *Pterocarya stenoptera*, while the LSP, P_{Nmax}, and saturation point of carbon dioxide (C_{iast}) of *T. sinense* in US were lower than those of *Acer pictum* and *Pterocarya stenoptera*. The specific leaf area (SLA) of *T. sinense* decreased with reduction in the irradiance. With increasing altitude, the P_{Nmax}, LSP, and SLA of young individuals of *T. sinense* (YT) increased; the LCP of YT or the LSP of mature individuals of *T. sinense* (MT) increased first and then decreased. The results showed that *1*) the photosynthetic capacity and adaptability of *T. sinense* were better in FG than that in FE and US; *2*) the photosynthetic capacity of *T. sinense* in FE and US was weaker than that of its associated species, and its ecological range of light adaptation was also narrower than that of its associated species, placing *T. sinense* at a competitive disadvantage, which may be one of the important reasons for its poor regeneration; and *3*) the environmental conditions at higher altitude can contribute to the growth and survival of *T. sinense.* Therefore, active artificial intervention should be undertaken to expand area of forest gap for *T. sinense* and transplant its seedlings to higher altitude to promote growth and population regeneration of *T. sinense.*

Keywords: *Acer pictum*, *Acer sterculiaceum*, altitude, irradiance, net photosynthetic rate, *Pterocarya stenoptera*, respiration rate, specific leaf area, *Tetracentron sinense.*

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Abbreviations: AQY - apparent quantum yield; CCP - carbon dioxide compensation point; CE - carboxylation efficiency; C_i - intercellular CO_2 concentration; C_{iast} - saturation point of carbon dioxide; E - transpiration rate; FE - forest edge; FG - forest gap; g_s - stomatal conductance; H - high altitude; L - low altitude; LA - leaf area; LCP - light compensation point; LL - leaf length; LM - leaf mass; LSP - light saturation point; LW - leaf width; M - middle altitude; MT - mature individuals of *T. sinense*; P_N - net photosynthetic rate; P_{Nmax} - the maximum net photosynthetic rate of the P_N-PAR; P^*_{Nmax} - the maximum net photosynthetic rate of the P_N-CO_2; R_D - dark respiration rate; R_p - light respiration rate; SLA - specific leaf area; US - understory; YT - young individuals of *T. sinense*.

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Introduction

Plant functional traits are measurable characteristics of organisms that influence the basic processes of growth, reproduction, and survival (Violle *et al*. 2007) and can describe mechanistic linkages between an organism and its environment (Lavorel and Garnier 2002, Reich *et al.* 2003, He *et al*. 2020). Among many functional traits in plants, leaf photosynthetic characteristics are key parameters influencing plant growth, survival, and reproduction (Westoby *et al*. 2002, Wright *et al*. 2004, Reich 2014), which is important for detecting the growth adaptability of plants under certain environmental conditions (Lodge 1993, Cleland *et al*. 2011, Chen and Huang 2018). The differences of photosynthetic physiological traits were relevant to environmental factors such as irradiance and altitude (Zhu *et al*. 2010, Liu 2017, Petrik *et al.* 2022). Assessment of the photosynthetic responses under a range of irradiances can reveal information about the tolerance and growth of species (Valladares *et al*. 2002). In general, endangered plants due to poor eco-physiological adaptability (especially of photosynthesis and respiratory metabolism) are often at a disadvantage in interspecific competition (Wang *et al*. 2000, Ma *et al*. 2007, Quero *et al*. 2008, Lanker *et al*. 2010, Jin *et al*. 2011, Iszkulo *et al*. 2012). Therefore, knowledge of the photosynthetic eco-physiological characteristics of endangered plants in different irradiances can help to understand why plants are endangered as well as to provide effective strategies for their conservation and management (Poorter 2002).

Tetracentron sinense Oliv. is the only tall deciduous tree in the *Tetracentraceae* family. It is mainly distributed in Southwest and Central China (Reynolds *et al*. 1997) as a relict species (Roháček 2002). Owing to its value in making ornaments, furniture, and medicine (Wang *et al.* 2006, Luo *et al*. 2010), the species has been excessively harvested, resulting in poor regeneration. It is listed as an endangered species in the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) Appendix III and is designated a national second-grade key protected plant in China (Fu and Jin 1992). To better conserve the endangered species, community and population ecology (Chen *et al*. 2008, Li 2015, Wang 2017, Li *et al*. 2018a, Tian *et al*. 2018, Zhang *et al*. 2020a), sporogenesis and gametophyte formation (Gan *et al*. 2012), pollination ecology (Gan *et al*. 2013), seed and seedling ecology (Wan 1986, Zhou 2007, Gan *et al*. 2008, Cao *et al*. 2012, Han *et al*. 2015, Li *et al*. 2015, Xu *et al*. 2015, Chen 2018, Tong *et al*. 2020, Li 2021, Lu 2021, Lu *et al*. 2021, Fan *et al*. 2022), and conservation genetics (Han *et al*. 2017, Li *et al*. 2018b, 2021) of *T. sinense* have been investigated extensively. Previous studies have shown that there are fewer young individuals and more middle and old-aged individuals in *T. sinense* natural populations, and the young individuals are mostly present in understory (US), whereas the middle and old-aged individuals in forest gap (FG) and forest edge (FE) (Li *et al*. 2015). In addition, there is a great niche overlap between *T. sinense* and its associated species, such as *Acer pictum* subsp. *mono*, *Acer sterculiaceum,* and *Pterocarya stenoptera*, leading to intense competition for radiation (Tian *et al*. 2018). The differences in the photosynthetic characteristics between *T. sinense* and its associated species under different irradiances can directly affect the adaptability and competitive potential of *T. sinense*, which may be closely related to the distribution of *T. sinense*. To date, little is known about the photosynthetic characteristics of *T. sinense* and its associated species under various irradiance.

Temperature, moisture, and solar radiation also vary at different altitudes, which further affect the photosynthesis, growth, and survival of species. Gale (1972a,b) found that the radiation increased, and the temperature generally decreased as the altitude increased. Anup and Ghimire (2015) found that a small increase of 1°C in the annual mean temperature is sufficient to cause major changes in the growth and regenerative ability of many tree species. Saccharide reserves appear to be higher near the lower altitudinal limits of a species (Mooney and Billings 1965). When the dry lapse rate (0.01°C m^{-1}) of air temperature was simulated, a significant decrease (up to 14%) in plant photosynthetic capability of CO_2 absorption was predicted from sea level up to 4 km elevation (Smith and Donahue 1991). Li *et al*. (2015) found that altitude is an important factor affecting the seed germination of *T. sinense*, but there are no relevant reports on the influence of altitude on the further growth and survival of *T. sinense*. The photosynthetic eco-physiological adaptation mechanisms of *T. sinense* to altitude is likely to significantly impact the growth and survival of this species at different altitudes.

In this study, the *Li-6400XT* portable photosynthetic system (*Li-COR*, Lincoln, NE, USA) was used to measure the photosynthetic characteristics of *T. sinense* and its associated species in different irradiances and altitudes. Our study aims to: *1*) examine the photosynthetic capacity of *T. sinense* and its dominant associated species in different irradiances and altitudes, *2*) understand the photosynthetic eco-physiological adaptation mechanisms of *T. sinense* to irradiance and altitude, and *3*) provide a scientific basis for the effective conservation and management of *T. sinense*.

Materials and methods

Study site was located in the Dafengding Nature Reserve (DNR), northeast of Meigu County, Sichuan Province (102°52′ - 103°20N, 28°30′ - 28°50E). This reserve has a subtropical monsoon climate, with an average annual precipitation of 1 110 mm, relative air humidity of 80%, and an average annual temperature of 11.4°C (Tian *et al*. 2018, Lu *et al*. 2021). The mountainous vertical distribution of vegetation in the reserve was obvious: evergreen broad-leaved forest (< 2 000 m), evergreen and deciduous mixed forest (2 000 - 2 400 m), coniferous and broad-leaved forest (2 400 - 2 800 m), coniferous forest (2 800 - 3 700 m), and alpine shrub meadow (> 3 700 m) (Sun *et al*. 2006). *Tetracentron sinense* Oliv. was mainly distributed in the evergreen deciduous mixed forest (2 000 - 2 400 m), along with *Acer* spp., *Viburnum* spp., and *Betula albosinensis* (Tian *et al.* 2018, Lu *et al.* 2021).

Field investigation: According to Fan *et al.* (2022), the photosynthetic capacity of *T. sinense* in the initial growth stage (20 cm ≤ diameter at breast height (DBH) < 30 cm) was significantly higher compared to that at other stages of the life cycle. In addition, there were many individuals at the initial growth stage distributed in forest gap (FG), forest edge (FE), and understory habitat (US) in the deciduous broad-leaved forest at an altitude of approximately 2 200 m, which is suitable for studying the variance in photosynthetic capacity of *T. sinense* and its associated species. *Pterocarya stenoptera* and *Acer sterculiaceum* were often associated with *T. sinense* in FE, *Acer pictum* and *Pterocarya stenoptera* were often associated in US, but there were no associated species with *T. sinense* in FG. Nine individuals of *T. sinense* were selected from three light habitats (three individuals per light habitat). Meanwhile, three individuals of *Pterocarya stenoptera* and *Acer sterculiaceum* from FE and three individuals of *P. stenoptera* and *Acer pictum* from US were also selected, respectively. A total of sixty-three leaves (three leaves per individual tree) of *T. sinense* and its associated species were collected for *in situ* photosynthetic measurements (Fan *et al.* 2022) (Fig. 1 Suppl.).

According to the elevation distribution of *T. sinense* in the DNR, three altitude gradients were set: L (low altitude: 1 996 - 2 014 m), M (middle altitude: 2 113 - 2 208 m), and H (high altitude :2 304 - 2 337 m). Based on the results of Li *et al.* (2015) and Fan *et al.* (2022), two age groups (YT: young tree, 5 cm ≤ DBH ≤ 10 cm, MT: mature tree, 35 cm ≤ DBH ≤ 45 cm) of *T. sinense* were selected at each altitude, and nine healthy leaves from three selected trees (three leaves per tree) per altitude were selected for photosynthetic tests (Fan *et al.* 2022).

P_N-PAR response curve: In clear weather, a *Li-6400XT* portable photosynthesis system was used to measure the net photosynthetic rate (P_N) and other photosynthetic parameters of *T. sinense* and its associated species in different irradiances and altitudes. The photosynthetic parameters of the fifth healthy mature leaf of the annual branch growing on the sunny side were determined (three times per leaf). To obtain daytime change of photosynthesis, the P_N was measured every 2 h from 9:00 to 17:30. Further, stomatal conductance (g_s), intercellular CO_2 concentration (C_i), and transpiration rate (E) were measured. Before measuring the radiation response curve with the red and blue radiation source of the instrument, leaves were induced for 15 min when the irradiance was 800 $\mu mol \cdot m^{-2} \cdot s^{-1}$, the temperature 23 - 26°C, the flow rate 500 $\mu mol\ m^{-2}\ s^{-1}$. The photosynthetic parameters were recorded from 9:00 to 12:00. The values of P_N were recorded at different photosynthetic photon flux densities: 2 000, 1 800, 1 600, 1 200, 1 000, 800, 600, 400, 200, 100, 80, 60, 40, 0 $\mu mol\ m^{-2}\ s^{-1}$. In this experiment, a modified rectangular hyperbola model (von Caemmerer and Farquhar 1981, von Caemmerer 2000, Ye 2007, Ye and Yu 2008) was used to fit radiation response curves of *T. sinense* and its associated species:

$$P_N(I) = \alpha \frac{1-\beta I}{1+\gamma I} I - R_D \tag{1}$$

$$P_{Nmax} = \alpha \left(\frac{\sqrt{\beta+\gamma}}{\gamma} - \frac{\sqrt{\beta}}{\gamma} \right)^2 - R_D \tag{2}$$

$$\mathrm{LSP} = \frac{\sqrt{(\beta+\gamma)/\beta - 1}}{\gamma} \tag{3}$$

$$\mathrm{LCP} = \frac{\alpha - R_D\gamma - \sqrt{(R_D\gamma - \alpha)^2 - 4\alpha\beta R_D}}{2\alpha\beta} \tag{4}$$

$$\mathrm{AQY} = \alpha \frac{1+(\gamma-\beta)\mathrm{LCP} - \beta\gamma \mathrm{LCP}^2}{(1+\gamma \mathrm{LCP}^2)} \tag{5}$$

Where P_{Nmax} is photosynthetic capacity, P_N is net photosynthetic rate, β and γ are coefficients, I is photosynthetically active radiation, R_D is dark respiration rate. LCP is light compensation point, LSP is light saturation point, AQY is apparent quantum yield. The calculated results are rounded after comparing with the measured values.

CO_2 response curve (P_N-CO_2): The leaves were selected as described in the previous section. The CO_2 response curves of *T. sinense* and its associated species were measured using a *Li-6400XT* portable photosynthetic system. The saturation radiation was used and CO_2 concentrations were set to 1 800, 1 500, 1 200, 1 000, 800, 600, 500, 400, 300, 200, 150, 100, 50 $\mu mol\ m^{-2}\ s^{-1}$. When measuring the CO_2 response curve, a small cylinder containing CO_2 was used to provide CO_2 raw material for photosynthesis. Before the measurement, the small cylinder needed to be calibrated each time to ensure that the CO_2 injection system could precisely control the CO_2 concentration in the leaf chamber. The leaves were subjected to irradiance for about 15 min and the interval of each CO_2 concentration was 300 s. The right angle hyperbolic modify model (Ye and Gao 2009) was used to fit the CO_2 response curve:

$$P_N = a \frac{1 - bC_i}{1 + cC_i} C_i - R_p \tag{6}$$

$$P^*_{Nmax} = a \left(\frac{\sqrt{b+c} - \sqrt{b}}{c} \right)^2 - R_p \tag{7}$$

$$C_{iast} \quad \frac{\sqrt{b \quad c/b} - 1}{c} \tag{8}$$

$$\mathrm{CCP} = \frac{a - R_p c - \sqrt{R_p{}^2 c^2 + a^2 - 2acR_p - 4abR_p}}{2ab} \tag{9}$$

Where P^{*}_{Nmax} is photosynthetic capacity, P_N is net photosynthetic rate, C_i is intercellular CO_2 concentration, R_p is photorespiration rate, a is the initial carboxylation efficiency of the CO_2 response curve, b and c are the coefficients, C_{iast} is saturation point of carbon dioxide, CCP is the CO_2 compensation point.

Specific leaf area (SLA): Five fully expanded and healthy leaves were collected from the same position as the measured photosynthetic parameters. After labeled and bagged, the leaf area (LA) was measured by a leaf area analyzer (*Microtek*, Haishang, China). Then the leaves were dried at 105°C for 30 min, followed by continuous drying for 48 h at 80°C using an oven. Afterwards, an electronic balance was used for determination of leaf mass (LM). The specific leaf area (SLA, cm^2 g^{-1}) was calculated according to the following formula:

$$SLA = LA/LM \tag{10}$$

Statistical analyses: The *SPSS14.0* (*IBM*, Armonk, New York, USA) was used for statistical analysis. One-way analysis of variance (*ANOVA*) was used for the significance analysis, *Simaplot 14.0* (*Systat*, San Jose, California, USA) and *R 4.1.2* (*R Core Team*, 2021) were used to plot the results. Based on the calculation of all species-mean performance variables, we carried out principal component analyses (PCA) separately for different habitats, different species, and different altitudes by *Factoextra* and *FactoMineR* packages (*R version 4.1.2*, Lê *et al.* 2008).

Results

As shown in Fig 1, the diurnal variation in P_N of *T. sinense* in both FG and FE exhibited a bimodal curve, and that of *T. sinense* in US showed a single peak curve. In general, the daily variation in P_N of *T. sinense* in FG and FE was higher than in US (Fig. 1*A*).

In US, the diurnal course of P_N of *A. pictum* and *P. stenoptera* also exhibited a bimodal curve (Fig. 1*B*), and the daily variation in P_N of *T. sinense* was lower than that of *P. stenoptera* and *A. pictum*. The daily average of P_N of *P. stenoptera* was four times of that of *T. sinense*.

In FE, there was a double peak curve observed for the daily average P_N of *P. stenoptera* and *A. sterculiaceum*. The daily average P_N of *P. stenoptera* was higher than that of *T. sinense* and *A. sterculiaceum* (Fig. 1*C*).

The diurnal variation of transpiration rate (*E*) was consistent with that of P_N of *T. sinense* in FG and FE (bimodal curves), whereas a single peak curve was observed in US habitat. Among different habitats, the *E* of *T. sinense* was maximal in FG, followed by FE and US (Fig. 2*A*).

In FE, the daily average E of both *P. stenoptera* and *A. sterculiaceum* showed a double peak curve. In US, the order of *E* was *P. stenoptera* > *A. pictum* > *T. sinense* (Fig. 2*B*), while in FE, the order of *E* was *P. stenoptera* > *T. sinense* > *A. sterculiaceum* (Fig. 2*C*).

Most of the photosynthetic parameters of *T. sinense* differed at different altitudes ($P < 0.05$, $n = 18$). There was no significant difference in C_i of the YT (Fig. 3*C*), however, the order of P_N was low (L) < moderate (M) < high (H) (Fig. 3*A*). The order of g_s was L < M < H (Fig. 3*B*), and of *E* was L < H < M (Fig. 3*D*). These parameters of MT did not differ significantly between L and H altitudes; however, the values in M were significantly lower than those in L and H.

The radiation response curves of *T. sinense* were significantly different in FG, US, and FE ($P < 0.05$, $n = 9$), and P_N for *T. sinense* in US was lower than in FE and FG (Fig. 4*A*). There were significant differences in the radiation response curves of *T. sinense* and its associated

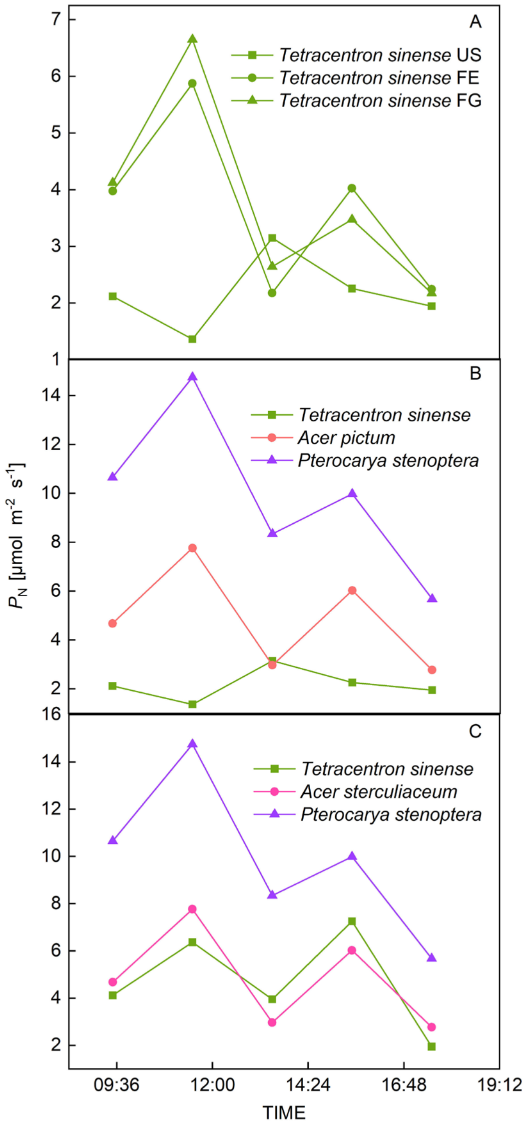

Fig. 1. The diurnal variation in P_N for *T. sinense* and its associated species in different habitats. *A* - The diurnal variation in the net photosynthetic rate (P_N) for *Tetracentron sinense* in forest gap (FG), forest edge (FE), understory (US). *B* - The diurnal variation in P_N for *Tetracentron sinense*, *Acer pictum*, and *Pterocarya stenoptera* at different times in understory. *C* - P_N values for *Tetracentron sinense*, *Pterocarya stenoptera*, and *Acer sterculiaceum* at different times in forest edge.

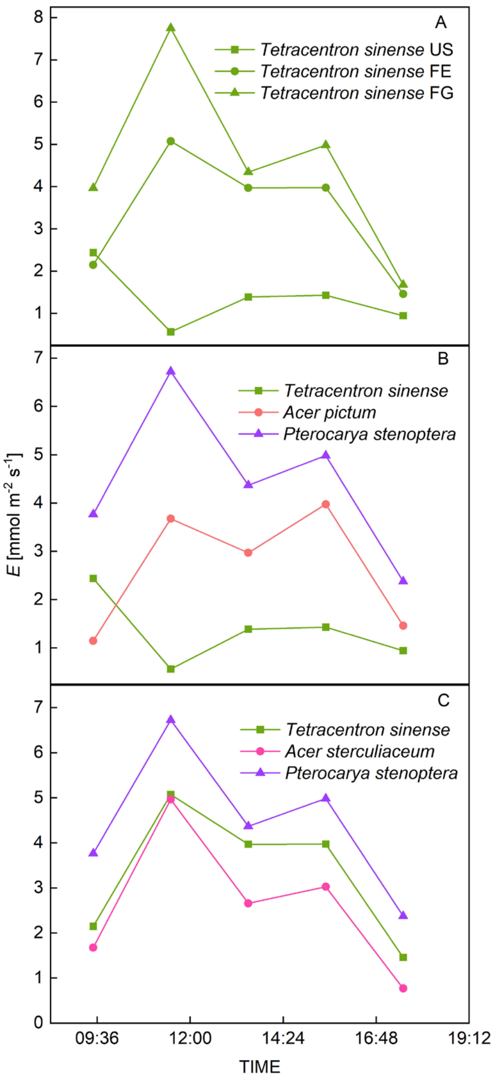

Fig. 2. The diurnal variation of E of *T. sinense* and its associated species in different habitats. *A* - The diurnal variation in transpiration rate (E) for *Tetracentron sinense* in forest gap (FG), forest edge (FE), understory (US). *B* - The diurnal variation of E for *Tetracentron sinense*, *Acer pictum*, and *Pterocarya stenoptera* at different times in understory. *C* - E values for different times of *Tetracentron sinense*, *Pterocarya stenoptera*, and *Acer sterculiaceum* in forest edge.

species in FE and US habitats ($P < 0.05$, $n = 18$). In US, the order in P_N was *P. stenoptera* > *A. pictum* > *T. sinense* (Fig. 4*B*), while the order in FE was *P. stenoptera* > *T. sinense* > *A. sterculiaceum* (Fig. 4*C*).

There were significant differences in LSP and P_{Nmax} of *T. sinense* among different habitats ($P < 0.05$, $n = 9$) (Table 1). The P_{Nmax} of *T. sinense* in US was lower than that in FE and FG, the order of LSP was FG > FE > US. The AQY, LCP, and R_D of *T. sinense* were not significantly different among different habitats.

In FE, there were significant differences in the LSP, LCP, and AQY of *T. sinense* and its associated species ($P < 0.05$, $n = 9$) (Table 1). The LCP and LSP of *T. sinense* were lower than those of *P. stenoptera*. No significant difference was observed in P_{Nmax} and R_D between *T. sinense* and its associated species, and the AQY of *P. stenoptera* was lower than that of *T. sinense* and *A. sterculiaceum*. In US, there were significant differences in LSP and P_{Nmax} between *T. sinense* and its associated species ($P < 0.05$, $n = 9$). The P_{Nmax} of *T. sinense* was lower than that of *P. stenoptera,* the LSP of *T. sinense* was lower than that of *A. pictum* and *P. stenoptera.* There was no significant difference in LCP, AQY, and R_D between *T. sinense* and its associated species.

With increasing altitude, the P_{Nmax} of YT increased, while that of MT decreased (Fig. 5). At the three different altitudes, the optimum P_N was found to be in the range of 800 µmol m^{-2} s^{-1} to 1 000 µmol m^{-2} s^{-1} in the YT.

There were significant differences in the LSP and LCP at different altitudes ($P < 0.05$, $n = 18$). With increasing altitude, the LSP of YT increased, whereas the LSP of MT first increased and then decreased, and the LCP of both the YT and MT first increased and then decreased (Tables 2 and 3).The R_D of MT at L and M was significantly higher than that at H, whereas the AQY of both YT and MT in L and M was significantly lower than that at H ($P < 0.05$, $n = 18$).

Different habitats affected the CO_2 response and P_N of *T. sinense* and its associated species ($P < 0.05$, $n = 21$). When the C_i was less than 500 µmol m^{-2} s^{-1}, the P_N of *T. sinense* and its associated species increased rapidly with increasing CO_2 concentration in each habitat. When P_N reached its maximum, the C_{iast} and P_N of *T. sinense* and its associated species remained unchanged or slightly decreased with increasing CO_2 concentration (Fig. 6).

The order in P_N of *T. sinense* in different habitats was FG > US > FE (Fig. 6*A*). In US and FE, the P_N value of *T. sinense* was lower than that of its associated species (*P. stenoptera*, *A. pictum*, and *A. sterculiaceum*) (Fig. 6*B*,*C*).

There were significant differences in the photosynthetic parameters of *T. sinense* among different habitats ($P < 0.05$, $n = 9$) (Table 4). The slope of the P_N-CO_2 response curve represents the carboxylation efficiency (CE). The CE, P^*_{Nmax}, R_p, CCP of *T. sinense* in FG were significantly higher than those of *T. sinense* in FE.

In FE and US, significant differences were observed in the photosynthetic parameters of *T. sinense* and its associated species ($P < 0.05$, $n = 18$). In FE, the P^*_{Nmax} of *T. sinense* was lower than that of *P. stenoptera* and *A. sterculiaceum*. In US habitat, the C_{iast} of *T. sinense* was lower than that of *P. stenoptera and A. pictum.*

There were significant differences in the LL, LA, LM, and SLA of *T. sinense* among the samples from different habitats ($P < 0.05$, $n = 9$) (Table 5). The order in LL and LM of *T. sinense* were FG > FE > US, and the SLA and LA of *T. sinense* in FG were significantly higher than in US and FE.

The SLA of YT and MT increased significantly with increasing altitude ($P < 0.05$, $n = 18$) (Tables 6 and 7). The LL of YT and MT at L was significantly lower than that at M and H ($P < 0.05$, $n = 18$). The LM of YT and MT

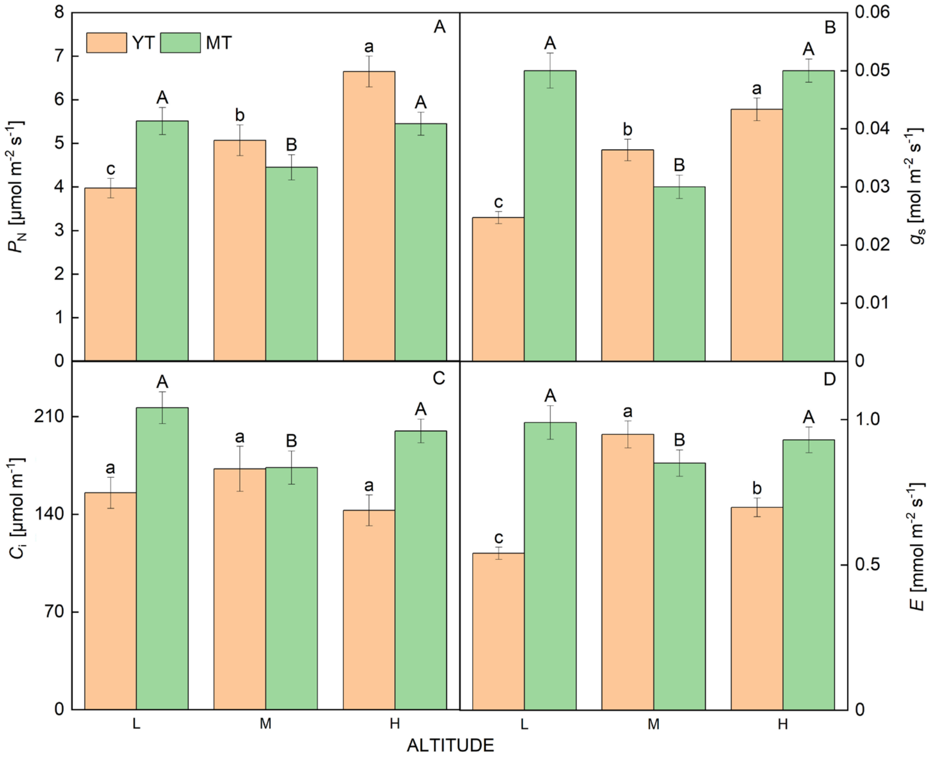

Fig. 3. Photosynthetic parameters of YT and MT for *T. sinense* at different altitudes. The net photosynthetic rate (P_N) (*A*), stomatal conductance (g_s) (*B*), intercellular CO$_2$ concentration (C_i) (*C*), and transpiration rate (*E*) (*D*) are shown. Different upper- or lowercase letters indicate significant differences in young tree or mature tree, respectively, $P < 0.05$.

at H was significantly lower than that at L and M altitudes (Tables 6 and 7). There was a significant difference in the LA of YT at different altitudes ($P < 0.05$, $n = 9$), and LA increased with increasing altitude (Table 4), but no significant difference was observed in the LA of MT at different altitudes.

Based on the PCA scatter plot under different irradiances, the first three principal components explained 70.2% of the variance. P^*_{Nmax} and LSP had significant positive relation with the PCA1, which embodies the difference between FG and FE. LCP and C_{iast} were positively associated with the PCA2. SLA had significant positive relation with the PCA3, which embodies the difference between FG and US (Fig. 2 Suppl.).

Based on the PCA scatter plot among different species, the first three principal components explained 65.4% of the variance. The AQY, P_{Nmax}, CE, and LSP had significant positive correlation with the PCA1.The CCP and C_{iast} were relevant to PCA2. CE has something to do with the PCA3. The PCA2 illustrated the difference between *T. sinense* and *P. stenoptera* (Fig. 3 Suppl.).

Based on the PCA scatter plot in different altitudes, the first two principal components explained 82.5% of the variance. The LA and SLA had significant positive correlation with the PCA1, the LSP, AQY, LCP were relevant to PCA2. The difference between low and high altitude was obvious on PCA (Fig. 4 Suppl.).

Discussion

Photosynthesis determines the energy absorption and material accumulation in plants. Generally, plant growth and photosynthetic characteristics differ under different irradiance (Pearcy 1987, Cheng *et al.* 2012). FG is the basic element for maintaining the long-term stability of forest ecosystems and is also the main manifestation of the forest cycle (Zhu *et al.* 2008). The average daily variation in P_N and *E* for *T. sinense* and its associated species in FG and FE showed a bimodal curve, indicating that *T. sinense* showed obvious the so-called "midday break" at midday (Wan *et al.* 2020). The reason may be that the temperature and irradiance were at their maximum at 11:30 h, when *E* was the highest. Generally, there was an optimal temperature for stomatal and leaf traits priming in plants. When the temperature exceeded the optimal temperature, stomatal conductance gradually decreased, leading to a decrease in P_N (Petrik *et al.* 2023). Therefore *T. sinense* and its associated species can adjust their physiological functions (Farquhar and Sharkey 1982, Shi *et al.* 2012) to adapt to high temperature and strong irradiance, which is consistent with the results obtained for *Torreya jackii* (Wang 2013). In the same habitat, a higher P_N of plants reflects a stronger photosynthetic capacity and adaptability of plants to the environment (Zhang and Liu 2008). In FE and US, the average daily variation

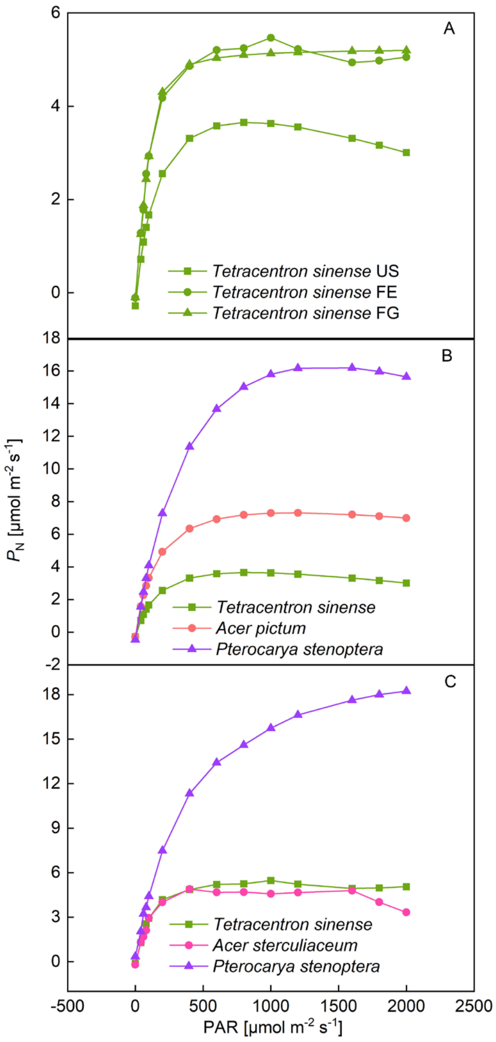

Fig. 4. Light response curves of *T. sinense* and its associated species in habitats. *A* - The light response curves of *Tetracentron sinense* in forest gap (FG), forest edge (FE), understory (US). *B* - The light response curves of *Tetracentron sinense*, *Acer pictum*, and *Pterocarya stenoptera* in understory. *C* - Light response curves of *Tetracentron sinense*, *Pterocarya stenoptera*, and *Acer sterculiaceum* in forest edge.

of P_N and *E* in *P. stenoptera* was greater than that in *T. sinense*, indicating weaker adaptability of *T. sinense* to the irradiance. The SLA value of *T. sinense* in FE and US was also less than that in FG. Kitao *et al.* (2000) showed that change in SLA was one of the main manifestations of plant adaptation to radiation, and a larger SLA may be a way to adapt to low irradiance. For *Daphhniphyllum macropodum*, weak radiation would reduce the chlorophyll content and increase of SLA (Park and Matsumoto 2018). Thus, *T. sinense* can improve its carbon assimilation under

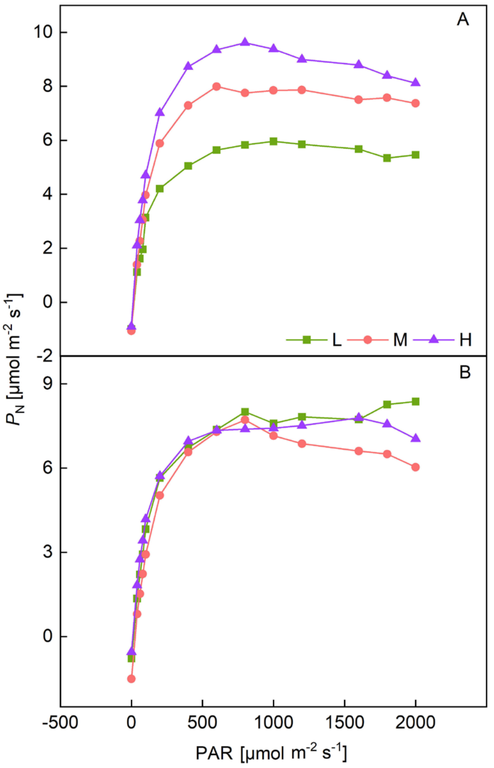

Fig. 5. Comparison of light response curves of YT and MT for *T. sinense* at different altitudes. *A* - The light response curves of YT for *Tetracentron sinense* at low, middle, high altitudes. *B* - The light response curves of MT for *Tetracentron sinense* at low, middle, and high altitudes.

Table 1. Photosynthetic parameters [μmol m^{-2} s^{-1}] from radiation response curves of *T. sinense* and its associated species at different habitats (FG - forest gap, FE - forest edge, US - understory). Means ± SEs, $n = 21$, different lowercase letters mark significant differences ($P < 0.05$). AQY - apparent quantum yield, P_{Nmax} - maximum net photosynthetic rate, LSP - saturation irradiance, LCP - radiation compensation point, R_D - dark respiration rate.

Habitat	Species	AQY	P_{Nmax}	LSP	LCP	R_D	R^2
FG	*Tetracentron sinense*	0.03±0.0034^{b}	6.77±4.60^{ab}	1225.58±372.23^{c}	22.73±5.23^{bc}	0.79±0.24^{ab}	0.9950
FE	*Tetracentron sinense*	0.05±0.0039^{b}	5.34±4.76^{bc}	944.94±399.43^{a}	19.06±4.84^{c}	0.59±0.24^{bc}	0.9943
	Acer sterculiaceum	0.05±0.0042^{b}	4.91±5.42^{bc}	791.82±408.81^{ab}	19.93±4.77^{c}	0.27±0.25^{bc}	0.9727
	Pterocarya stenoptera	0.05±0.0035^{a}	6.47±5.07^{bc}	1637.16±382.34^{c}	31.74±4.75^{a}	0.74±0.20^{ab}	0.9932
US	*Tetracentron sinense*	0.05±0.0033^{b}	3.49±5.10^{c}	540.39±375.31^{b}	23.62±10.23^{abc}	0.47±0.23^{bc}	0.9930
	Acer pictum	0.04±0.0033^{b}	5.76±4.74^{bc}	1687.99±264.79^{c}	22.63±11.09^{abc}	0.61±0.16^{ab}	0.9878
	Pterocarya stenoptera	0.03±0.0021^{ab}	8.25±4.54^{a}	1197.50±256.82^{c}	24.39±13.36^{abc}	0.8±1.27^{ab}	0.9881

Table 2. Photosynthetic parameters [μmol m^{-2} s^{-1}] from radiation response curves of young individuals for *T. sinense* under different altitudes. Means ± SEs, *n* = 9, different lowercase letters mark significant differences ($P < 0.05$). P_{Nmax} - maximum net photosynthetic rate, LSP - saturation irradiance, LCP - radiation compensation point, R_{D} - dark respiration rate, AQY - apparent quantum yield.

Altitude	P_{Nmax}	LSP	LCP	R_{D}	AQY
Low	5.961±1.684^{a}	657.56±12.76^{a}	23.64±0.98^{a}	0.987±0.034^{a}	0.0431±0.0046^{a}
Moderate	7.854±1.783^{b}	736.84±23.67^{b}	25.34±1.08^{b}	1.061±0.056^{a}	0.0532±0.0057^{a}
High	9.626±2.013^{c}	813.24±29.44^{c}	18.63±1.47^{c}	0.940±0.021^{a}	0.0791±0.0072^{b}

Table 3. Photosynthetic parameters [μmol m^{-2} s^{-1}] from radiation response curves of mature individuals for *T. sinense* under different altitudes. Means ± SEs, *n* = 9, different lowercase letters mark significant differences ($P < 0.05$). P_{Nmax} - maximum net photosynthetic rate, LSP - saturation irradiance, LCP - radiation compensation point, R_{D} - dark respiration rate, AQY - apparent quantum yield.

Altitude	P_{Nmax}	LSP	LCP	R_{D}	AQY
Low	7.593±1.231^{a}	824.55±36.44^{a}	27.54±0.44^{a}	0.91±0.043^{a}	0.0704±0.0055^{a}
Moderate	7.711±1.883^{a}	863.26±32.44^{b}	36.17±2.04^{b}	1.28±0.084^{a}	0.0794±0.0035^{a}
High	7.273±1.663^{a}	804.12±43.26^{a}	23.34±1.86^{a}	0.65±0.063^{b}	0.0956±0.0048^{b}

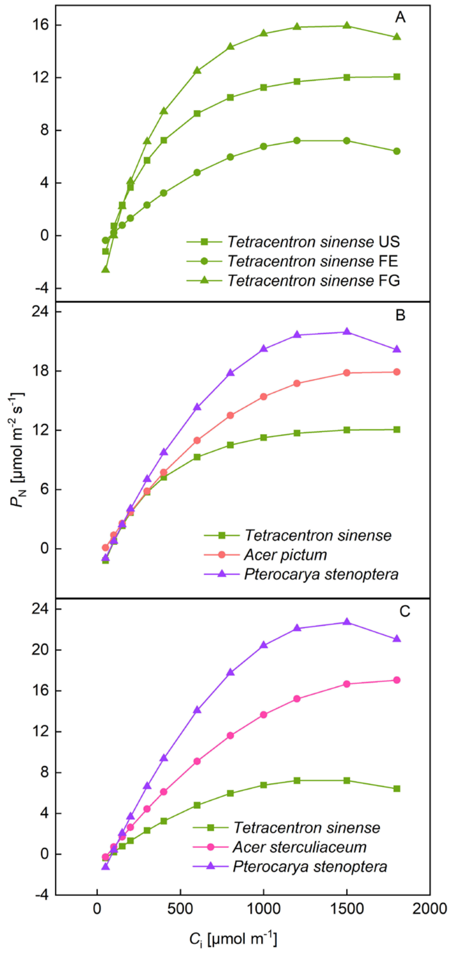

Fig. 6. CO_2 response curves of *T. sinense* and its associated species in different habitats. *A* - The CO_2 response curves of *Tetracentron sinense* in forest gap (FG), forest edge (FE), understory (US). *B* - The CO_2 response curves of *Tetracentron sinense*, *Acer pictum*, and *Pterocarya stenoptera* in understory. *C* - The CO_2 response curves of *Tetracentron sinense*, *Pterocarya stenoptera*, and *Acer sterculiaceum* in forest edge.

a weak radiation by increasing its SLA (Luan 2008), leading to good growth and better regeneration in the FG.

The P_{Nmax} and LSP of *T. sinense* in FG were higher than those in US and FE, indicating that *T. sinense* has the ability to utilize strong irradiance (Lv and Liu 2018) and is suitable for growth in environment with high irradiance (Wang *et al.* 2014). In FE, the LSP and LCP values of *T. sinense* were significantly lower than those of its associated species *P. stenoptera*. In US, the P_{Nmax} and LSP values of *T. sinense* were significantly lower than those of *P. stenoptera*. These results indicate that the photosynthetic capacity of *T. sinense* was significantly lower than that of *P. stenoptera*, leading to lower adaptability to low irradiance, and thus a disadvantage in interspecific competition (Zhang 1999, Zhu *et al.* 2008, Jin *et al.* 2011, Xiong *et al.* 2012).

CO_2 is the basic compound for plant photosynthesis as it is a substrate of ribose 1, 5-diphosphate carboxylase (Cui 2013). Both C_{iast} and R_{p} are important indicators of CO_2 utilization capacity of plants (Lv *et al.* 2016). The carboxylation efficiency (CE) reflects the ability of plants to assimilate CO_2. The lower the CE, the poorer is the ability to assimilate CO_2. The R_{p}, P_{N}, P^{*}_{Nmax}, CCP, and CE values of *T. sinense* in FE were lower than those of *T. sinense* in FG. The results showed that *T. sinense* in FG adapted to a wide range of CO_2 concentrations and had the strongest ability to accumulate photosynthetic products, indicating suitability for growth under high radiation, which is consistent with the results from radiation-response curves.

In FE, the P^{*}_{Nmax} value of *T. sinense* was lower than that of *A. sterculiaceum* and *P. stenoptera*. In US habitat, the C_{iast} of *T. sinense* was lower than that of *A. pictum* and *P. stenoptera*. The results indicate that *T. sinense* had a relatively lower ability for CO_2 utilization and photosynthetic produts accumulation compared to its associated species (Dong *et al.* 2007), which is a disadvantage in interspecific competition.

Altitude is an important ecological factor that affects plant growth and development, material metabolism,

Table 4. The multiple comparison test among different habitats (FG - forest gap, FE - forest edge, US - understory) for parameters from CO_2 response curves of *T. sinense* and its associated species. Means ± SEs, $n = 21$, different lowercase letters mark significant differences ($P < 0.05$). CE - carboxylation efficiency, P^{*}_{Nmax} - maximum net photosynthetic rate, C_{iast} - saturation point of carbon dioxide, CCP - carbon dioxide compensation point, R_p – respiration rate under irradiance.

Habitat	Species	CE [μmol m^{-2} s^{-1}]	P^{*}_{Nmax} [μmol m^{-2} s^{-1}]	C_{iast} [μmol mol^{-1}]	CCP [μmol mol^{-1}]	R_p [μmol m^{-2} s^{-1}]	R^2
FG	*Tetracentron sinense*	0.07 ± 0.01^{a}	15.97 ± 4.30^{bc}	$1\,388.57\pm244.60^{b}$	99.79 ± 20.64^{a}	5.73 ± 1.25^{a}	0.9558
FE	*Tetracentron sinense*	0.01 ± 0.01^{bc}	7.32 ± 4.58^{a}	$1\,348.37\pm251.40^{b}$	69.87 ± 21.21^{bc}	2.97 ± 0.92^{b}	0.9613
	Acer sterculiaceum	0.02 ± 0.01^{bc}	17.06 ± 4.42^{bc}	$1\,356.25\pm277.39^{b}$	63.68 ± 20.46^{bc}	1.31 ± 0.86^{bc}	0.9924
	Pterocarya stenoptera	0.03 ± 0.02^{b}	22.77 ± 4.57^{b}	$1\,429.59\pm282.47^{ab}$	87.19 ± 22.02^{ab}	3.05 ± 0.90^{ab}	0.9627
US	*Tetracentron sinense*	0.03 ± 0.01^{ab}	12.08 ± 3.83^{c}	$1\,106.61\pm300.20^{bc}$	63.66 ± 25.12^{bc}	1.09 ± 0.89^{ab}	0.9559
	Pterocarya stenoptera	0.05 ± 0.01^{ab}	15.08 ± 3.99^{c}	$1\,706.62\pm236.68^{a}$	79.66 ± 18.19^{ab}	3.59 ± 0.96^{ab}	0.9559
	Acer pictum	0.04 ± 0.00^{bc}	11.97 ± 4.00^{bc}	$1\,676.54\pm235.93^{a}$	45.54 ± 15.81^{bc}	1.20 ± 0.15^{bc}	0.9894

Table 5. Leaf morphological characteristics of *T. sinense* under different habitats (FG - forest gap, FE - forest edge, US - understory). Means ± SEs, $n = 9$, different lowercase letters mark significant differences ($P < 0.05$). LL - leaf length, LA - leaf area, LM - leaf mass, SLA - specific leaf area.

Habitat	LL [cm]	LA [cm^2]	LM [g]	SLA [cm^2 g^{-1}]
FG	11.966 ± 0.801^{a}	62.834 ± 5.040^{a}	0.52 ± 0.03^{a}	121.994 ± 11.859^{a}
FE	10.276 ± 0.556^{b}	47.929 ± 4.545^{b}	0.41 ± 0.03^{b}	102.448 ± 5.366^{b}
US	9.612 ± 0.258^{c}	38.778 ± 1.610^{b}	0.30 ± 0.03^{c}	100.911 ± 11.731^{b}

Table 6. Leaf morphological characteristics of young individuals of *T. sinense* at different altitudes. Means ± SEs, $n = 9$, different lowercase letters mark significant differences ($P < 0.05$). LL - leaf length, LW - leaf width, LM - leaf mass, LA - leaf area, SLA - specific leaf area.

Altitude	Stage	LL [cm]	LW [cm]	LM [g]	LA [cm^2]	SLA [cm^2 g^{-1}]
Low	YT	8.97 ± 0.38^{a}	6.03 ± 0.17^{a}	0.34 ± 0.05^{a}	36.73 ± 2.23^{a}	108.35 ± 22.15^{a}
Moderate	YT	11.42 ± 0.27^{b}	5.89 ± 0.08^{b}	0.32 ± 0.05^{a}	45.17 ± 1.78^{b}	155.48 ± 33.56^{b}
High	YT	12.47 ± 0.34^{b}	5.85 ± 0.13^{b}	0.24 ± 0.04^{b}	50.06 ± 2.05^{c}	190.58 ± 26.34^{c}

Table 7. Leaf morphological characteristics of mature individuals of *T. sinense* at different altitudes. Means ± SEs, $n = 9$, different lowercase letters mark significant differences ($P < 0.05$). LL - leaf length, LW - leaf width, LM - leaf mass, LA - leaf area, SLA - specific leaf area.

Altitude	Stage	LL [cm]	LW [cm]	LM [g]	LA [cm^2]	SLA [cm^2 g^{-1}]
Low	MT	9.38 ± 0.27^{a}	6.08 ± 0.16^{a}	0.35 ± 0.04^{a}	41.20 ± 2.08^{a}	119.34 ± 22.58^{a}
Moderate	MT	10.39 ± 0.41^{b}	6.06 ± 0.18^{a}	0.33 ± 0.03^{a}	42.86 ± 1.97^{a}	130.29 ± 12.45^{b}
High	MT	10.49 ± 0.21^{b}	5.97 ± 0.21^{a}	0.30 ± 0.06^{b}	43.45 ± 2.45^{a}	143.40 ± 18.05^{c}

structure, and function (Woodward 1986). For young individuals of *T. sinense* (YT), the photosynthetic parameters, except C_i, varied significantly at different altitudes, indicating the significant effect of altitude on the growth of YT. In case of the mature individuals of *T. sinense* (MT), there was no significant difference in P_{Nmax} at different altitudes. With increasing altitude, the P_{Nmax} and LSP of YT increased, whereas the LCP first increased and then decreased. The results indicate that the ability of YT to use strong radiation gradually increased with the increase of altitude, and its ability to use weak radiation firstly decreased and then increased with the increase of altitude (Osmond *et al.* 1980, Shi *et al.* 2011, Ma *et al.* 2012, Santos *et al.* 2013, Ling *et al.* 2016). The AQY of YT in high altitude was higher than that in low altitude, indicating a higher utilization efficiency of sun radiation at high altitudes. Shi *et al.* (2006) also found that compared with plants at low altitudes, LSP and AQY of plants at high altitudes were higher, the LCP and R_D were lower.

SLA (SLA = 1/LMA) reflects the ability of plants to obtain resources. Plants with low SLA can better adapt to the environment of poor resources and drought, while plants with high SLA have the ability to maintain high concentrations of nutrients within their leaves (Wilson *et al*. 1999). Our results suggested that the SLA of *T. sinense* YT and MT was reduced with the decrease of altitude. Wright *et al.* (2004) and Zhu *et al.* (2010) also observed the same phenomenon in *Ceratoides latens*. In general, increasing SLA appears to be an adaptive response of plant leaf morphology to the low irradiance, a larger leaf area per unit dry mass can enhance the radiation capture ability of plants under low irradiance and improve carbon assimilation (Li and Lin 1986, Lu and Ben 1995, Chen *et al*. 2011). The climate in the study area was humid, especially with sufficient precipitation in the growing season, and the density of clouds and fog gradually increased with the increasing altitude, so the irradiance was low and its duration was rather short at higher altitudes. To adapt to these environmental conditions, the SLA of *T. sinense* gradually increased with increasing altitude. Therefore, considering the limitations of the study area, future studies on the impact of *T. sinense* in different habitats and altitudes maybe be considered in different regions.

Based on the PCA scatter plot in different irradiance, obvious differences between FG and FE or US were illustrated by PCA1 or PCA3. Moreover, P^*_{Nmax}, LSP, or SLA had strong correlations with PCA1 or PCA3, respectively. The results showed that the P^*_{Nmax}, LSP, SLA can be used as important indices reflecting the adaptation of *T. sinense* to different habitats (Aleric and Kirkman 2005, Chen *et al*. 2013, Wang *et al*. 2014). The PCA scatter plot at different species showed obvious differences between *P. stenoptera* and *T. sinense* explained by PCA2, the CCP and C_{iast} had significant positive correlation with PCA2. Hence, the CCP and C_{iast} can be used as important indices to reflect the adaptability of *T. sinense* and its associated species. The altitude PCA indicated significant differences between low and high altitude by PCA1, and the LA and SLA were relevant to PCA1. Therefore, LA and SLA can be used as important indicators reflecting the adaptation of *T. sinense* to different elevations (Wright *et al*. 2004, Poorter *et al*. 2008, Hao *et al*. 2018, Liang *et al*. 2019, Zhang *et al*. 2020b).

Conclusions

The photosynthetic capacity of *T. sinense* were better in FG than that in FE and US. In US and FE, the rather low photosynthetic capacity of *T. sinense* was a disadvantage in the interspecific competition with its associated species. The photosynthetic capacity of YT was most suitable at high altitudes. Moreover, we also found that the P^*_{Nmax}, LSP, and SLA can be used as important indexes reflecting the adaptation of *T. sinense* to different irradiance, the CCP and C_{iast} can be used as important indexes to detect the adaptability difference of *T. sinense* and its associated species, and LA and SLA can be used as important indicators to measure the adaptation of *T. sinense* to different elevations. In order to promote the growth and establishment of *T. sinense*, active artificial intervention should be undertaken to expand area of forest gap for *T. sinense* and transplant *T. sinense* seedlings to higher altitude.

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