Gas exchange and resource utilization in two alpine oaks at different altitudes in the Hengduan Mountains

Shi-Bao Zhang, Zhe-Kun Zhou, Hong Hu, and Kun Xu

Abstract: The evergreen sclerophyllous broadleaf forests composed of alpine oaks in the Hengduan Mountains of southwest China are mainly distributed at altitudes of 1700–4800 m. Gas exchange and related leaf traits of Quercus guyavifolia H. Lev. and Quercus pannosa Hand.-Mazz. were measured at eight sites along an altitudinal gradient to understand their physiological adaptabilities. Both Q. guyavifolia and Q. pannosa showed a significant midday depression in the photosynthesis rate (Pn) due to a high vapor pressure deficit and high temperature around noon. The optimum temperature for photosynthesis for the two oak species ranged from 17 to 23 °C depending on altitude. When the temperature exceeded 25 °C, Pn decreased sharply. However, Ps was not depressed by high irradiance. As altitude increased, the leaf dry mass per unit area of the two oaks increased but the chlorophyll content decreased, while the maximum values of daily mean photosynthesis rate (Pd), maximum photosynthesis rate (Pmax), Pd/Pmax, water-use efficiency, and photosynthetic nitrogen use efficiency occurred at altitudes of 3240–3610 m. Although the photosynthetic capacities of the two oaks were higher in August than in May, altitudinal trends did not change with season. The altitudinal range from 3240 to 3610 m would be optimal for the growth and development of these two alpine oaks in the Hengduan Mountains.

Résumé : Les forêts de feuillus sclérophyllous à feuilles persistantes composées de chênes alpins dans les monts Hengduan du sud-ouest de la Chine se retrouvent surtout à des altitudes variant de 1700 à 4800 m. Les échanges gazeux et les caractéristiques foliaires associées ont été mesurés sur des individus de Quercus guyavifolia H. Lév. et Quercus pannosa Hand.-Mazz. établis sur huit stations le long d’un gradient altitudinal dans le but de comprendre leur capacité d’adaptation physiologique. Une diminution significative du taux de photosynthèse a été observée à mi-journée chez Quercus guyavifolia et Quercus pannosa en raison des forts déficits de pression de vapeur et des températures élevées vers midi. La température optimale pour la photosynthèse des deux espèces de chêne variait de 17 à 23 °C selon l’altitude. Lorsque la température dépassait 25 °C, le taux de photosynthèse diminuait abruptement. Toutefois, les fortes valeurs d’irradiation n’ont pas entraîné de diminution du taux de photosynthèse. La masse foliaire anhydre par unité de surface foliaire des deux chênes augmentait avec l’altitude alors que le contenu en chlorophylle diminuait. Les valeurs maximales du taux journalier moyen de photosynthèse (Pd), du taux maximal de photosynthèse (Pmax), de Pd/Pmax, de l’efficacité d’utilisation de l’eau et de l’efficacité de l’utilisation de l’azote pour la photosynthèse ont été mesurées à des altitudes allant de 3240 à 3610 m. Bien que la capacité photosynthétique des deux chênes ait été plus élevée en août qu’en mai, la tendance observée en fonction de l’altitude ne changeait pas selon la saison. Les stations situées à des altitudes allant de 3240 à 3610 m offraient des conditions optimales pour la croissance et le développement de ces deux chênes alpins dans les monts Hengduan.

Introduction

Every species is limited both geographically and ecologically to a range of habitats. Understanding the patterns and processes governing plant distribution is a central goal of ecology, yet for many species the reasons for distribution limits are unclear (Angert 2006). Altitudinal gradients provide unique experimental opportunities to study the morphological and physiological responses of plants to environments and describe species richness from low to high elevations, because altitudinal changes in environmental factors have important effects on plant distribution and leaf physiology and

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Abbreviations: AQE, apparent quantum efficiency (mol carbon dioxide (CO2)·mol−1 photon); Chl, total chlorophyll content per unit area (mg·dm−2); Ci, intercellular CO2 concentration (μmol·mol−1); δ13C ratio, stable carbon isotope ratio; E, transpiration rate; Jmax, light-saturated rate of electron transport (μmol·m−2·s−1); LMA, leaf dry mass per unit area (g·m−2); LNC, leaf N content (g·m−2); Pn, photosynthesis rate (μmol·m−2·s−1); Ps, daily mean PN (μmol·m−2·s−1); Pmax, light-saturated PN (μmol·m−2·s−1); PNUE, photosynthetic N use efficiency (μmol·s−1·CO2·g−1 N); PPFD, photosynthetic photon flux density (μmol·m−2·s−1); PPN, photosynthetic net carbon assimilation (μmol·m−2·s−1); Tair, air temperature (°C); Tleaf, leaf temperature (°C); Topt, optimum temperature for photosynthesis (°C); Vmax, maximum carboxylation rate by ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco) (μmol·m−2·s−1); WUE, water-use efficiency (μmol CO2·mmol−1·H2O).


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morphology (Hovenden and Brodribb 2000). Species’ altitudinal limits may be partly due to metabolic limitations on growth, because both the morphological and the physiological characteristics of plants enable them to survive or reproduce better in a particular environment. Photosynthetic traits governing carbon acquisition have an integral role in vegetative growth, and thus may affect individual fitness (Angert 2006). A good relationship between $P_N$ and relative growth rate has been observed in seedlings (Pattison et al. 2001; Lajzerowicz et al. 2004), and a correlation between photosynthesis and the percentage of ground covered was found in Chaparral species (Oechel et al. 1981). A large investment in resources leads to a maximum $P_N$. Efficient use of resources is also important for the growth, survival, and competition of plants in changing environments (Hirose and Bazzaz 1998).

The sclerophyllous broadleaf evergreen forests composed of alpine oaks in the Hengduan Mountains of southwestern China are mainly distributed at altitudes of 1700–4800 m, and are considered to effectively conserve water and soil in the upriver regions of China’s major river systems. Usually, sclerophyllous evergreen oaks occur in arid zones of the world, such as the Mediterranean area. However, the oak species belonging to Quercus sect. Heterobalanus are distributed in cold, moist habitats of the Himalayas (Zhou et al. 2003), but retain obvious xerophytic characters, such as dense hairs, a thick cuticle, and low stomatal density (He et al. 1994). The relationships between the altitudinal distribution of alpine oaks and environmental factors in the Hengduan Mountains are of great interest to plant physiologists and ecologists (He et al. 1994; Zhou et al. 2003; Li et al. 2006). In alpine regions, temperature is thought to be one of the primary determinants of species distribution and growth along altitudinal gradients (Cabrera et al. 1998; Lajzerowicz et al. 2004). Several authors have suggested that alpine oaks adapt to low temperature because of their xerophytic characters, and an altitudinal range from 2400 to 3600 m is their optimum distribution zone (He et al. 1994; Zhou et al. 2003). However, physiological evidence for this hypothesis is lacking. A previous study showed that an altitude near 2800 m could be optimal for growth and development of Quercus aquifolioides Rehder & E.H. Wilson, and that specific leaf area and stomatal length increased with increasing altitude below 2800 m, but exhibited a converse tendency above 2800 m (Li et al. 2006). Zhang et al. (2005) found that the photosynthetic capacity of Quercus pannosa Hand.-Mazz. decreased from 3240 to 4170 m in the Hengduan Mountains. However, the photosynthetic capacity of this oak below 3240 m was not investigated.

To gain further understanding of altitudinal trends in the morphology and physiology of alpine oaks in the Hengduan Mountains, leaf gas exchange and resource-use efficiency in Quercus guyavifolia H. Lév. and Q. pannosa were investigated at eight sites along an altitudinal gradient. The aims were to determine altitudinal variations in photosynthetic capacity and resource-use efficiency in alpine oaks, and to understand the relationship between their ecophysiological adaptability and geographical distribution. It was hypothesized that the two alpine oak species have greater photosynthetic capacities and resource-use efficiencies in the middle part of altitudinal range than at lower and higher altitudes because the environment is more favorable for their growth and development.

### Materials and methods

#### Field sites and species

The study was carried out at eight sites in the Hengduan Mountains. The locations and $T_a$ of the sites are given in Table 1. The climate is continental, with cold winters and hot, moist summers. Because no long-term climatic data from the sampling sites are available, the $T_a$ values listed in Table 1 were calculated from the decrease in $T_a$ with altitude (7.1 °C / 1000 m) in this region (Zhang 1998). May to October is the rainy season (87% of annual rainfall from 1959 to 2000), while November to April is the dry season. The soil type at all sites was brown soil with similar fertility levels and pH 7.5–8.5.

**Quercus guyavifolia** is an endemic tree that occurs at altitudes between 2500 and 4000 m above sea level, while **Q. pannosa** is distributed at altitudes ranging from 2600 to

### Table 1. Locations and air temperatures of eight experimental sites where Quercus guyavifolia and Quercus pannosa were studied.

<table>
<thead>
<tr>
<th>Altitude (m)</th>
<th>Longitude (E)</th>
<th>Latitude (N)</th>
<th>Temp. (°C)</th>
<th>Tree density (no./ha)</th>
<th>Upper canopy</th>
<th>Midcanopy</th>
<th>Understory</th>
</tr>
</thead>
<tbody>
<tr>
<td>2720</td>
<td>99°26.69’</td>
<td>28°07.57’</td>
<td>9.6</td>
<td>475</td>
<td>Q. guyavifolia, Pinus armandi</td>
<td>Q. guyavifolia</td>
<td>Sabina squamata, Campylotropis polyantha</td>
</tr>
<tr>
<td>3180</td>
<td>99°34.90’</td>
<td>27°57.99’</td>
<td>5.8</td>
<td>673</td>
<td>Q. guyavifolia, Q. longisipica, Picea likiangensis</td>
<td>Q. longisipica</td>
<td>Salix delavayana, Contoneaster franchetii</td>
</tr>
<tr>
<td>3560</td>
<td>99°36.81’</td>
<td>27°56.03’</td>
<td>2.8</td>
<td>704</td>
<td>Q. guyavifolia, Picea likiangensis, Rhododendron racemosum, Viburnum cylindricum</td>
<td>Q. guyavifolia</td>
<td>Deutzia longifolia, Rhododendron euryphilum</td>
</tr>
<tr>
<td>3920</td>
<td>99°39.77’</td>
<td>27°53.01’</td>
<td>1.6</td>
<td>598</td>
<td>Q. guyavifolia, Picea likiangensis, Deutzia longifolia, Rhododendron euryphilum</td>
<td>Q. guyavifolia</td>
<td>Prunus conduradnae, Lonicera chlamydata, Ribes glanduliferum</td>
</tr>
<tr>
<td>2870</td>
<td>99°43.80’</td>
<td>28°09.23’</td>
<td>8.1</td>
<td>627</td>
<td>Q. pannosa, Sorbus pallescens</td>
<td>Q. pannosa, Acer robusta</td>
<td>Prunus cerasoides, Lonicera chlamydata, Ribes glanduliferum</td>
</tr>
<tr>
<td>3240</td>
<td>99°38.80’</td>
<td>27°46.10’</td>
<td>5.4</td>
<td>736</td>
<td>Q. pannosa, Sorbus pallescens</td>
<td>Q. pannosa, Acer robusta</td>
<td>Prunus cerasoides, Lonicera chlamydata, Ribes glanduliferum</td>
</tr>
<tr>
<td>3650</td>
<td>99°42.46’</td>
<td>28°00.15’</td>
<td>5.5</td>
<td>693</td>
<td>Q. pannosa, Sorbus rupestris</td>
<td>Q. pannosa, P. likiangensis</td>
<td>Prunus cerasoides, Lonicera chlamydata, Ribes glanduliferum</td>
</tr>
<tr>
<td>4170</td>
<td>99°49.75’</td>
<td>28°32.57’</td>
<td>-0.2</td>
<td>568</td>
<td>Q. pannosa, P. likiangensis</td>
<td>Q. pannosa, P. likiangensis</td>
<td>Prunus cerasoides, Lonicera chlamydata, Ribes glanduliferum</td>
</tr>
</tbody>
</table>

**Note:** Air temperatures were calculated according to the altitudinal lapse rate of 7.1 °C / 1000 m.

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4300 m. Both are important components of the sclerophyllous broadleaf evergreen forests in the southwest of China.

**Photosynthesis measurements**

Diurnal variations in gas exchange were measured on three mature, fully expanded leaves from sun-exposed, upper canopies (3–4 m high) of trees sampled at the eight sites at approximately 1 h intervals from 08:00 to 19:00 on the clear days in May 2004. All leaves were carefully selected from branches of the same age to avoid differences in photosynthetic capacity associated with leaf age. $P_N$, $E$, stomatal conductance, and $C_i$ were measured using a portable infrared gas exchange system with a PLC-B leaf chamber (CIRAS-1, PP Systems, Hitchin, UK) in an open-system configuration. Meanwhile, a data logger (Li-1400, Li-Cor, Lincoln, Nebraska) was used to record irradiance (PPFD), $T_a$, and relative air humidity hourly. $T_a$ and relative humidity were used to calculate VPD. WUE was calculated as the ratio between $P_N$ and $E$.

The photosynthetic response curves to CO$_2$ and light plus temperature were measured two times in May and August 2004, respectively. These measurements were also made on mature, fully expanded leaves from the upper canopy. Sampled leaves were allowed to acclimate to a PPFD of 1200 $\mu$mol-m$^{-2}$-s$^{-1}$ about 15 min before measurements. Photosynthetic responses to PPFD were measured on three fully expanded and sun-exposed leaves at 14 light intensities using a CIRAS-1 infrared gas analyzer. $T_i$ was adjusted to 20 °C using the internal heating/cooling system built into the CIRAS-1. After the initial measurement at 0 $\mu$mol-m$^{-2}$-s$^{-1}$, PPFD was increased to produce the subsequent light intensities. Following a 5–6 min equilibration period at each light intensity, $P_N$ was recorded when stomatal conductance and CO$_2$ uptake stabilized. Data were fit by a nonrectangular hyperbola (Prioul and Chartier 1977). Using this function, AQE and $P_{\text{max}}$ were estimated by means of Photosyn Assistant® software (version 1.1, Dundee Scientific, Dundee, UK).
Fig. 2. Photosynthesis rates ($P_N$) for *Quercus guyavifolia* and *Quercus pannosa* at different altitudes depending on temperature. Vertical bars indicate the error of the mean for three measurements.

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Fig. 3. Photosynthetic responses of *Quercus guyavifolia* and *Quercus pannosa* to photosynthetic photon flux density (PPFD). Vertical bars indicate the error of the mean for three measurements.
Fig. 4. Effects of vapor pressure deficit (VPD) on photosynthesis rate ($P_N$) for Quercus guyavifolia and Quercus pannosa. Vertical bars indicate the errors of the mean for three measurements ($Q. \text{guyavifolia}: P_N = 5.286 + 1.390 \text{VPD} - 0.640 \text{VPD}^2, n = 48, R^2 = 0.336, P < 0.001; Q. \text{pannosa}: P_N = 5.845 - 1.159 \text{VPD} - 0.292 \text{VPD}^2, n = 48, R^2 = 0.367, P < 0.001$).

Following $P_N$–PPFD curves, the CO$_2$ responses of photosynthesis were determined using a range of CO$_2$ concentrations at a PPFD of 1200 µmol·m$^{-2}$·s$^{-1}$ and 20°C. Preliminary measurements showed that the $P_N$ values for the two alpine oak species were light-saturated at an intensity of 1200 µmol·m$^{-2}$·s$^{-1}$. CO$_2$ was injected into the circuit using the injection system built into the gas analyzer. After the initial measurements at 2000 µmol·mol$^{-1}$, the CO$_2$ concentration was reduced to produce other levels at which $P_N$ was recorded. Using $P_N$–C$_i$ curves, $V_{\text{max}}$ and $J_{\text{max}}$ were calculated using Photosyn Assistant® software according to the biochemical model of von Caemmerer and Farquhar (1981).

The dependence of photosynthesis on temperature was examined on fully mature leaves in the morning between 0800 and 1100. $T_1$ was adjusted using the internal heating and cooling system. During measurements, the CO$_2$ concentration in the chamber was kept at 350 µmol·mol$^{-1}$ and PPFD at 1200 µmol·m$^{-2}$·s$^{-1}$. The measurements started at 10°C and increased by 1°C increments up to 35°C. A second-order polynomial equation was used to fit $T_{\text{opt}}$.

Measurement of LMA
Following the determination of photosynthetic responses, 100 leaves were harvested from the sampled trees at each site and divided into 10 groups. In the laboratory, leaf areas were measured using a leaf-area meter (LI-3000A, Li-Cor). Dry mass was determined after oven-drying for 48 h at 70°C. LMA was calculated in grams per square metre.

Nitrogen analysis
After LMA was measured, the same leaves were analyzed for LNC using a N analyzer (Leco Corporation, St. Joseph, Michigan). PNUE was calculated as the ratio of $P_{\text{max}}$ to LNC.

Determination of chlorophyll content
Chlorophyll was extracted from leaf disks from sampled trees with N,N-dimethylformamide. Chlorophyll contents were analyzed with a spectrophotometer (UV-2550, Shimadzu, Japan) and calculated using the method of Inskell and Bloom (1985). Three replicates were made for each measurement.

Stable carbon isotope analysis
The relationship between $\delta^{13}$C ratio and WUE has led to the widespread use of isotopic analysis in plant physiological ecology. In the present study, the sun-exposed leaves were harvested from the upper part of sampled trees for $\delta^{13}$C analysis. The $\delta^{13}$C ratio of leaf tissues was determined using a mass spectrometer (Finnigan MAT 253, Gainesville, Florida). The $\delta^{13}$C ratio is expressed in delta notation: $\delta^{13}$C (%) compared with a standard (Pee Dee Belemnite). The precision of the analysis was ±0.3‰.

Statistical analysis
Statistical analysis was performed using SPSS® Version 10.0 (SPSS Inc., Chicago, Illinois). Normality of distribution and homogeneity of variance were checked prior to any further statistical analyses by a one-sample Kolmogorov–Smirnov test. Following standard statistical protocols, differences in leaf morphological and physiological variables among sites were determined using one-way analysis of variance (ANOVA) and a LSD test for multiple comparisons, and between May and August by an independent-samples t test. The relationships between photosynthetic parameters and leaf traits were addressed using regression analysis.

Results
At eight sites, maximum PPFD, $T_a$, and VPD were observed at midday (Fig. 1). There was no statistical difference in average daily PPFD among altitudes ($F_{[7,22]} = 0.602, p = 0.754$). However, both $T_a$ ($F_{[7,22]} = 8.466, p = 0.000$) and VPD ($F_{[7,22]} = 4.434, p = 0.000$) decreased as altitude increased.

Across all study sites, the two oaks showed a significantly midday depression in photosynthesis each day (Fig. 1). The average $P_N$ values for the three leaves sampled at different altitudes peaked rapidly after dawn before subsiding during the middle of the day. Values reached a maximum at about 10:00–11:00, increased gradually again after 14:00, and reached a second peak in the late afternoon. The diurnal var-
Temperature had an important influence on photosynthesis in the two oaks at all sites. $T_{\text{opt}}$ for both species decreased as altitude increased (Fig. 2). The two oaks were able to attain higher $P_N$ values between 17 and 23 °C. At all sites, net photosynthesis decreased sharply when $T_1$ was above 25 °C. There was no significant variation in $T_{\text{opt}}$ among species ($t = 0.102, p = 0.919$) or between values in May and August ($t = 2.038, p = 0.054$).

$P_N$ values were light-saturated at a PPFD of 900–1050 μmol·m$^{-2}$·s$^{-1}$ for $Q.$ guyavifolia and at 840–990 μmol·m$^{-2}$·s$^{-1}$ for $Q.$ pannosa (Fig. 3). The light-saturated PPFD (at which 95% of $P_{\text{max}}$ is achieved) was higher for $Q.$ guyavifolia than for $Q.$ pannosa ($t = 2.833, p = 0.001$), but there was no significant difference in photosynthetic light-saturated PPFD among sites ($Q.$ guyavifolia: $F_{[3,10]} = 2.752, p = 0.0012; Q.$ pannosa: $F_{[3,10]} = 1.462, p = 0.296$) or between May and August ($t = 0.332, p = 0.743$).

The relationship between VPD and $P_N$ was analyzed using measurements of diurnal variation (Fig. 4). VPD had an important effect on photosynthesis in the two oaks ($Q.$ guyavifolia: $R^2 = 0.336, p < 0.0001; Q.$ pannosa: $R^2 = 0.367, p < 0.0001$). A high VPD significantly reduced $P_N$. Chl values for the two oaks decreased with increasing altitude, while LMA increased. Although LNC values for the two oaks were higher at lower and higher altitudes, there was no significant difference among species ($t = 0.088, p = 0.930$) and between May and August ($t = 2.338, p = 0.029$).

Discussion

In the Hengduan Mountains, both $Q.$ guyavifolia and $Q.$ pannosa experienced a pronounced midday depression in photosynthesis ($P_N$), which was similar to the responses of sclerophyllous Mediterranean oaks ($Quercus suber$) (Tenhunen et al. 1984). Although the diurnal variation in photosynthesis exhibited an inverse relationship to that of PPFD, $T_1$, and VPD, the two alpine oaks could withstand a high PPFD without photosynthesis decreasing substantially, provided the temperature was favorable. On the other hand, when $T_1$ went above 25 °C, which typically occurred from 1100 to 1400, photosynthesis in the two oaks decreased sharply. A high $T_1$ resulted in the increase in VPD ($R^2 = 0.845, p = 0.000$), and therefore reduced stomatal conductance (Iio et al. 2004) and CO$_2$ supply from the atmosphere to the intercellular spaces. Photosynthesis would also be inactivated by high $T_1$ at midday (Berry and Björkman 1980). This experiment provided evidence of the important role of high $T_1$ and high VPD on photosynthetic depression in the two oaks at midday (Fig. 4).

Despite many studies on altitudinal trends in photosynthesis and leaf traits, there was no clear consensus. Most studies in the literature have reported that photosynthetic capacity and carboxylation efficiency decreased with increasing altitude (Cabrera et al. 1998; Rada et al. 1998). It has been considered that the lower $P_N$ values at higher altitude are caused by significantly thicker leaf pubescence and lower stomatal conductance, photosynthetic-pigment content, and leaf N content (Cabrera et al. 1998; Rada et al. 1998). However, in many studies it has been reported that photosynthetic capacity increased with altitude (Woodward 1986; Körner and Diemer 1987). These results could be explained by the increase in carboxylation efficiency, leaf N content, chlorophyll content, and stomatal conductance with altitude (Körner and Diemer 1987; Friend et al. 1989). This discrepancy would be due to the differences in equipment, plant material, environmental conditions, and altitudinal range (Rada et al. 1998).

The present study showed that individuals of the two oak

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Table 2. Results of statistical analysis of photosynthetic variables and related leaf traits in $Quercus guyavifolia$ and $Quercus pannosa$ at different altitudes.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Site</th>
<th>Season</th>
<th>Site</th>
<th>Season</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>$P_{\text{max}}$</td>
<td>12.323</td>
<td>0.002</td>
<td>2.572</td>
<td>0.017</td>
<td>4.300</td>
</tr>
<tr>
<td>AQE</td>
<td>8.761</td>
<td>0.007</td>
<td>2.950</td>
<td>0.007</td>
<td>8.454</td>
</tr>
<tr>
<td>$V_{\text{cmax}}$</td>
<td>7.920</td>
<td>0.009</td>
<td>1.386</td>
<td>0.180</td>
<td>8.682</td>
</tr>
<tr>
<td>$J_{\text{max}}$</td>
<td>8.341</td>
<td>0.008</td>
<td>3.980</td>
<td>0.001</td>
<td>6.083</td>
</tr>
<tr>
<td>LNC</td>
<td>0.747</td>
<td>0.554</td>
<td>0.929</td>
<td>0.363</td>
<td>1.771</td>
</tr>
<tr>
<td>PNUE</td>
<td>4.296</td>
<td>0.044</td>
<td>2.338</td>
<td>0.029</td>
<td>5.294</td>
</tr>
<tr>
<td>Chl</td>
<td>22.316</td>
<td>0.000</td>
<td>2.304</td>
<td>0.031</td>
<td>38.958</td>
</tr>
<tr>
<td>LMA</td>
<td>5.514</td>
<td>0.024</td>
<td>1.198</td>
<td>0.244</td>
<td>2.819</td>
</tr>
<tr>
<td>$\delta^{13}$C ratio</td>
<td>15.250</td>
<td>0.001</td>
<td>—</td>
<td>—</td>
<td>5.586</td>
</tr>
<tr>
<td>WUE</td>
<td>10.750</td>
<td>0.004</td>
<td>—</td>
<td>—</td>
<td>5.174</td>
</tr>
</tbody>
</table>

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species growing in the middle of their altitudinal range displayed greater photosynthetic capacity ($P_{\text{max}}$) than those growing at the upper and lower ends of the altitudinal range. Angert (2006) suggested that two *Mimulus* species attained the greatest aboveground biomass and $P_N$ values when grown at a temperature characteristic of the middle of their altitudinal range. The highest $P_{\text{max}}$ values for *Pinus sylvestris* were found in the middle of the distribution area, and $P_{\text{max}}$ decreased towards both ends of the transect (Luoma 1997). Although the altitudinal difference in photosynthesis could have been caused by differences in photosynthetic-pigment content, chlorophyll content was not correlated with the $P_{\text{max}}$ values for the two alpine oaks ($r^2 = 0.049$, $p = 0.131$).

Most studies have shown that LNC increases with altitude (Friend et al. 1989; Cordell et al. 1999). For the two oaks, LNC was higher in the middle of the altitudinal range than at other sites, but there was no significant difference among altitudes. However, PNUE values in the middle of the altitudinal range were higher than at higher and lower altitudes. LNC was significantly correlated with $P_{\text{max}}$ ($R^2 = 0.587$, $p = 0.000$). This has been confirmed by many studies (Evans 1989; Cordell et al. 1999; Hikosaka et al. 2002). The strong relationship was due to the large proportion of leaf N present in the photosynthetic apparatus.

Photosynthesis depends partly on leaf metabolic capacity, which can be partitioned into the activity of the enzyme ribulose-1,5-bisphosphate (RuBP) carboxylase–oxygenase.
In the Hengduan Mountains, the photosynthetic capacities and WUE values of the two oaks were similar to those of Mediterranean oaks (Mediavilla et al. 2001). The LMA values of the two alpine oaks were higher than those of Mediterranean oaks (203–253 versus 86–242 g m\(^{-2}\)) (Damesin et al. 1997; Mediavilla et al. 2001) and similar to that of Quercus semecarpifolia from the Himalayas (Delillis et al. 2004). Lower temperatures could have reduced leaf extension in the alpine oaks in the Hengduan Mountains, resulting in thicker leaves (Kao and Chang 2001).

Temperature determines the altitudinal distribution of trees in at least two ways: it reduces survival through freezing or by a negative carbon balance through a lower \( P_N \) (Cavieres et al. 2000). Diminished growth at low temperatures in subalpine forests was associated with less photosynthesis (Lajzerowicz et al. 2004). Usually, sclerophyllous oaks were distributed in xerothermic regions, but Q. guyavifolia occurred in the relatively cold, moist habitats in the Hengduan Mountains. \( T_{opt} \) values for the two alpine oaks were significantly lower than that for the Mediterranean sclerophyllous oak (18–23 versus 25–30 °C) (Gratani et al. 2000). Sakai (1981) reported that Q. semecarpifolia could resist temperatures down to –15 °C.

The species richness of sclerophyllous oaks in the Hengduan Mountains peaked in the altitudinal range from 2400 and 3600 m (Fig. 6). Li et al. (2006) further confirmed that an altitude near 2800 m could be the optimum zone for growth and development of Q. aquifoloides. This species had higher genetic variability at altitudes between 2400 and 3300 m (Li et al. 1998). In this study, individuals of the two oak species in the middle of the altitudinal range (3240–3610 m) exhibited greater photosynthetic capacity and resource-use efficiency. The degree to which plants adapt to their environment can affect their utilization of environmental resources. Efficient use of resources could lead to maximum \( P_{N} \). Photosynthetic capacity would affect competition and survival of species (Nagel and Griffin 2004). The unfavorable environments at lower or higher altitudes would limit carbon assimilation, growth, and competition by plants (Zu et al. 1998), while a high \( P_{N} \) achieved by maximizing the biochemical capacity for photosynthesis could contribute to the success of certain genotypes under stressful conditions (Wu and Campbell 2006). These results indicate that the two alpine oaks were able to fulfill their photosynthetic and competitive potential at altitudes of 3240–3610 m. This is also confirmed by the \( P_{g}/P_{max} \) ratio, which expresses the effect of the currently prevailing environment on photosynthesis.

In conclusion, altitude has a major effect on LMA and the physiology of the two oak species studied. LMA increased with altitude, while chlorophyll content decreased. \( P_{max} \), PNU, and WUE values were highest in the middle of their altitudinal ranges and decreased towards both ends of their altitudinal ranges. The altitudinal trend in photosynthesis was linked to biochemical efficiency and LNC. Altitudes from 3240 to 3610 m would be optimal for the growth and development of these two oak species.

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