热带亚热带植物学报　2008,16(3):205 ~211
*Journal of Tropical and Subtropical Botany*

# 广西猫儿山中山森林共生的常绿和落叶阔叶树光合特性的季节变化

廖德宝[1]，　白坤栋[2*]，　曹坤芳[2]，　蒋得斌[1]
(1. 广西猫儿山国家级自然保护区管理局，广西桂林 541316；2. 中国科学院西双版纳热带植物园昆明分部，昆明 650223)

**摘要**：研究分析了广西猫儿山中山森林中 3 种落叶阔叶树(亮叶水青冈 *Fagus lucida*;青榨槭 *Acer davidii* ;缺萼枫香 *Liquidambar acalycina*)和 4 种常绿阔叶树(铁椎栲 *Castanopsis lamontii*;曼青冈 *Cyclobalanopsis oxyodon*;桂南木莲 *Manglietia chingii*;银木荷 *Schima argentea*)光合特性的季节性变化。除青榨槭外,在雨季饱和光照下,落叶树与常绿树的最大净光合速率($P_{max}$)差异不明显,而落叶树的最大气孔导度($G_{max}$)要比常绿树高;在旱季,落叶树的 $P_{max}$ 和 $G_{max}$ 下降幅度远大于常绿树,这伴随前者暗呼吸速率和光补偿点的大幅提高。常绿树和落叶树的表观量子效率(AQY)和凌晨光系统 II 潜在最大光化学效率($F_v/F_{m\text{-}predawn}$)在雨季差异不明显;在旱季,落叶树的 AQY 和$F_v/F_{m\text{-}predawn}$小于常绿树,说明前者遭受较严重的光抑制。此外,光合速率与气孔导度呈显著直线相关,但常绿树的直线斜率要比落叶树大,说明前者光合水分利用效率较高,这有利于常绿植物在干旱和低温条件下生存。光合速率与电子传递速率和温度也呈显著直线相关,但常绿树的直线斜率都小于落叶树,这说明常绿植物可以调节电子传递速率的变化来适应温度的宽幅的季节性变化。总之,落叶阔叶树需要相对较高的温度和水分供应才能满足光合作用的需要,而在干旱和低温条件下,落叶阔叶树尽管可以通过气孔和光系统 II 的调节来适应环境的变化,但还是无法避免严重的光抑制从而导致叶片脱落;与之相反,常绿植物却可以通过气孔调节提高水分利用效率和通过电子分配耗散多余能量来适应干旱和低温的胁迫而使叶片维持四季常绿。

**关键词**：广西；猫儿山；落叶阔叶树；常绿阔叶树；光合作用；低温效应；光抑制
**中图分类号**:Q945.11　　**文献标识码**:A　　**文章编号**:1005-3395(2008)03-0205-07

# Seasonal Changes in Photosynthetic Traits of the Co-occurring Evergreen and Deciduous Broad-leaved Species in a Montane Forest of Mao'er Mountain, Guangxi

LIAO De-bao[1],　BAI Kun-dong[2*],　CAO Kun-fang[2],　JIANG De-bing[1]
(1. *Bureau of Guangxi Mao'er Mountain Nature Reserve*, Guilin 5413162, China;
2. *Kunming Division, Xishuangbanna Tropical Botanical Garden, the Chinese Academy of Sciences*, Kunming 650223, China)

**Abstract**: The Seasonal changes in photosynthetic characteristics of three deciduous broad-leaved species (*Fagus lucida*, *Acer davidii*, and *Liquidambar acalycina*) and four evergreen broad-leaved species (*Castanopsis lamontii*, *Cyclobalanopsis oxyodon*, *Manglietia chingii*, and *Schima argentea*) in Guangxi Mao'er Mountain were studied. Except of *Acer davidii*, there was not significant difference in maximum photosynthetic rate at saturating light ($P_{max}$) between the deciduous and evergreen species, but maximum stomatal conductance at saturating light ($G_{max}$) was higher in the deciduous species than the evergreen species in rainy season. However, in dry season, the decreases of $P_{max}$ and $G_{max}$ were greater in the deciduous species than the evergreen species, as accompanied by

**收稿日期**:2007-06-18　　**接受日期**:2007-12-10
**基金项目**：国家自然科学基金项目(30670320)资助
* 通讯作者 Corresponding author

the larger increases in dark respiration rate and light compensation point in the former. The deciduous and evergreen species had slight difference in apparent quantum yield (*AQY*) and predawn maximum photochemical efficiency of photosystem II ($F_v/F_{m\text{-predawn}}$) in rainy season. However, in dry season, the deciduous species showed lower *AQY* and $F_v/F_{m\text{-predawn}}$ than the evergreen species, suggesting that the deciduous species suffered greater photoinhibition. Furthermore, there was a significant linear relationship between *P* and *G*, and the evergreen species showed lower slope, indicating that the evergreen species had higher photosynthetic water use efficiency and this would help them to survive in dry and cold conditions. Also, the significant linear correlations of *P* with electron transport rate and leaf temperature were observed in both the deciduous and evergreen species, and the evergreen species exhibited lower slope; this indicates that the evergreen species could adjust the electron transport rate through alternative electron pathways to adapt to the wide range of seasonal temperatures. In conclusion, the results obtained here suggest that the deciduous species required relatively higher temperature and water supply than the evergreen species to meet the needs of photosynthesis; under dry and cold situations, it's therefore unavoidable for them to suffer greater photoinhibition and shed their leaves finally, although the coordinated adjustments in stomata and photosystem II occurred in them. By contrast, the evergreen species could adapt to dry and cold stresses and maintain green leaves by promoting photosynthetic water use efficiency through stomatal control and dissipating excessive light energy via electron allocation.

**Key words**: Guangxi; Mao'er Mountain; Deciduous broad-leaved species; Evergreen broad-leaved species; Photosynthesis; Photoinhition; Low temperature effects

在热带有季节性干旱的森林中和我国东部亚热带中山地带阔叶混交林中,共存着常绿和落叶阔叶树[1–2]。这两类树种一个鲜明的对比性特征是落叶阔叶树的叶片在秋季枯黄脱落,叶片寿命较短,而常绿阔叶树却能保留叶片越冬,叶片寿命较长[3–4]。据报道:与常绿植物相比,在光温条件适宜情况下,落叶植物具有较高的光合速率[5]。然而,落叶植物对干旱以及冬季低温等自然胁迫环境采取了一种极端适宜策略—落叶[6]。常绿植物保留叶片越冬,从而在冬季低温条件下可能遭受严重的光抑制和光氧化损伤[7]。但是,在早春和晚秋季节,常绿阔叶树可能保持相当高光合速率,增加碳积累。研究表明,落叶植物的光合作用对季节性大气温度变化响应比较敏感,而常绿植物相对不敏感[8]。

常绿植物在相对无明显季节性变化、养分贫瘠或者生长季节短而且冬季温度低的北方寒温带地区和热带亚热带高山和亚高山地区占优势,而落叶植物在干旱或季节性变化明显的环境中占优势[9–11]。位于中国中亚热带的广西猫儿山在海拔1 300～1 800 m处的中山暖温带气候条件下分布着水青冈(*Fagus*)占优势的落叶阔叶树林带,伴生的常绿阔叶树有壳斗科(Fagaceae)的曼青冈(*Cyclobalanopsis oxyodon*)和铁椎栲(*Castanopsis lamontii*)、樟科的华东润楠(*Machilus leptophylla*)和木兰科的桂南木莲(*Manglietia chingii*)等[12–13]。

猫儿山属中亚热带山地气候,四季分明,并且有一个明显的旱季和干冷季。本研究以猫儿山中山暖温带气候下生长的常绿和落叶阔叶树为研究对象,分析常绿和落叶阔叶树光合生理的季节性变化特征,以探讨常绿和落叶阔叶树光合能力适应外界季节性环境变化的差异;试图分析在猫儿山中山地带暖温带气候条件下落叶阔叶树占优势,常绿阔叶树不占优势的可能的光合生理原因。本研究将为估测我国中亚热带中山森林对大气$CO_2$的固定以及预测这类森林对全球气候变暖的响应提供重要科学依据。

## 1 研究区域概况

猫儿山位于广西的东北部,地理坐标为25°48′～25°58′ N,110°20′～110°35′ E。最高峰海拔2 141.5 m,相对高差1 862 m,系华南第一高峰,亦是南岭山脉越城岭的主峰。猫儿山属中亚热带山地气候,山顶的年均温7℃,山脚年均温16～18℃,大于10℃的年积温为6 000℃左右。年降水量在2 100 mm以上,每年的2～6月为雨季。猫儿山的降雨和温度有明显的季节性变化(图1)。5月降雨量最大,8月以后降雨量急剧下降,11月降雨

量最小,此后降雨量逐渐增加;7 月温度最高,2 月温度最低。成土母质为花冈岩[14]。猫儿山林区是我国中亚热带保存较好并有一定代表性的天然林区,地带性植被类型为常绿阔叶林。植被的垂直分布较明显,从山脚到山顶,依次出现的植被类型为常绿阔叶林和常绿针阔叶人工林、常绿落叶阔叶混交林、常绿针阔叶混交林、山顶矮林和山顶灌草丛[15]。

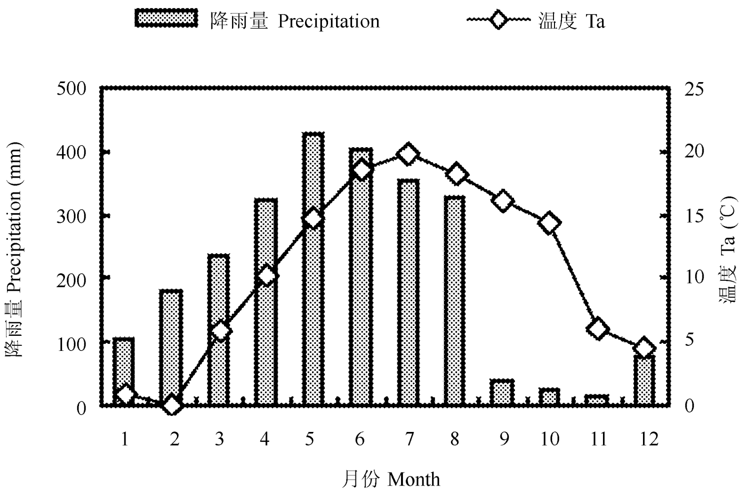


图 1　1991 ~ 2005 年猫儿山的月均降雨量和月均温。
Fig. 1 Mean monthly precipitation and air temperature from 1991 to 2005 in Mao’er Mountain Nature Reserve, Guangxi
气象数据在海拔 1 200 m 处采集 Data were recorded by the Weather Station at 1200 m.

# 2 材料和方法

## 2.1 研究地点和样树选择

本研究在位于猫儿山南坡中山地带水青冈混交林中进行,主要的落叶阔叶树优势树种有壳斗科(Fagaceae)的亮叶水青冈(*Fagus lucida*)和长柄水青冈(*Fagus longipetiolata*)、槭树科的青榨槭(*Acer davidii*)、金缕梅科的缺萼枫香(*Liquidambar acalycina*);伴生的常绿阔叶树有壳斗科的曼青冈和铁锥栲、樟科的华东润楠和木兰科的桂南木莲等[13]。我们选择的样地在海拔 1 500 m 处,选择的树种是落叶的亮叶水青冈、青榨槭和缺萼枫香以及常绿的铁椎栲、曼青冈、桂南木莲和银木荷(*Schima argentea*)。

## 2.2 光合作用和荧光参数测定

参考 Morecroft 和 Roberts[16] 的方法,每树种在全光下选择 5 ~ 7 株已能开花结果的成熟植株(高约 3 ~ 7 m)做好标记。在雨季(5 月上旬)、旱季(9 月中旬)和干冷季(12 月中旬)的晴天,用便携式光合作用测定仪(Licor-6400, USA)测定它们冠层阳生枝条最近成熟叶片(尽量减少不同季节叶龄的差异)的光合作用日进程,同时用 FMS2 型脉冲调制荧光仪(Hansatech, UK)测定叶绿素荧光参数的日变化,测定的荧光参数为 $F_v/F_m$(光系统 II 潜在的最大光化学效率)和 ETR(电子传递速率);另外,用 Licor-6400 的自带光源(6400-02B)测定冠层叶片的光-光合作用响应曲线。

## 2.3 数据分析与统计

根据 Peek 等[17] 的方法,光-光合作用响应曲线通过非线性关系模拟,并进而计算最大净光合速率($P_{max}$)、表观量子效率(AQY)、饱和光下的气孔导度($G_{max}$)、暗呼吸速率($R_d$)和光补偿点(LCP)。我们采用单因素方差分析(One-way ANOVA),即以树种或者季节为因素来比较不同树种在某一季节下的光合作用差异或者同一树种在不同季节下的光合作用的差异。我们还采用线性回归分析探讨树种光合速率和气孔导度、电子传递速率以及温度的相互关系。所有数据的统计与分析采用 Microsoft Excel 和 SPSS 软件。

# 3 结果和分析

从表 1 可见,在雨季饱和光照下,除青榨槭外,落叶阔叶树亮叶水青冈和缺萼枫香与 4 种常绿阔

叶树的最大净光合速率($P_{max}$)差异不明显。在旱季,落叶阔叶树与常绿阔叶树的 $P_{max}$ 下降,分别下降了 32% 和 12%。总的来看,饱和光照下落叶阔叶树的气孔导度($G_{max}$)要比常绿阔叶树高。旱季与雨季相比,落叶阔叶树和常绿阔叶树的 $G_{max}$ 分别下降了 35% 和 21%。无论在雨季还是旱季,落叶阔叶树的暗呼吸速率($R_d$)大于常绿阔叶树,但落叶阔叶树和常绿阔叶树的 $R_d$ 在旱季比雨季分别增加了 40% 和 58%。3 种落叶阔叶树的光补偿点(LCP)比 4 种常绿阔叶树高,无论常绿阔叶树还是落叶阔叶树,旱季要比雨季的 LCP 增高,且增加的幅度差异不大。3 种落叶阔叶树与 4 种常绿阔叶树的表观量子效率(AQY)在雨季的差异不明显,但在旱季常绿阔叶树 AQY 稍高于落叶阔叶树。7 种植物在雨季凌晨的光系统 II 潜在最大光化学效率($F_v/F_{m\text{-}predawn}$)没有明显差异,但在旱季凌晨,常绿阔叶树的 $F_v/F_{m\text{-}predawn} > 0.80$,而落叶阔叶树的 $F_v/F_{m\text{-}predawn} < 0.71$。到了干冷季,落叶阔叶树已枯黄落叶,而常绿阔叶树的 $P_{max}$、$G_{max}$、AQY、$F_v/F_{m\text{-}predawn}$ 均大幅度地下降,而 $R_d$、LCP 却大幅度地上升。

**表 1 常绿和落叶阔叶树光合参数的季节性变化**

Table 1 Seasonal changes in photosynthetic traits of evergreen and deciduous broad-leaved species

| 植物 Species | 季节 Season | $P_{max}$ ($\mu$mol m$^{-2}$s$^{-1}$) | $G_{max}$ (mmol m$^{-2}$s$^{-1}$) | Rd ($\mu$mol m$^{-2}$s$^{-1}$) | LCP ($\mu$mol m$^{-2}$s$^{-1}$) | AQY | $F_v/F_{m\text{-}predawn}$ |
|---|---|---|---|---|---|---|---|
| 铁椎栲 | RS | 9.55 ±0.56 | 174.55 ±4.84 | 0.48 ±0.04 | 10.23 ±1.00 | 0.048 ±0.002 | 0.839 ±0.002 |
| *Castanopsis lamontii* | DS | 8.12 ±0.47 | 130.92 ±3.63 | 0.70 ±0.06 | 17.45 ±1.70 | 0.040 ±0.002 | 0.806 ±0.002 |
| | DCS | 2.23 ±0.08 | 49.53 ±3.02 | 0.86 ±0.07 | 31.85 ±4.69 | 0.028 ±0.002 | 0.541 ±0.002 |
| 银木荷 | RS | 11.67 ±0.71 | 120.87 ±3.13 | 0.43 ±0.05 | 8.63 ±1.21 | 0.051 ±0.002 | 0.838 ±0.002 |
| *Schima argentea* | DS | 10.75 ±0.77 | 110.87 ±3.13 | 0.81 ±0.06 | 18.66 ±1.27 | 0.044 ±0.002 | 0.804 ±0.002 |
| | DCS | 1.99 ±0.13 | 49.53 ±3.02 | 0.89 ±0.05 | 27.92 ±2.64 | 0.033 ±0.002 | 0.543 ±0.002 |
| 桂南木莲 | RS | 9.33 ±0.60 | 67.85 ±5.41 | 0.29 ±0.0 | 5.81 ±0.85 | 0.051 ±0.002 | 0.837 ±0.003 |
| *Manglietia chingii* | DS | 7.93 ±0.51 | 50.89 ±4.06 | 40.42 ±0.06 | 9.90 ±1.44 | 0.043 ±0.002 | 0.803 ±0.002 |
| | DCS | 2.69 ±0.19 | 22.90 ±1.83 | 0.83 ±0.07 | 22.39 ±1.53 | 0.037 ±0.002 | 0.612 ±0.001 |
| 曼青冈 | RS | 9.58 ±0.41 | 119.62 ±4.34 | 0.53 ±0.05 | 10.52 ±1.39 | 0.052 ±0.002 | 0.835 ±0.003 |
| *Cyclobalanopsis oxyodon* | DS | 8.14 ±0.35 | 89.72 ±3.26 | 0.77 ±0.07 | 17.95 ±2.36 | 0.044 ±0.002 | 0.801 ±0.003 |
| | DCS | 2.39 ±0.14 | 40.37 ±1.47 | 0.94 ±0.10 | 30.12 ±3.73 | 0.032 ±0.002 | 0.541 ±0.001 |
| 亮叶水青冈 | RS | 12.39 ±0.88 | 286.87 ±13.18 | 0.55 ±0.06 | 10.63 ±1.25 | 0.052 ±0.002 | 0.840 ±0.003 |
| *Fagus lucida* | DS | 7.96 ±0.50 | 186.47 ±8.56 | 0.87 ±0.05 | 23.27 ±2.20 | 0.038 ±0.002 | 0.714 ±0.002 |
| 青榨槭 | RS | 6.67 ±0.39 | 149.58 ±6.83 | 0.57 ±0.09 | 12.92 ±2.47 | 0.046 ±0.00 | 0.837 ±0.003 |
| *Acer davidii* | DS | 5.02 ±0.33 | 97.23 ±4.44 | 0.84 ±0.07 | 26.54 ±3.91 | 30.033 ±0.002 | 0.711 ±0.003 |
| 缺萼枫香 | RS | 10.26 ±0.38 | 175.15 ±5.83 | 0.76 ±0.06 | 14.94 ±0.84 | 0.051 ±0.003 | 0.838 ±0.002 |
| *Liquidambar acalycina* | DS | 6.88 ±0.49 | 113.86 ±3.80 | 0.92 ±0.10 | 25.10 ±3.11 | 0.037 ±0.002 | 0.712 ±0.002 |
| 常绿树 | RS | 10.03 ±0.34 | 120.72 ±8.14 | 0.43 ±0.03 | 8.80 ±0.65 | 0.050 ±0.001 | 0.837 ±0.001 |
| Evergreen | DS | 8.74 ±0.35 | 95.40 ±6.52 | 0.68 ±0.04 | 15.99 ±1.10 | 0.043 ±0.001 | 0.804 ±0.001 |
| | DCS | 2.33 ±0.08 | 42.93 ±2.94 | 0.88 ±0.04 | 28.07 ±1.73 | 0.032 ±0.001 | 0.559 ±0.006 |
| 落叶树 | RS | 9.75 ±0.66 | 203.87 ±15.50 | 0.63 ±0.04 | 12.83 ±1.00 | 0.050 ±0.002 | 0.838 ±0.001 |
| Deciduous | DS | 6.62 ±0.38 | 132.52 ±9.94 | 0.88 ±0.04 | 24.97 ±1.74 | 0.036 ±0.001 | 0.712 ±0.001 |

n = 6. $P_{max}$:最大净光合速率 Maximum net photosynthetic rate;$G_{max}$:饱和光照下的气孔导度 Maximum stomatal conductance;$R_d$:暗呼吸速率 Dark respiration rate;LCP:光补偿点 Light compensation point;AQY:表观量子效率 Apparent quantum yield;$F_v/F_{m\text{-}predawn}$:凌晨光系统 II 潜在最大光化学效率 Predawn maximum photochemical efficiency of photosystem II. RS:雨季 Rainy season;DS:干季 Dry season;DCS:干冷季 Dry and cold season.

从表 2 可见,在自然光照下,落叶阔叶树和常绿阔叶树在雨季的光合速率差异不明显,但在旱季常绿阔叶树高于落叶阔叶树,且两者对光照日变化的响应特征相似。落叶阔叶树和常绿阔叶树的气孔导度对光照日变化的响应特征也相似,但落叶阔叶树的气孔导度总比常绿阔叶树高。无论在雨季

还是在旱季,常绿阔叶树日间光系统Ⅱ的潜在最大光化学效率($F_v/F_m$)总比落叶阔叶树高,但落叶阔叶树和常绿阔叶树的 $F_v/F_m$ 对光照日变化的响应特征相似。到了干冷季,落叶阔叶树已枯黄落叶;常绿阔叶树净光合速率、气孔导度以及 $F_v/F_m$ 都下降到很低的水平。

**表 2　常绿和落叶阔叶树净光合速率(P)、气孔导度(G)以及光系统Ⅱ潜在最大光化学效率($F_v/F_m$)的日变化**

Table 2　Diurnal changes in net photosynthetic rate (P), stomatal conductance (G), and maximum photochemical efficiency of photosystem Ⅱ ($F_v/F_m$) in evergreen and deciduous broad-leaved species

| 季节 Season | 时间 Time | P (μmol $m^{-2}s^{-1}$) | | G (mmol $m^{-2}s^{-1}$) | | $F_v/F_m$ | |
|---|---|---|---|---|---|---|---|
| | | 常绿树 Evergreen | 落叶树 Deciduous | 常绿树 Evergreen | 落叶树 Deciduous | 常绿树 Evergreen | 落叶树 Deciduous |
| RS | 08:00 | 9.34 ±1.49 | 9.05 ±2.26 | 125.0 ±31.0 | 210.0 ±60.6 | 0.820 ±0.032 | 0.782 ±0.029 |
| | 10:00 | 10.03 ±1.64 | 9.75 ±2.79 | 120.7 ±38.9 | 203.8 ±64.9 | 0.732 ±0.036 | 0.670 ±0.035 |
| | 12:00 | 7.07 ±1.00 | 7.69 ±1.60 | 73.1 ±34.4 | 127.6 ±54.4 | 0.614 ±0.031 | 0.552 ±0.032 |
| | 14:00 | 8.14 ±1.36 | 8.69 ±1.90 | 85.9 ±37.8 | 165.0 ±58.8 | 0.688 ±0.027 | 0.634 ±0.035 |
| | 16:00 | 8.46 ±1.64 | 9.02 ±2.08 | 96.9 ±35.2 | 180.0 ±60.6 | 0.782 ±0.034 | 0.747 ±0.027 |
| | 17:00 | 8.14 ±1.64 | 8.53 ±2.31 | 89.3 ±45.3 | 174.3 ±57.5 | 0.795 ±0.016 | 0.766 ±0.030 |
| DS | 08:00 | 7.23 ±1.46 | 5.02 ±1.23 | 104.0 ±41.3 | 140.0 ±25.6 | 0.751 ±0.045 | 0.655 ±0.025 |
| | 10:00 | 8.74 ±1.73 | 6.62 ±1.60 | 93.5 ±31.9 | 132.5 ±42.2 | 0.631 ±0.035 | 0.543 ±0.043 |
| | 12:00 | 6.16 ±1.28 | 3.34 ±0.64 | 63.8 ±28.5 | 96.1 ±38.8 | 0.508 ±0.032 | 0.437 ±0.020 |
| | 14:00 | 6.91 ±1.62 | 4.61 ±0.95 | 78.2 ±24.3 | 115.6 ±41.3 | 0.584 ±0.022 | 0.537 ±0.029 |
| | 16:00 | 7.26 ±1.60 | 5.22 ±1.05 | 83.3 ±21.8 | 120.7 ±42.8 | 0.720 ±0.020 | 0.611 ±0.038 |
| | 17:00 | 6.65 ±1.39 | 4.25 ±0.87 | 75.7 ±23.5 | 113.1 ±34.8 | 0.740 ±0.025 | 0.636 ±0.031 |
| DCS | 08:00 | 1.09 ±0.25 | | 44.2 ±15.0 | | 0.580 ±0.063 | |
| | 10:00 | 1.92 ±0.61 | | 42.9 ±14.4 | | 0.480 ±0.070 | |
| | 12:00 | 0.82 ±0.14 | | 25.5 ±5.0 | | 0.357 ±0.045 | |
| | 14:00 | 1.27 ±0.31 | | 35.7 ±8.8 | | 0.466 ±0.043 | |
| | 16:00 | 1.37 ±0.38 | | 30.6 ±4.4 | | 0.487 ±0.056 | |
| | 17:00 | 0.92 ±0.24 | | 23.0 ±5.6 | | 0.510 ±0.047 | |

n = 6. RS:雨季 Rainy season; Ds:干季 Dry season; DCS:干冷季 Dry and cold season.

从表 3 可知,光合速率与气孔导度呈显著直线相关,常绿阔叶树的直线斜率要比落叶阔叶树大,这说明常绿阔叶树比落叶阔叶树有较高的光合水分利用效率。光合速率与电子传递速率和温度都呈显著直线相关,但常绿阔叶树的直线斜率远小于落叶阔叶树,这说明常绿植物可以调节电子传递速率的变化来适应温度的宽幅的季节性变化。

## 3 讨论

有研究报道,落叶植物比常绿植物有较高光合速率和随之而来的较高的生长潜力[18–19]。与上述已报道的结果不同的是,猫儿山中山地带的落叶阔叶树,无论在雨季还是在旱季,并不比常绿阔叶树具有较高的光合速率(表 1)。在旱季,常绿和落叶阔叶树两者都部分关闭气孔以减少水分蒸发从而导致光合速率下降;同时,季节性温度的下降也会降低两者的光合速率(表 3)。总的来看,常绿阔叶树的气孔导度要比落叶阔叶树低(表 1),说明常绿阔叶树光合水分利用效率高,而落叶阔叶树光合水分利用效率低,这与已有的报道结果认为落叶阔叶树以高水分散失为代价获得高光合速率是一致的[10]。为减少在旱季水分损失,落叶阔叶树在旱季对气孔的关闭程度要比常绿阔叶树高,结果导致落叶阔叶树在旱季比常绿阔叶树的光合速率还低(表 1),这与已有的报道结果相符[11];另外,落叶树叶片在旱季时已经到了开始衰老的时候,叶片养分开始转移也会导致光合速率的下降[16]。

落叶阔叶树的 $R_d$ 和 LCP 明显高于常绿阔叶树(表 1),这表明落叶阔叶树比常绿阔叶树对高光照的适应性较强。落叶阔叶树与常绿阔叶树在雨季

**表3 常绿和落叶阔叶树光合速率(P)与气孔导度(G)、电子传递速率(ETR)和温度($T_a$)的回归分析**

Table 3 The regression analysis of photosynthetic rate (P) to stomatal conductance (G), electron transport rate (ETR), and temperature ($T_a$), respectively, in evergreen and deciduous broad-leaved species

| 树种 Species | G | ETR | $T_a$ |
|---|---|---|---|
| 铁椎栲 | $P=0.13G-4.10$ | $P=0.08\ ETR-4.31$ | $P=0.82T_a-7.13$ |
| *Castanopsis lamontii* | ($R^2=0.94$) | ($R^2=0.71$) | ($R^2=0.68$) |
| 银木荷 | $P=0.10G-1.74$ | $P=0.06\ ETR-0.84$ | $P=0.63T_a-5.40$ |
| *Schima argentea* | ($R^2=0.90$) | ($R^2=0.54$) | ($R^2=0.80$) |
| 桂南木莲 | $P=0.13G+0.44$ | $P=0.04\ ETR+1.81$ | $P=0.75T_a-6.00$ |
| *Manglietia chingii* | ($R^2=0.76$) | ($R^2=0.44$) | ($R^2=0.56$) |
| 曼青冈 | $P=0.07G-2.25$ | $P=0.05\ ETR-0.99$ | $P=0.66T_a-6.58$ |
| *Cyclobalanopsis oxyodon* | ($R^2=0.88$) | ($R^2=0.67$) | ($R^2=0.80$) |
| 亮叶水青冈 | $P=0.05G-0.56$ | $P=0.08\ ETR-2.50$ | $P=1.22T_a-19.09$ |
| *Fagus lucida* | ($R^2=0.51$) | ($R^2=0.51$) | ($R^2=0.62$) |
| 青榨槭 | $P=0.03G-2.59$ | $P=0.06\ ETR-0.63$ | $P=0.65T_a-9.07$ |
| *Acer davidii* | ($R^2=0.48$) | ($R^2=0.61$) | ($R^2=0.84$) |
| 缺萼枫香 | $P=0.06G+0.59$ | $P=0.05\ ETR+1.24$ | $P=1.05T_a-15.20$ |
| *Liquidambar acalycina* | ($R^2=0.81$) | ($R^2=0.82$) | ($R^2=0.80$) |
| 常绿树 | $P=0.06G+1.59$ | $P=0.05\ ETR-0.42$ | $P=0.66T_a-5.35$ |
| Evergreen | ($R^2=0.51$) | ($R^2=0.57$) | ($R^2=0.65$) |
| 落叶树 | $P=0.04G+1.90$ | $P=0.07ETR-1.03$ | $P=1.10T_a-17.37$ |
| Deciduous | ($R^2=0.74$) | ($R^2=0.79$) | ($R^2=0.52$) |

的$F_v/F_{m\text{-predawn}}$无明显差异；在旱季，落叶阔叶树的$F_v/F_{m\text{-predawn}}$降到0.66(表1)，这说明落叶阔叶树光系统II受到了较严重的胁迫。从气孔导度与光合速率直线相关(表3)可以得知常绿阔叶树要比落叶阔叶树有更大的气孔限制，这说明与常绿阔叶树相比，落叶阔叶树光合速率的高低更加依赖光合酶活性的高低以及光合底物的多寡。温度过低或过高都将使光合酶的活性降低从而导致植物光合速率下降，但在一定的温度范围内，植物的光合速率与温度直线相关(表3)；落叶阔叶树直线的斜率比常绿阔叶树大，即温度的变化对落叶阔叶树的光合速率的影响要比对常绿阔叶树的光合速率的影响大。另外，在干冷季，落叶阔叶树枯黄落叶，可以视为落叶阔叶树对不利环境干旱和低温采取的一种极端适应措施；然而，常绿阔叶树尽管可以通过气孔调节提高水分利用效率和通过电子分配耗散多余能量来降低光合机构的损伤(表3)，但是不耐冰凌和雪灾还是使其生长受到严重制约从而限制其在群落中成为优势种[13]。

# 4 结论

猫儿山中山地带暖温带气候条件下的落叶阔叶树和常绿阔叶树两者对季节性环境变化采取了不同的光合适应性策略。当雨季结束旱季来临时，两者的光合速率下降，这与气孔的部分关闭和光系统II活性的下降有显著的关系。气孔的部分关闭有利于减少在旱季的水分蒸腾损失，但落叶阔叶树气孔关闭的程度明显高于常绿阔叶树。另外，常绿阔叶树通过气孔调节提高水分利用效率和通过电子分配耗散多余能量来降低干旱和低温的危害，但是冬天的冰凌和雪灾还是造成了生物量的损失，不利于其在当地环境下占优势。

**致谢** 中国科学院西双版纳热带植物园的博士研究生陈军文、朱俊杰和硕士研究生李伟以及广西猫儿山国家级自然保护区的张建国先生和罗远周先生参加了部分或全部野外调查和测定，在此表示诚挚的谢意！

## 参考文献

[1] Sobrado M A. Cost-benefit relationships in deciduous and evergreen leaves of tropical dry forest species [J]. Funct Ecol, 1991, 5: 608–616.

[2] Quigley M E, Platt W J. Composition and structure of seasonally forests in the Americas [J]. Ecol Monogr, 2003, 73(1): 87–106.

[3] Kikuzawa K. A cost-benefit analysis of leaf habit and leaf longevity of trees and their geographical pattern [J]. Amer Natrual, 1991, 138: 1250–1263.

[4] Kikuzawa K, Ackerly D. Significance of leaf longevity in plants [J]. Plant Spec Biol, 1999, 14: 39−45.

[5] Monk C D. An ecological significance evegreenness [J]. Ecology, 1966, 47: 504−505.

[6] Mooney H A. The carbon balance of plants [J]. Ann Rev Ecol System, 1972, 2: 315−346.

[7] Chapin F S. The mineral nutrition of wild plants [J]. Ann Rev Ecol System, 1980, 11: 233−260.

[8] Aerts R. The advantages of being evergreen [J]. Trends Ecol Evol, 1995, 10: 402−407.

[9] Salleo S, Nardini A, Logullo A M. Is sclerophylly of Mediterranean evergreens and adaptation to drought? [J] New Phytol, 1997, 135: 603−612.

[10] Givnish T J. Adapative significance of evergreen vs. deciduous leaves: solving the triple paradox [J]. Silva Fenn, 2002, 36(3) : 703−743.

[11] Eamus D. Ecophysiological traits of deciduous and evergreen woody species in the seasonally dry tropics [J]. Trends Ecol Evol, 1999, 14: 11−16.

[12] Wang X P(王献溥), Li X X(李信贤). Vegetations of Miaoer Nature Reserve, Xingan County, Guangxi [J]. Guihaia(广西植物), 1986, 6: 79−91.(in Chinese)

[13] Cao K F. Morphology and growth of evergreen and deciduous saplings under different light conditions in a Chinese beech forest with dense bamboo undergrowth [J]. Ecol Res, 2001, 16(3): 509−517.

[14] Li G Z(李光照). A preliminary study of Maoershan flora [J]. Guihaia(广西植物), 1985, 5(3): 211−226.(in Chinese)

[15] Li G Z(李光照). A study of Maoershan flora [J]. Guihaia(广西植物), 2001, 21(Suppl.): 4−17.(in Chinese)

[16] Morecroft M D, Roberts J M. Photosynthesis and stomatal conductance of mature canopy oak (*Quercus robur*) and sycamore (*Acer pseudoplatanus*) trees throughout the growing season [J]. Funct Ecol, 1999, 13: 332−342.

[17] Peek M S, Russek-Cohen E, Wait D A, et al. Physiological response curve analysis using nonlinear mixed models [J]. Oecologia, 2002, 132: 175−180.

[18] Reich P B, Walters M B, Ellsworth D S. Leaf life-span in relation to life, plant, and stand characteristics among diverse ecosystems [J]. Ecol Monogr, 1992, 62: 365 392.

[19] Cornelissen J H C, Castro D P, Hunt R. Seedling growth, allocation and leaf attributes in a wide range of woody plant species and types [J]. J Ecol, 1996, 84: 755−765.