

生长环境光强对两种热带雨林树种 幼苗光合作用的影响

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摘要:以西双版纳热带雨林中演替后期种绒毛番龙眼和先锋树种山黄麻为材料, 于雾凉季测定了不同光强下生长的 2 种树苗叶片最大净光合速率($P_{\max}$)、叶绿素荧光参数以及光合色素含量和比叶重(LMA), 探讨了不同生态习性热带雨林树种幼苗对光强的适应及光保护机制。发现在一定光强范围内随生长环境光强的增加, 2 种树苗 LMA、荧光的非化学猝灭(NPQ)、类胡萝卜素(Car)含量、Car 与叶绿素(Chl)之比升高, 光饱和点和光补偿点也有随生长环境光强的增大而升高的趋势, Chl 含量降低, 2 种树苗均能通过形态和生理特性的变化适应不同的光强环境。相同的生长光强下, 绒毛番龙眼光抑制明显比山黄麻重, 山黄麻适应强光的能力强。随生长环境光强的增加, 山黄麻 NPQ 增加不显著, 热耗散较少, 相同光强下其 $P_{\max}$ 显著高于绒毛番龙眼。绒毛番龙眼则相反, 其热耗散随生长环境光强的升高显著增多, 但 $P_{\max}$ 差异不显著。表明先锋种山黄麻主要通过提高 $P_{\max}$ 利用光能防止光合机构光破坏, 而演替后期种绒毛番龙眼却较大程度通过增强非光化学猝灭来耗散过量光能。上午人为降低光强度对先锋种山黄麻影响不大, 但可以明显缓解绒毛番龙眼的光抑制, 表明上午一定程度的遮光(如有雾)可减缓绒毛番龙眼光抑制。

关键词:光抑制; 光适应; 最大净光合速率; 热耗散; 色素含量; 热带雨林树种

Effects of growth light intensities on photosynthesis in seedlings of two tropical rain forest species

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Abstract: Acclimation to growth light intensities and the strategies of photoprotection were explored in seedlings of two tropical rainforest tree species, *Pometia tomentosa* and *Trema orientalis*. The former is a late-successional species in forest, and its seedlings distribute in understory or small canopy gap. Whereas the latter is a pioneer tree species, and its seedlings occur in canopy gap. The plant materials were raised under four light regimes [a. 3.1%/12.5% (Before/after fog disappear, percent of sunshine); b. 12.5%/12.5%; c. 9%/36%; d. 25%/36%] for about 3 months during the foggy and cool season in 2002 at Xishuangbanna, Yunnan Province, China. Then maximum net photosynthetic rate ($P_{\max}$), chlorophyll fluorescence parameters, chloroplast pigments content, and lamina mass per unit area (LMA) were measured. We manipulated morning light intensities to simulate the effect of fog which could shield sunlight for about 60%~90% in the morning. Fog presents almost every day in this season. The main purpose of this study was to determine whether decreasing morning light intensity (the effect of fog) could ameliorate photoinhibition of photosynthesis when the light intensity was the same in the afternoon. If so, we could conclude that fog could protect tropical rainforest tree species from photoinhibition through screening sunlight in Xishuangbanna.

For the two species, with the increase of growth light intensity LMA, non-photochemical quenching coefficient (NPQ),

基金项目:中国科学院“百人计划”资助项目

收稿日期:2003-10-22; **修订日期:**2004-05-21

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Foundation item: the Program of 100 Distinguished Young Scientists of the Chinese Academy of Sciences

Received date: 2003-10-22; **Accepted date:** 2004-05-21

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the carotenoid content expressed as unit leaf dry weight and expressed as unit chlorophyll, light saturation point and light compensation point increased, while chlorophyll concentration decreased. Seedlings of the two species could acclimate to different growth light regimes in this study through changes of physiological and morphological traits. Diurnal photoinhibition of photosynthesis, as judged by maximum efficiency of PS II photochemistry, was significantly severer in *P. tomentosa* than in *T. orientalis* in all growth light regimes. The acclimation capacity to high light regimes was stronger in *T. orientalis* than in *P. tomentosa*. With the increase of growth light intensity, $P_{\max}$ increased significantly, but NPQ not in *T. orientalis*. While the reverse trends occurred in *P. tomentosa*. At the same light regimes thermal dissipation was much lower, but $P_{\max}$ was much higher in *T. orientalis* than in *P. tomentosa*. This indicates that photodamage was avoided mainly through increasing light energy utilization by photosynthesis in *T. orientalis*, a pioneer tree species, but through increasing thermal dissipation in *P. tomentosa*, a late-successional species. In addition, photosynthetic pigments content and LMA were lower in *T. orientalis* than in *P. tomentosa*, indicating that the percent of light energy absorbed by the former is lesser. This can ameliorate excitation pressure on photosystem II. The effects of decreasing light intensity in the morning was significant in *P. tomentosa*, but not in *T. orientalis*. Decreasing light intensity in the morning could ameliorate diurnal photoinhibition of photosynthesis significantly in *P. tomentosa*, but not in *T. orientalis*. Fog can decrease light intensity by 60%~90% in the morning in foggy and cool season in Xishuangbanna. Shading by fog in the morning might be important to *P. tomentosa* and other late-successional species, especially to chilling sensitive species. So we hypothesized that fog be important to the existence of tropical rainforest in Xishuangbanna, and one of its role be to ameliorate photoinhibition of photosynthesis through decreasing light intensity in the morning.

Key words: photoinhibition of photosynthesis; light acclimation; maximum net photosynthetic rate; thermal dissipation; chloroplast pigment content; tropical rainforest tree species

文章编号:1000-0933(2005)01-0023-08 中图分类号:Q142,Q945,Q948 文献标识码:A

光是重要的生态因子,很大程度上植物适应光环境变化的能力决定了它的分布模式和物种丰度^[1]。当植物叶片吸收的光能不能完全用于光合作用时,过量的光能会引起植物光化学效率的降低,发生光合作用的光抑制^[2~5]。热带雨林中不同生态习性树种的更新对光环境的要求不同。荫生植物捕光能力较强,光合能力较低,对光抑制特别敏感^[6~8]。强光下阳生植物能提高光合速率,利用更多的光能^[9~12];另一方面增加热耗散,消耗掉过剩光能^[13,7],防止光破坏^[14]。西双版纳处于热带北缘,在雾凉季对植物造成寒害的夜间低温时常出现,有时还会出现霜冻^[15,16],低温结合强光导致植物光抑制^[17~21],甚至光氧化破坏^[22]。虽然如此,本区却有典型的热带雨林,推测雾对该地区热带雨林的存在起着不可忽视的作用。本区低温季节几乎天天上午有雾,雾使光强降低 60%~90%。本文以演替后期物种绒毛番龙眼(*Pometia tomentosa*)和先锋树种山黄麻(*Trema orientalis*)两种需光特性不同的树苗为材料,研究不同光照条件下它们对光能的利用与耗散,探讨不同生态习性的热带雨林树种幼苗对光强的适应及光保护机制,同时人们还关注:下午光强相同条件下,上午光强高低对植物光合机构的不同影响,以探讨雾使上午光强减弱对西双版纳地区热带植物的可能影响。

1 材料与方法

1.1 自然概况

实验在中国科学院西双版纳热带植物园进行,该园位于 21°56'N,101°15'E,海拔 570 m,属北热带西南季风气候,一年中有明显的干季(11~翌年 4 月份)和雨季(5~10 月份)之分。西双版纳地区年均气温 21.7℃,年均相对湿度 86%,年平均降雨量 1 500~1 600 mm,降雨多集中在雨季,占全年降雨量的 83%~87%,干季占 13%~17%。本区是有名的静风多雾区,年雾日数 170 d 左右,主要出现在干季(80%以上),这在一定程度上弥补了干季雨量的不足。根据有雾与否,可把干季进一步分为雾凉季(11~翌年 2 月份)和干热季(3~4 月份),雾凉季天天有雾,一般 22:00 雾生,第 2 天 11:30 雾散,因此上午光线较弱^[23]。

1.2 实验材料与处理

通过黑色尼龙网遮阳,使 3 个荫棚内的相对光强(RI)分别为 50%、36%、12.5%,另外一个光强为全光照,即 100%。本研究所用材料为绒毛番龙眼[*Pometia tomentosa* (Bl.) Teysm. et Binn. (Sapindaceae)]和山黄麻[*Trema orientalis* (Linn.) Bl. (Ulmaceae)],绒毛番龙眼是西双版纳原始热带季节雨林的冠层树种,广泛分布于海拔 900 m 以下的沟谷雨林中^[24],其幼苗在林窗和林冠下都可见,山黄麻是热带季节雨林先锋树种。2002 年 7 月收集 2 种热带雨林树种的种子,播于 12.5%光照下的砂床中萌发。8 月底 2 种幼苗均有 2 片以上真叶后移栽到内径 30 cm、深 23 cm、容积约为 15 L 的花盆中,每盆 1 株,土壤为林内 10 cm 以上表土(砖红壤)。幼苗在 RI 为 12.5%的荫棚中生长 1 个月后,选取大小一致、长势良好的小苗随机分成 4 组,每组 20 盆,

处理光照强度为:a. 12.5%/12.5%(雾散前/雾散后,自然环境光强的百分比(%),下同,每天约 11:30 雾散);b. 50%/12.5%;c. 36%/36%;d. 100%/36%,处理时间 3 个月,除雨天外,每日 18:00 浇饱水 1 次,每月施复合肥 1 次,随时除草。对所选取的 2 种树苗充分浇水,即忽略雾对植物的水分效应,只考虑雾降低光强的作用。

西双版纳的雾可使上午光强降低 60%~90%,假定上午雾的遮光率为 75%,上午有雾时自然光强的 12.5%、50%、36%和 100%分别相当于无雾时太阳光强的 3.1%、12.5%、9%和 25%,下午无雾自然光强与太阳光强相同。以太阳光强的百分比表示时,4 种处理分别为 a. 3.1%/12.5%(雾散前/雾散后,无雾时太阳光强百分比(%),下同,每天约 11:30 雾散);b. 12.5%/12.5%;c. 9%/36%;d. 25%/36%,为直观本文用此方式表示处理光强。处理 a 和 b、c 和 d 的光强分别相当于林内小、大林窗中的光强,下午 a 和 b、c 和 d 的光强相同,上午 a 的光强是 b 的 25%,c 的光强是 d 的 36%,a 和 c 相当于上午有雾,b 和 d 相当于上午无雾。

1.3 叶绿素荧光参数的测定

用 FMS2.01 型脉冲调制荧光仪(英国 Hansatech 公司)于晴天测定光系统 II (PS II)最大光能转换效率 (F_v/F_m)和非光化学猝灭系数 (NPQ)= $(F_m - F'_m)/F'_m$ ^[25]的日变化,测定方法见冯玉龙等^[23]。本文以 F_v/F_m 为指标判断是否发生光合作用光抑制^[3],以 NPQ 为指标判断植物热耗散的多少^[3,23]。

1.4 光合作用光响应曲线的测定

用 Li-6400 便携式光合系统 (Li-Cor, Inc, 美国)测定叶片的净光合速率 (P_n),使用开放气路,空气流速为 0.5 L/min,温度 25℃,相对湿度 50%,CO₂ 浓度 360 $\mu\text{mol}/\text{mol}$ 。测定从 2000 $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$ 光强开始,依次降为 1500、1000、800、600、400、200、100、50 和 0 $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$,测定时每一光强下停留 3 min。测定前叶片在 600~1200 $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$ 光强(依植物种类及生长光强而定)下诱导 30 min,叶片与光源之间具 8 cm 厚的流动隔热水层,以减少叶片升温。以光量子通量密度(PFD)为横轴, P_n 为纵轴绘出光合作用光响应曲线 (P_n - PFD 曲线),依据 Bassman 和 Zwier^[26]的方法拟合 P_n - PFD 的曲线方程:

$$P_n = P_{\max}(1 - C_0 e^{-\alpha PFD/P_{\max}})$$

式中, $P_{\max}$ 为最大净光合速率,即光合能力, α 为弱光下光量子利用效率,即表观量子效率(AQY), C_0 为度量弱光下净光合速率趋近于 0 的指标。通过适合性检验,若拟合效果良好,则可用下式计算光补偿点(LCP):

$$LCP = P_{\max} \ln(C_0)/\alpha$$

假定 P_n 达到 $P_{\max}$ 的 99% 时的 PFD 为光饱和点(LSP),则:

$$LSP = P_{\max} \ln(100C_0)/\alpha$$

1.5 叶绿体色素含量的测定

用一定面积的打孔器在成熟叶片上,避开主叶脉,打下 5 个叶圆片,按 Lichtenthaler 和 Wellburn^[27]的方法测定叶绿素和类胡萝卜素含量。

1.6 比叶重(LMA)的测定

LMA 的测定见冯玉龙等^[1]。用一定面积的打孔器打下 50 个叶圆片,120℃处理 30 min,80℃烘干 24 h 后,用电子天平称干重,计算 LMA (单位面积叶干重, g/m^2)。

测定时选取不同处理植株成熟叶片为测定叶(每株 1 片),每一处理重复 3~5 株,除叶绿素荧光参数外,所有测定均在 8:30~11:30 进行,此期间由于有雾,光线较弱,且变化不大,植物各生理参数随时间的变化较小,可比性较强。各参数均以平均值加减 1 个标准误差表示。用 t 检验不同处理之间的差异, $P < 0.05$,差异显著。

2 结果

2.1 生长环境光强对两种植物光合作用光抑制的影响

一天中黎明光系统 II 最大光能转换效率 (F_v/F_m)最高,随日间光强的升高, F_v/F_m 降低,下午光最强时即 14:00 左右 F_v/F_m 降到最底点,之后随光强的减弱缓慢回升,18:00 光照强度较弱时,各光强下生长的绒毛番龙眼的 F_v/F_m 仍未恢复到天亮前的水平,3.1%/12.5%和 12.5%/12.5%光强下生长的山黄麻 F_v/F_m 基本恢复,但 9%/36%和 25%/36%光强下仍未恢复(图 1)。表明在日间 2 种植物均发生了光抑制,相同光强下生长的绒毛番龙眼的日间光抑制明显比山黄麻重。而且上午光强的降低均能明显缓解绒毛番龙眼的光抑制,但对山黄麻的影响不太明显(图 1)。

不同光强下生长的绒毛番龙眼表观量子效率(AQY)差异不显著,12.5%/12.5%、9%/36%和 25%/36%光强下生长的山黄麻的 AQY 显著高于 3.1%/12.5%光强下的值。同一光强下生长的山黄麻 AQY 显著高于绒毛番龙眼(表 1)。表明绒毛番龙眼对光抑制较敏感。

2.2 生长环境光强对 2 种植物气体交换参数的影响

不同光强下生长的山黄麻最大净光合速率($P_{\max}$)显著高于绒毛番龙眼(表 2)。山黄麻 $P_{\max}$ 随生长环境光强升高而增大,这

与其它需高光植物是一致的^[12,28,1];不同光强下生长的绒毛番龙眼 P_{max} 差异不显著。

9%/36%和 25%/36%以及 3.1%/12.5%和 12.5%/12.5%光强下生长的山黄麻的光饱和点 (LSP) 差异不显著,但 9%/36%和 25%/36%光强下的值均显著高于 3.1%/12.5%和 12.5%/12.5%光强下的值。绒毛番龙眼的 LSP 随生长光强变化不明显。相同光强下生长的山黄麻 LSP 显著高于绒毛番龙眼(图 2)。山黄麻的光补偿点 (LCP) 随生长光强的增大而升高,9%/36%和 25%/36%光强下的绒毛番龙眼 LCP 高于 3.1%/12.5%和 12.5%/12.5%光强下的值。相同光强下生长的 2 种树苗的 LCP 差异不显著(图 2)。

表 1 不同光环境下生长的绒毛番龙眼和山黄麻幼苗表观量子效率

Table 1 Apparent quantum yield for the seedlings of <i>P. tomentosa</i> and <i>T. orientalis</i> grown under different light regimes				
树种 Species	光环境(雾散前/雾散后, RI) Light regimes (Before/after fog disappear, percent of sunshine without fog) *			
	3.1%/12.5%	12.5%/12.5%	9%/36%	25%/36%
绒毛番龙眼 <i>P. tomentosa</i>	0.017±0.0057A,a	0.0160±0.0019A,a	0.022±0.0027A,a	0.0198±0.0027A,a
山黄麻 <i>T. orientalis</i>	0.0417±0.0015A,b	0.0476±0.0013B,b	0.0508±0.0012B,b	0.0482±0.0024B,b

* 3~5 个重复的平均值±标准误差 Mean±standard error (SE) of 3~5 separate experiments; 不同大、小写字母分别表示同种不同光下和相同光下不同物种间差异显著 ($P<0.05$) Different upper- and lowercase letters indicate significant different among the light regimes of the same species and between different species in the same light regime ($P<0.05$, student's t -test), respectively;下同 the same below

表 2 不同光环境下生长的绒毛番龙眼和山黄麻幼苗的最大净光合速率 ($\mu\text{mol}/(\text{m}^2 \cdot \text{s})$)

Table 2 Maximum net photosynthetic rate for seedlings of <i>P. tomentosa</i> and <i>T. orientalis</i> grown under different light regimes				
树种 Species	光环境 Light regimes			
	3.1%/12.5%	12.5%/12.5%	9%/36%	25%/36%
绒毛番龙眼 <i>P. tomentosa</i>	4.1824±1.5270A,a	3.9625±0.3824A,a	3.1044±0.1978A,a	4.5837±0.8073A,a
山黄麻 <i>T. orientalis</i>	14.9417±1.3477A,b	15.4952±0.4929A,b	20.8699±0.3809B,b	22.4585±0.5112B,b

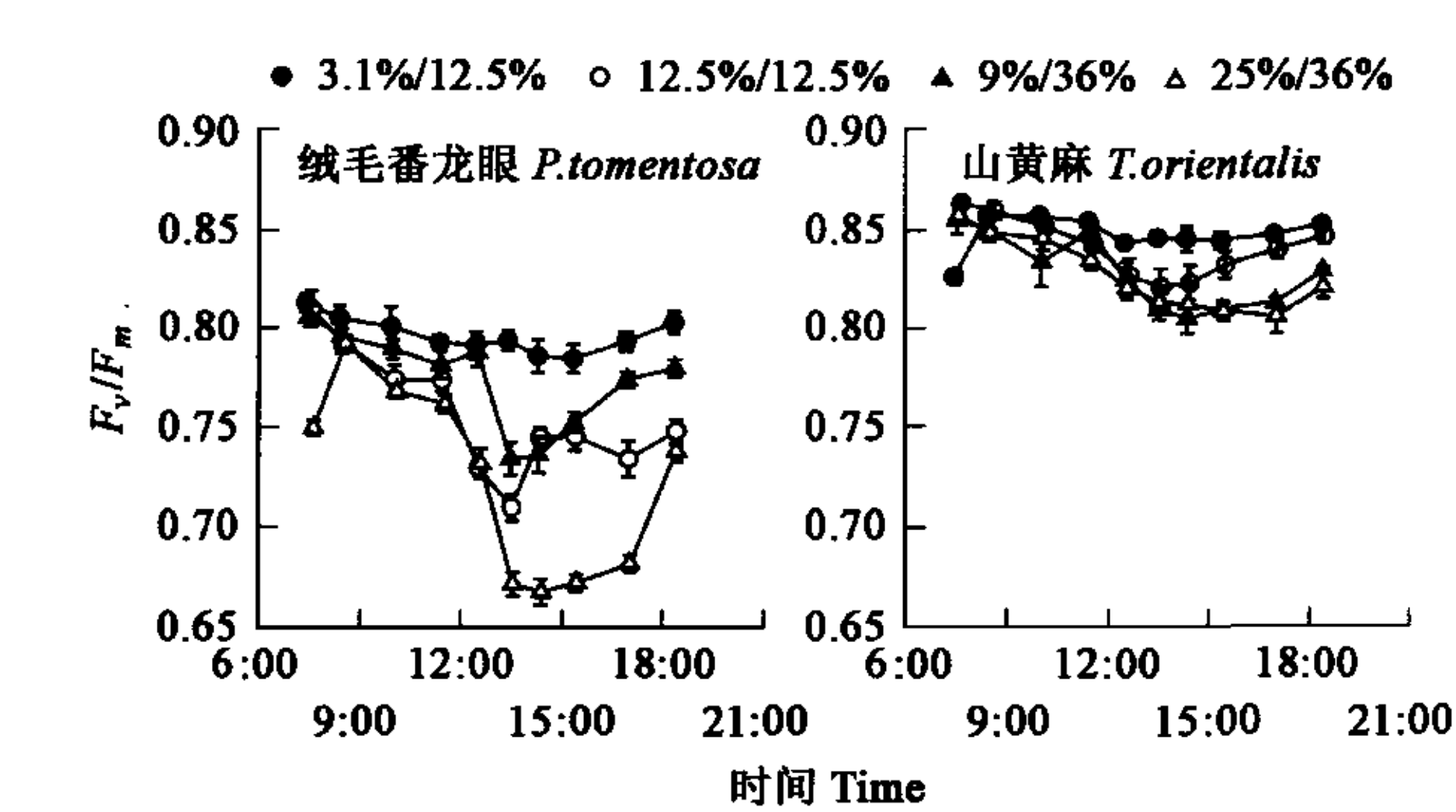


图 1 不同光环境下生长的绒毛番龙眼和山黄麻幼苗光系统 I 最大光能转换效率 (F_v/F_m) 日变化

Fig. 1 The diurnal changes of maximum efficiency of PS I photochemistry (F_v/F_m) for *P. tomentosa* and *T. orientalis* grown under different light regimes

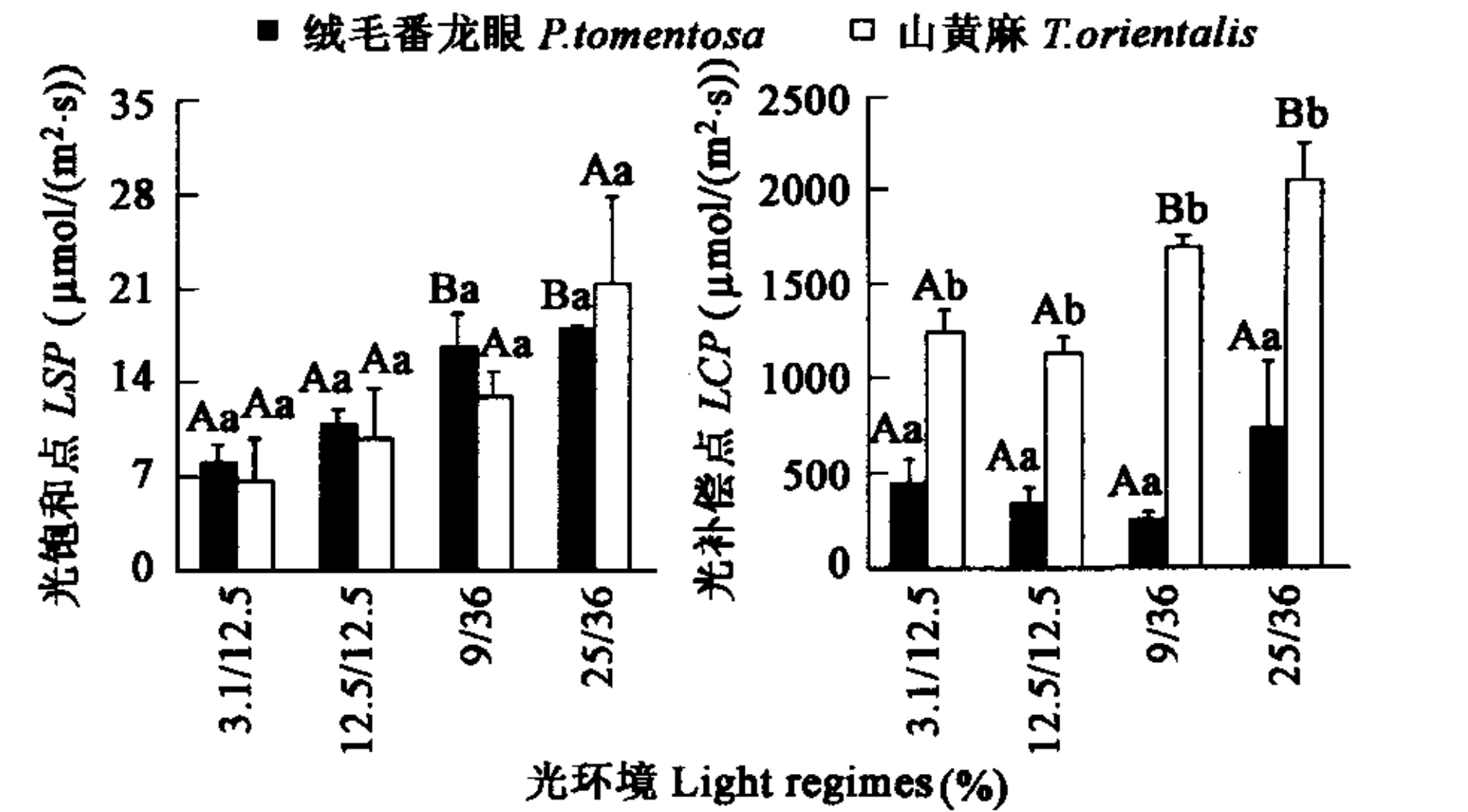


图 2 不同光环境下生长的绒毛番龙眼和山黄麻幼苗光饱和点 (LSP) 和光补偿点 (LCP)

Fig. 2 Light saturation point (LSP) and light compensation point (LCP) for *P. tomentosa* and *T. orientalis* grown under different light regimes

2.3 生长环境光强对 2 种植物热耗散速率的影响

各光强下生长的绒毛番龙眼和山黄麻非光化学猝灭系数 (NPQ) 的日变化表明(图 3), 上午热耗散随日间光强的增大而增多, 达最大值后随光强的减弱而减少。强光下生长的植物热耗散多于弱光下生长的同种植物, 25%/36%和 12.5%/12.5%光强下生长的 2 种植物的热耗散分别多于 9%/36%和 3.1%/12.5%光强下的同种植物。相同光强下绒毛番龙眼热耗散多于山黄麻, 并且人为调节上午光强对绒毛番龙眼热耗散的影响明显大于对山黄麻的影响。

2.4 生长环境光强对 2 种植物光合色素含量和比叶重 (LMA) 的影响

随生长光强的增大, 山黄麻叶绿素 (Chl) 含量降低, 9%/36%和 25%/36%光强下的值显著低于 3.1%/12.5%光强下的值; 各生长光强下绒毛番龙眼 Chl 含量差异则不显著。相同光强下 2 种植物 Chl 含量差异不显著(表 3)。

随生长光强的增大, 山黄麻类胡萝卜素 (Car) 含量降低。生长在 9%/36%和 25%/36%光强下的值均显著低于生长在 3.1%/12.5%光强下的值。但随生长光强的变化绒毛番龙眼 Car 含量差异不显著。3.1%/12.5%和 9%/36%光强下, 两种植物 Car 含量差异显著; 12.5%/12.5%和 25%/36%光强下, 两种植物 Car 含量差异不显著。 Car 可耗散过剩光能, 清除活性

氧^[29,30],从而保护光合机构。为了解不同光强下生长的 2 种植物光能吸收与光保护的关系,测定了叶片叶绿素/类胡萝卜之比(Car/Chl)。结果表明,随生长光强的增大 2 种植物 Car/Chl 呈升高趋势,保护功能逐渐增强,9%/36%和 25%/36%光强下生长的山黄麻 Car/Chl 均显著高于 3.1%/12.5%光强下的值(表 3)。

2 种植物 3.1%/12.5%和 12.5%/12.5%光强之间、9%/36%和 25%/36%光强之间的色素含量差异不显著(但 12.5%/12.5%光强下生长的绒毛番龙眼 Car 含量显著高于 3.1%/12.5%光强下生长的绒毛番龙眼,25%/36%光强下的山黄麻 Car/Chl 显著高于 9%/36%光强下生长的山黄麻)。

随着生长环境光强的减弱,2 种植物的 LMA 显著降低(表 4)。弱光强下 LMA 降低,单位干重叶面积增大,导致干重叶的捕光能力增强,利于在弱光环境中生长^[1]。随生长环境光强的减弱,山黄麻变化更明显。相同光强下,绒毛番龙眼 LMA 显著大于山黄麻。

表 3 不同光环境下生长的绒毛番龙眼和山黄麻幼苗叶片单位干重叶绿素(Chl)、类胡萝卜素(Car)含量和 Chl/Car
Table 3 Contents of chlorophyll (Chl) and carotenoid (Car) per unit dry weight, and Chl/Car for seedlings of *P. tomentosa* and *T. orientalis* grown under different light regimes

树种 Species	参数 Parameters	光环境 Light regimes			
		3.1%/12.5%	12.5%/12.5%	9%/36%	25%/36%
绒毛番龙眼 <i>P. tomentosa</i>	Chl(mg/g)	5.1587±0.4404Aa	4.1803±0.1691Aa	4.2140±0.3156Aa	4.3952±0.6664Aa
	Car(mg/g)	1.8739±0.0971Aa	1.4448±0.0498Ba	1.6334±0.1243ABa	1.7525±0.2030ABa
	Car/chl	0.3655±0.0149Aa	0.3930±0.0078Aa	0.3876±0.0056Aa	0.4039±0.0171Aa
山黄麻 <i>T. orientalis</i>	Chl(mg/g)	4.5325±0.1779Aa	3.7296±0.4181ABa	3.4967±0.1265Ba	2.9451±0.3375Ba
	Car(mg/g)	1.5184±0.0630Ab	1.2808±0.1284ABa	1.2074±0.0433Bb	1.1238±0.1101Ba
	Car/chl	0.3350±0.0018Aa	0.3442±0.0039ABb	0.3453±0.0031Bb	0.3834±0.0089Ca

表 4 不同光环境下生长的绒毛番龙眼和山黄麻幼苗比叶重(g/m²)
Table 4 Lamina mass per unit area for *P. tomentosa* and *T. orientalis* grown under different light regimes

树种 Species	光环境 Light regimes			
	3.1%/12.5%	12.5%/12.5%	9%/36%	25%/36%
绒毛番龙眼 <i>P. tomentosa</i>	36.0042±0.3575Aa	37.4934±0.3317Ba	44.1427±0.1568Ca	46.0851±0.2882Da
山黄麻 <i>T. orientalis</i>	23.7183±0.2578Ab	26.7628±0.3530Bb	35.8032±0.3532Cb	44.3575±0.5338Db

3 讨论

各光环境下生长的山黄麻均发生了日间光抑制,但 F_v/F_m 降幅较小,日间光抑制不强,即使在 25%/36%光强下下午光最强时 F_v/F_m 也在 0.8 以上,且随光强的减弱基本能恢复到黎明前的水平(图 1),表明没有发生光合机构的破坏^[13]。12.5%/12.5%、9%/36%和 25%/36%光强下生长的绒毛番龙眼 F_v/F_m 降幅较大,25%/36%光强下下午光最强时 F_v/F_m 降到了 0.7 以下,且 19:00 光照强度较弱时仍未恢复到天亮前的水平。相同光环境下绒毛番龙眼光抑制均较山黄麻重。上午人为降低光强均能缓解绒毛番龙眼光合作用光抑制,而对山黄麻影响不大(图 1)。

随生长环境光强的增大 2 种植物的热耗散均增多,这与文献的报告是一致的^[10,32,25,33],但先锋种山黄麻热耗散增加不显著,在日间光强最高时 NPQ 也没超过 1,演替后期物种绒毛番龙眼热耗散增加显著,25%/36%光强下其 NPQ 达 3 以上(图 3)。热耗散可以保护光合机构^[34,35,25]。25%/36%和 9%/36%光强下,山黄麻 P_{max} 分别为 22.46 和 20.87 $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$,显著高于 12.5%/12.5%和 3.1%/12.5%光强下的值(分别为 15.50 和 14.94 $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$)。但各光环境下生长的绒毛番龙眼 P_{max} 差异不显著,维持在 4 $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$ 左右。其它耐荫树种,如玉蕊和滇南红厚壳等^[1,36]也有相似情况,随生长环境光强的增大 P_{max} 升高也不显著。相同光强下先锋种山黄麻 P_{max} 显著高于绒毛番龙眼。不同光环境下其它需光植物,如团花树^[1,36]、野桐、紫茎泽兰^[37]、飞机草、兰花菊三七^[38]等的 NPQ 和 P_{max} 也与山黄麻的变化规律相似,即随生长环境光强的增大, P_{max} 显著升高,而 NPQ 增加不显著。Scholes 等^[10]发现强光下热带先锋树种和需强光的龙脑香科植物主要是通过提高 P_{max} 来保护光合机构,而它们的

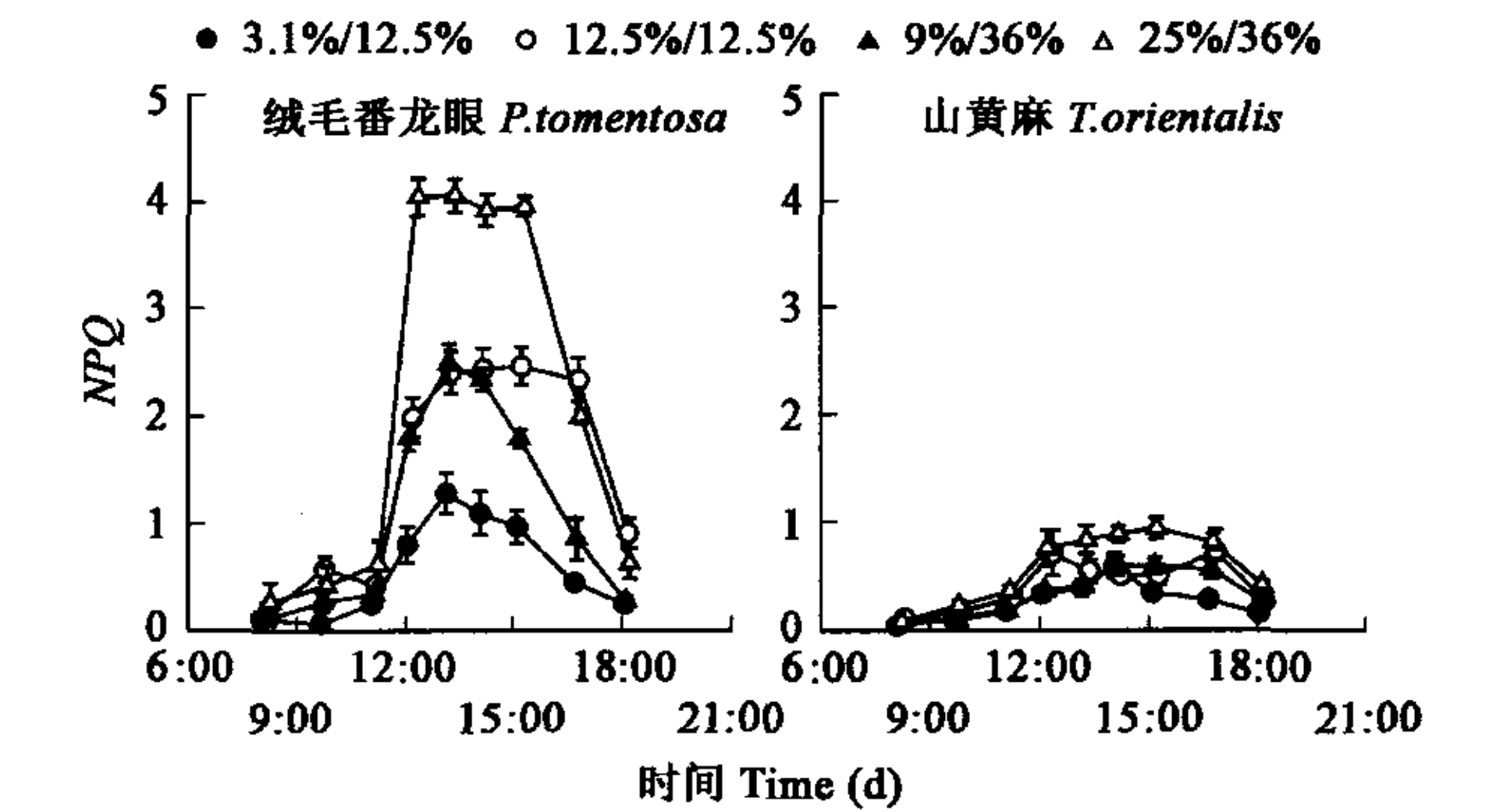


图 3 不同光环境下生长的绒毛番龙眼和山黄麻幼苗非光化学猝灭系数(NPQ)的日变化
Fig. 3 The diurnal changes of non-photochemical quenching efficiency (NPQ) for *P. tomentosa* and *T. orientalis* grown under different light regimes

热耗散并不比耐荫树种多,这与先锋树种山黄麻情况相似。可以推测,需光种主要通过提高 $P_{\max}$ 利用光能、而耐荫种主要是通过耗散光能适应强光环境的。

绒毛番龙眼热耗散较多与其具有较高的 Car 含量有关(表 3),Car 中的一些组分是热耗散所必需的^[30]。随着生长光强的增大,2 种植物的 Car/Chl 比均升高。Garcia-Plazaola 等^[39],Munné-Bosch 和 Alegre^[40]认为,胁迫时植物能通过增加叶片 Car/Chl 比来保护光合机构免受光破坏。 LMA 与叶片厚度有关,一般情况下 LMA 低的叶片就薄。叶片吸收的光能是光合色素含量和叶片厚度的函数,色素含量低、叶片薄吸收的光能就少。相同光强下山黄麻的 Chl、Car 含量(表 3)和 LMA (表 4)均低于绒毛番龙眼,表明单位面积叶片山黄麻吸收的光能少于绒毛番龙眼。山黄麻较高的 $P_{\max}$ 基本能利用掉叶片吸收的光能,可以有效地防止光合机构的光破坏。强光下植物降低叶绿素含量也是一种适应强光的保护策略。

LMA 与植物叶片长期生长的光环境密切相关^[41]。弱光环境下 LMA 降低(表 4),单位干重叶的面积增大、捕光能力增强,增加叶片同化组织对输导组织和结构组织的相对比例^[42],利于碳的净积累^[43],是植物对弱光环境做出的典型的形态学反应^[12]。山黄麻低的 LMA 不仅可以减少单位面积叶片吸收的光能防止光抑制发生、增加单位干重叶光合速率^[1],还可以使它用等量的干物质制造更大的叶面积,从而利于植株水平的光能截获和碳积累。

虽然绒毛番龙眼的热耗散较多,但由于其 $P_{\max}$ 较低,25%/36%和 9%/36%光强下没有及时有效地利用和耗散掉吸收的光能,导致光抑制的发生。光抑制可以降低叶片或植株水平碳的积累。表明绒毛番龙眼幼苗不适宜在强光环境下生长,这与其在林下的分布是一致的。25%/36%和 9%/36%光强下山黄麻 $P_{\max}$ 较高(表 2),光抑制不严重(图 1),表明先锋种山黄麻适宜生长在强光环境下,这与其在林窗等光较强的环境中的分布是一致的。本研究结果支持树种的生理生态特性决定了其演替状况和生境选择的假说。演替早期种都是一些不耐荫的种类,光合速率高,生长快,寿命短,具有适应高光强的形态与生理特征。而演替后期树种光合速率低,生长慢,寿命长,幼苗对光抑制较敏感,不能生长在开阔的地方。随着演替早期树种的生长群落下层光强逐渐降低,这种荫蔽环境为演替中、后期物种的进入提供了条件,并且这些物种最终能替代先锋种。

上午光强度的改变对先锋树种山黄麻影响不大,对演替后期树种绒毛番龙眼影响较大。下午光强相同,上午两种光强下山黄麻光抑制程度、热耗散和光合能力等差异均不大;上午光强低时绒毛番龙眼光抑制比光强高时轻且易恢复、热耗散比光强高时少,下午处理光越强这种趋势越明显。表明上午一定程度的遮光(如有雾)可减缓绒毛番龙眼光抑制。如遇低温上午遮荫的效果更明显^[44],雾凉季西双版纳地区有夜间低温,夜间低温可以加剧热带植物光抑制。上午雾使光强减弱,缓解了低温、强光对本区敏感植物的危害,推测雾与本区热带雨林和热带作物的分布有一定的关系。

4 结论

在一定光强范围内随生长环境光强的升高,山黄麻和绒毛番龙眼幼苗 LMA 、 NPQ 、Car 含量、Car/Chl 比升高, LSP 和 LCP 也有随生长环境光强的增大而升高的趋势,Chl 含量降低,2 种树苗均能通过形态和生理特性的改变适应不同的光强环境。相同的生长光强下,演替后期种绒毛番龙眼光抑制明显比先锋种山黄麻重,山黄麻适应强光的能力强。先锋种山黄麻主要通过提高 $P_{\max}$ 利用光能,而演替后期种绒毛番龙眼却较大程度地通过增强非光化学猝灭来耗散过量光能防止光合机构光破坏。上午人为降低光强度对先锋种山黄麻影响不大,但可以明显缓解演替后期树种绒毛番龙眼的光抑制,表明雾使上午光强降低可缓解绒毛番龙眼的光抑制。

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