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栲树冠层光合生理特性的空间异质性*

孟 陈[1] 徐明策[1] 李俊祥[1,2]** 高三平[1]
([1]华东师范大学环境科学系, 上海 200062; [2]华东师范大学上海市城市化生态过程与生态恢复重点实验室, 上海 200062)

摘 要 森林冠层在能量传输、光合有效辐射和微气象等方面的差异可导致冠层光合生产力空间分布的变化. 叶片光合生理特性在空间上的差异对精确估算森林冠层的初级生产力十分重要. 本文以亚热带常绿阔叶林优势种——栲树(*Castanopsis fargesii*)为对象, 研究叶片光合生理特性在冠层空间上的变化. 结果表明: 1)在垂直方向上, 冠层北向叶的饱和光合速率(A_{max})、光饱和点(LSP)和 CO_2 羧化效率(CCE)均表现为上部>中部>底部, 且依次平均降低19.4%、18.1%和37.1%; 光补偿点(LCP)、光下暗呼吸(R_d)以及冠层南向叶的饱和光合速率、光饱和点和 CO_2 羧化效率均表现为上部>底部>中部, 上部比中部和底部高出12.3%～71.4%; 表观量子效率(AQY)表现为底部>上部>中部, 底部分别是顶部和中部叶的1.2和1.3倍; 2)在水平方向上, 冠层上部和底部南向叶的饱和光合速率、光饱和点和 CO_2 羧化效率比北向叶高0.9%～31.5%; 冠层中部北向叶的饱和光合速率等6个参数比南向叶高9.6%～63.2%. 因此, 在冠层水平上模拟和估算植物生产力时, 必须考虑冠层光合生理特性的空间差异.

关键词 亚热带常绿阔叶林 栲树 光合生理特性 林冠 空间异质性
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Spatial heterogeneity of photosynthetic characteristics of *Castanopsis fargesii* canopy. MENG Chen[1], XU Ming-ce[1], LI Jun-xiang[1,2], GAO San-ping[1] ([1]*Department of Environmental Science, East China Normal University, Shanghai* 200062, *China*; [2]*Shanghai Key Laboratory of Urbanization and Ecological Restoration, East China Normal University, Shanghai* 200062, *China*). -*Chin. J. Appl. Ecol.*, 2007, **18**(9): 1932-1936.

Abstract: The vertical and horizontal differences in the energy transmission, photosynthetically active radiation, and micrometeorological characteristics of forest canopy can lead to a considerable heterogeneity, which should be analyzed when estimating forest primary productivity. With *Castanopsis fargesii*, the dominant species in the subtropical evergreen broad-leaved forest in Tiantong National Forest Park of Zhejiang Province as test object, this paper studied the vertical and horizontal variations of photosynthetic characteristics of its canopy. Vertically, the photosynthetic indices such as maximum photosynthetic rate (A_{max}), light saturation point (LSP), and carboxylation efficiency (CCE) of north-facing leaves in the canopy all declined in the sequence of top canopy > mid-canopy > bottom canopy. The mean values of light compensation point (LCP), respiration in light (R_d), and A_{max} from top canopy to bottom canopy reduced by 19.4%, 18.1% and 37.1%, respectively. The LSP and CCE of south-facing leaves followed the pattern of top canopy > bottom canopy > mid-canopy. These two indices decreased by 12.3% in bottom canopy and 71.4% in mid-canopy, compared with those in top canopy. The apparent quantum yield (AQY) of leaves followed the sequence of bottom canopy > top canopy > mid-canopy, being 1.1 and 1.3 times higher at bottom canopy than at top- and mid-canopy, respectively. Horizontally, the A_{max}, LSP and CCE of south-facing leaves at top- and bottom canopy were 0.9%-31.5% higher than those of north-facing leaves. In mid-canopy however, the values of test six indices of north-facing leaves were 9.6%-63.2% higher than those of south-facing leaves. It was suggested that in order to estimate and model forest primary productivity accurately, the vertical and horizontal heterogeneity of photosynthetic characteristics of forest canopy should be analyzed.

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**通讯作者. E-mail: jxli@des.ecnu.edu.cn
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Key words: subtropical evergreen broad-leaved forest; *Castanopsis fargesii*; photosynthetic characteristic; forest canopy; spatial heterogeneity.

1 引 言

林冠是森林与外界环境相互作用最直接和最活跃的界面层,是当今生物多样性和全球气候变化研究的焦点[7,15,22]. 由于林冠结构和几何特征对太阳辐射和降水的影响[13],使能量传输和分配在冠层呈现空间异质性[14,18,29],从而导致光合作用在冠层空间上的变化. 国外对冠层光合作用的研究进行的较早[6,8-9,16,19-20,23],并相应发展了冠层光合作用模型,如大叶片模型[1](big leaf model)、分层模型[11](multilayer model)和二叶模型[12,21](two-leaf model)等. 它们以植物生理和物理过程为基础,耦合叶片光合作用、气孔导度和蒸腾作用等子模型对冠层光合作用进行模拟,主要考虑生理和环境参数在垂直方向上的梯度变化,并假定水平方向上的状态参量是匀质的[25]. 国内肖文发[24]、张小全等[26-27,29]对杉木(*Cunninghamia lanceolata*)冠层光合作用进行了较系统的研究. 但对亚热带常绿阔叶林冠层光合作用的研究鲜见报道. 亚热带常绿阔叶林是我国面积最大的森林类型,在世界森林植被中具有重要的作用和地位[17]. 栲树是亚热带常绿阔叶林的优势树种之一,周莉等[31]、丁圣彦等[4-5]和赵广东等[30]对其光合作用的日动态、不同演替阶段和不同叶龄的光合生理生态特性进行了研究和对比,但没有涉及冠层光合生理特性的空间异质性. 本文定量研究了栲树冠层光合生理特性在冠层空间上的差异,旨在为在冠层水平上精确估算植物生产力,以及进一步估算亚热带常绿阔叶林生产力的尺度推绎和模型耦合提供参考.

2 研究方法

本研究在浙江省宁波市鄞州区天童国家森林公园内进行, 自然概况参见文献[5]. 选择当地演替顶级群落——栲树 +木荷群落(*Castanopsis fargesii* + *Schima superba community*)内的优势种——栲树成年个体为研究对象,在 30 m高的铁塔活动平台上对其冠层不同部位叶片的生理生态特征进行观测. 栲树冠层在垂直方向分为顶部(20 m)、中部(18 m)和底部(16 m)3个部分;在水平方向,根据冠层受光情况,分为南向叶和北向叶.

在栲树 +木荷群落中,选择铁塔南北两侧两株冠形和年龄相似的栲树为标准木,按照冠层的空间分层部位,每个处理选择 3～5片长势良好的同龄功能叶进行生理生态观测. 在 2006年 4月 17—21日(晴天无云)的 9:00—15:00,分别观测栲树冠层各叶片的光、CO_2 反应曲线. 光反应曲线:利用 Li-6400便携式光合作用仪红蓝光源控制实验叶室中的光量子通量密度(*PPFD*),在 0～2 000 μmol·m^{-2}·s^{-1}内设定若干梯度测定净光合速率,环境温度为 21 ℃～25 ℃;大气 CO_2 浓度为 377～386 μmol CO_2·mol^{-1}. 利用模型拟合计算光合作用的光补偿点(light compensation point, *LCP*)和表观光合量子效率等指标[10].

$$P_n = \frac{AQY \cdot PPED + A_{max} - \sqrt{\{(AQY \cdot PPFD + A_{max})2 - 4K \cdot AQY \cdot A_{max}\}}}{2K} - R_d$$

式中: P_n 为净光合速率(net photosynthesis rate, P_n); *AQY*为表观光合量子效率(apparent quantum yield, *AQY*); *PPFD* 为光量子通量密度(photosynthetic photon flux density); A_{max}为饱和光合速率(maximum photosynthetic rate); *K*为曲线的弯曲程度(convexity); R_d 为光下暗呼吸速率(respiration in light).

CO_2 反应曲线:在饱和光强 800 μmol·m^{-2}·s^{-1}下,利用 Li-6400-01液化钢瓶控制参比叶室中的 CO_2 浓度,在 0～800 μmol CO_2·mol^{-1}内设定若干浓度梯度测定净光合速率,环境温度为 21 ℃～25 ℃. 选择胞间 CO_2 浓度(C_i)小于 200 μmol CO_2·mol^{-1}时做 CO_2 反应曲线,直线斜率为 CO_2 羧化效率(carboxylation efficiency, *CCE*)[10].

3 结果与分析

3.1 光反应曲线在栲树冠层空间上的变化

从图 1可以看出:从冠层上部到底部,光反应曲线的曲率增大,从光抑制到光饱和的变化幅度增大,表明冠层中部和底部叶片对强光的适应能力较差;和冠层垂直变化相比,水平方向上叶片的光反应曲线变化差异相对较小. 同时,通过对光、CO_2反应曲

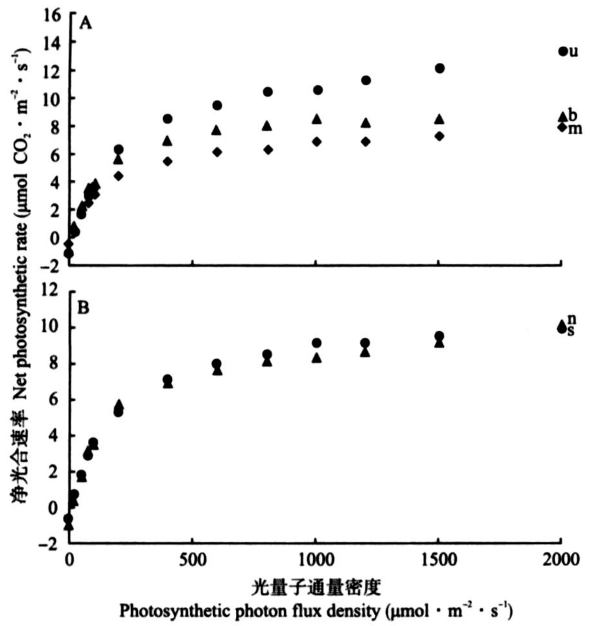

图 1 枹树冠层不同空间位置的光响应曲线

Fig. 1 P_n-*PPFD* curves in different positions in the canopy of *C. fargesii*

A:垂直方向 Vertical; B:水平方向 Horizontal u、m、b表示冠层垂直方向的上部、中部和底部; s、n表示冠层水平方向的南向和北向. 不同组合表示不同的位置,如 us表示冠层上部南向叶. The u, m and b showed the top, middle and bottom position of the canopy in vertical, respectively; the s and n denoted the southern and northern sides of the forest canopy. Their combinations represented the different positions in the forest canopy, *e. g.* us was the southern position at the top canopy. 下同 The same below.

线的数学拟合可以得到饱和光合速率 (A_{max})、表观量子效率 (*AQY*)和 CO_2羧化效率 (*CCE*)等参数,从而定量地反映冠层不同空间位置上叶片对光和 CO_2 变化的响应特征.

3.2 光合生理特性在枹树冠层空间上的变化

从图 2可以看出:在垂直方向上,枹树冠层光合生理特性的饱和光合速率、光饱和点、CO_2 羧化效率、光下暗呼吸和光补偿点的最高值均出现在冠层上部,分别为 16.90 μmol CO_2 · m^{-2} · s^{-1}、209.33 μmol · m^{-2} · s^{-1}、0.049、1.10 μmol CO_2 · m^{-2} · s^{-1} 和 16.85 μmol · m^{-2} · s^{-1},最高值出现在冠层底部的只有表观量子效率,为 0.07 mol CO_2 · mol^{-1};冠层北向叶的饱和光合速率、光饱和点和 CO_2 羧化效率呈上部 >中部 >底部,从冠层上部到底部依次平均降低 19.4%、18.1%和 37.1%;光补偿点、光下暗呼吸,以及冠层南向叶的饱和光合速率、光饱和点、CO_2 羧化效率表现为上部 >底部 >中部,上部比中部和底部高 12.3%～71.4%;表观量子效率表现为底部 >上部 >中部,底部表观量子效率分别是上部和中部的 1.2和 1.3倍. 表明在枹树冠层垂直方向上,冠层上部叶片的光合活性和生产力较高,但表观量子效率较低,对强光适应能力强;冠层底部光合活性和生产力较低,但具有较高的光能利用效率,可以充分利用冠层底部的散射光进行物质生产.

枹树冠层光合生理特性水平方向上的分布规律为:冠层上部南向叶的饱和光合速率、光饱和点和 CO_2 羧化效率分别比北向叶高 27.8%、11.6%和 6.6%,而光下暗呼吸、光补偿点和表观量子效率则

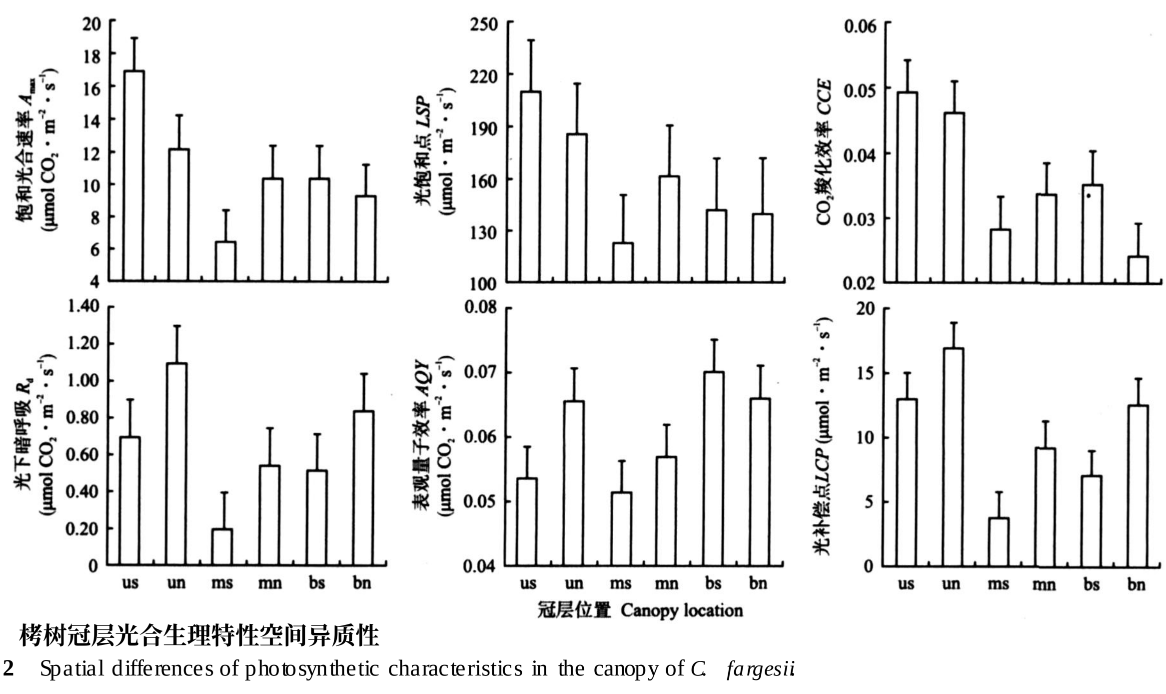

图 2 枹树冠层光合生理特性空间异质性

Fig. 2 Spatial differences of photosynthetic characteristics in the canopy of *C. fargesii*

为南向叶低于北向叶,分别低 36.2%、22.9%和 18.4%;冠层中部的饱和光合速率等 6个参数均表现为北向叶高于南向叶,分别高 9.6%～63.2%;冠层底部,饱和光合速率、光饱和点、CO_2 羧化效率和表观量子效率表现为南向叶大于北向叶,分别高 10.9%、0.9%、31.5%和 5.6%,光补偿点和光下暗呼吸则南向叶比北向叶分别低 43.4%和 38.9%. 表明冠层上部和底部南向叶的光合活性和生产力高于北向叶,但光能的利用效率南向叶低于北向叶.

4 讨　论

从以上分析可以看出,楮树冠层垂直方向上,饱和光合速率、CO_2 羧化效率、光补偿点、光饱和点和光下暗呼吸速率表现为冠层上部高于冠层中部和底部,而表观量子效率的变化趋势却相反,与前人的研究结果相似[8,11-12,21,24,26-28]. 其中,楮树冠层上部叶片的光合潜力最大,分别是中部和底部的 1.73和 1.50倍,杉木冠层垂直方向上也表现出相似的变化特征,冠层上部叶片的饱和光合速率是中部和底部的 1.1～1.7倍[24,26]; Gonzalez-Real等[6]研究玫瑰(*Rosa hybrida*)冠层垂直方向变化的范围在 1.1～1.8倍之间; Harley等[8]测定白橡(*Quercus alba*)和红枫(*Acer rubrum*)冠层上部叶的饱和光合速率(30 m)是底部叶(3～4 m)的 1.4倍. 可见,冠层光合生理特性在垂直方向上具有显著的差异,但在不同的生态系统和物种之间存在差异. 在本研究中,冠层水平方向上南向叶和北向叶的饱和光合速率的差异也在 1.1～1.4倍之间. 因此,研究森林冠层光合特性的空间异质性,对森林冠层光合生产力的尺度推绎和生产力精确估算模型的建立具有重要意义.

光补偿点、光饱和点和表观量子效率是指示植物光响应特征的重要指标. 光补偿点越低,对弱光的适应能力越强;饱和点越高,利用强光的能力越强;表观量子效率则反映叶片对光能的利用效率. 通过三者在楮树冠层空间上的变化,可以看出:楮树冠层上部叶片光合活性高,对强光利用能力强;而冠层中部和底部光合活性低但对弱光适应能力强. 从而使冠层整体光能的利用效率最高.

影响冠层光合生理特性空间异致性分布的原因很多,但主要是光环境的差异[3,24,26-27,29]. 由于冠层结构的几何特征,光在冠层中的传输和分配符合比尔定律[2,29],从冠层上部到底部光通量呈指数函数衰减;同时由于冠层上部叶片对光合有效辐射的选择性吸收和反射,冠层中部和底部的光合有效辐射显著下降,底部的光合有效辐射不足冠层上部的 10%[10]. 叶片在新老交替的过程中,新叶生长位置的光环境会直接影响叶片的形态建成和光合生理特性. 光斑出现的几率和持续的时间对冠层的光环境也具有重要的影响[18],再加上叶龄[24,26,30]、季节变化[26]等对叶片光合生理特性的影响,使冠层光合作用的研究变得更为复杂和具有挑战性.

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作者简介 孟 陈,男,1979生,硕士研究生.主要从事植物生理生态、景观生态研究,发表论文 1篇. E-mail: dingdong936@163.com

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