

人工林生产力年龄效应及衰退机理研究进展

毛培利¹, 曹帮华^{2,*}, 田文侠³, 孟凤芝³

(1. 中国科学院烟台海岸带研究所滨海湿地生态实验室, 中国科学院、山东省海岸带环境过程重点实验室 烟台 264003;
2. 山东农业大学农业生态与环境重点实验室, 泰安 271018; 3. 山东省林业监测规划院 济南 250014)

摘要: 同龄林林分郁闭后, 地上部净初级生产量随着林龄增加而降低的现象近几十年引起了林业工作者的兴趣和注意并成为研究热点。多数研究试图通过光合生理、林分营养、生物量分配和林分结构等随林龄的变化规律来解释林分生产力衰退机理。研究认为, 林分郁闭后水分传输阻力的增加减少了树木的光合能力; 林地养分的减少使得根系生物量分配增加, 导致林分叶面积减少, 树木光合能力下降; 对资源的竞争使得树木优势度发生变化, 资源利用率降低。光合能力、林分叶面积和资源利用率的降低以及根系生物量分配的增加是林分生产力衰退的关键, 而林分呼吸和林木衰老的作用不大。今后深入研究树木水分运输及其补偿机制、逆境下根系的生长过程及适应机制, 并跟踪研究林分生长规律, 更有助于揭示人工林生产力衰退的实质。

关键词: 生长过程; 林龄; 地上部净初级生产量

Advances in research on the mechanisms of age-related productivity decline of planted forests

MAO Peili¹, CAO Banghua^{2,*}, TIAN Wenxia³, MENG Fengzhi³

1 Laboratory of Coastal Wetland Ecology Key Laboratory of Coastal Zone Environment Processes, CAS, Shandong provincial Key Laboratory of Coastal Zone Environment Processes, Yantai Institute of Coastal Zone Research, Chinese Academy of Sciences, Yantai 264003, China

2 Key Laboratory of Agricultural Ecology and Environment, Shandong Agricultural University, Taian 271018, China

3 Shandong Provincial Academy of Forestry, Jinan 250014, China

Abstract: In forestry, it is of both economic and ecological significance to study the growth dynamics of plantations. In an even-aged plantation, the above-ground net primary productivity usually decreases with age following the canopy closure. The mechanisms and potential causes conducive to the decline in above-ground net primary productivity have attracted considerable attentions from forest ecologists and resource managers during the recent decades, and has become a hot topic of research in recent years. A number of hypotheses have been proposed, attempting to explain the net primary productivity decline through the change in foliage photosynthetic capacity, tree nutrition, allocation of above- and below-ground biomass, and stand structure, etc accompanying stand age. The decrease in leaf area following canopy closure is believed to be one of the significant contributing factors of reduced above-ground net primary productivity. The hydraulic limitation hypothesis ascribes the decrease in above-ground net primary productivity to reduced foliage photosynthetic capacity resulting from the increase in xylem hydraulic resistance as trees grow taller. But it fails to explain the rapid decrease in net primary productivity following canopy closure, which may be related to the compensation mechanisms adopted by trees of varied sizes. As a compensation for the decrease in hydraulic conductance as a tree grows taller, it usually increases its sapwood area in relation to foliage area, and accordingly, increases respiration of woody tissues. However, there is lack of experimental data to support the hypothesis that the increase in woody tissue respiration contributes the decrease in stand productivity. The nutrient limitation hypothesis postulates that gradual depletion of soil nutrient reserves may cause the decrease in net primary productivity of plantations. Because soil nutrient depletion may directly increase below-ground root

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* 通讯作者 Corresponding author. E-mail: caobh@sdau.edu.cn

biomass and relatively decrease leaf area and foliage photosynthetic capacity. This hypothesis may explain the decrease in net primary productivity observed in some old stands. There are other evidences that intense intra-specific competition for limited resources and resultant tree discrimination among individuals may, to certain extent, result in the decrease in resource utilization efficiency and net primary productivity. Although senescence-associated genetic variation as a tree is aging plays an important role in the decrease in tree growth, it appears tree size rather than age is more closely related to tree growth. In summary, the decrease in foliage photosynthetic capacity, foliage area and resource utilization efficiency as well as the increased allocation of below-ground root biomass are the major contributing factors of the decrease in net primary productivity of plantations, whereas tree respiration and senescence only play a marginal role in the decline of stand growth. In the future, it will be beneficial to understanding of the mechanisms of the decline in net primary productivity and plantation growth to study hydraulic conductivity and compensation mechanisms, root growth and adjustment under stressed environment, and monitor the dynamics of plantation growth.

Key Words: growth process; stand age; above-ground net primary production

随着林龄的增加, 同龄林地上部净初级生产量随着林分叶面积的增加而迅速增加, 在林分叶面积达到最大值时地上部净初级生产量也达到最大值, 随后迅速下降, 林分叶面积也随之降低。人工林郁闭后地上部净初级生产量降低的现象被称为生产力衰退。人工林生产力衰退是一个复杂的过程, 影响因素很多。林分郁闭后叶面积的降低会引起林分碳吸收的减少, 但树木生长效率和叶面积的变化并不同步^[1], 说明叶面积的降低不是林分净初级生产量降低的唯一原因^[2]。立地质量、林分密度以及树木个体的生长规律都对同龄林净初级生产量有着重要影响。立地质量越高, 林分净初级生产量达到最大值越快, 随后净初级生产量下降速度也越快^[2]; 林分密度越大, 林分净初级生产量下降越早^[1]; 树木个体随树龄增加生长效率也逐渐降低^[3-4]。

近几十年关于人工林生产力衰退研究很多^[2, 5-6], 近年来逐步成为一个研究热点^[7-9], 研究主要集中在林分光合生理、林分营养、林分生物量分配、林分结构随林龄变化的规律。提出的假说主要包括: (1) 林分光合与呼吸的不平衡变化^[5]; (2) 水力限制假说^[10]; (3) 细胞膨压的降低^[11]; (4) 营养可利用性的减少^[12]; (5) 林分地下部碳分配的增加^[13]; (6) 遗传程序决定的树木顶端分生组织老化^[14]; (7) 林分发育过程中优势木的变化^[15]。尽管如此, 目前人们对其机理还不明确。充分理解林分生长规律, 对全球碳循环、陆地森林生产量、森林病虫害和经济林产量预测都有着重要的意义^[2]。

1 林分光合生理

1.1 光合作用

树木捕获和利用太阳能的能力决定了光合产物和固定碳的数量。在林分发育过程中, 光合作用的降低是引起林分净初级生产量降低的重要原因, 主要包括 3 个方面: 叶面积的减少、光合能力和光合性能的降低。

叶面积的多少直接决定了林分光合作用的能力。林分郁闭后叶面积的降低是林分净初级生产量降低的重要原因。在林分叶面积达到最大值后, 3 种机理可以解释叶面积的降低: 林分营养元素的变化、树冠之间磨损及死亡树木个体的增加。对 *Pinus contorta* 同龄林的研究表明, 随着林龄的增加, 林地的营养元素可利用性降低^[12], 叶面积的变化与营养可利用性密切相关^[16]。氮可利用性的降低通常会造树木增加地下部生物量的分配以便获得更多的营养元素。营养可利用性降低会使叶片光合酶浓度降低, 造成光合能力和碳固定量降低, 进而造成叶片生物量分配降低, 减少新生叶片。树高的增加引起叶片细胞膨压降低, 限制了叶片和分枝的生长^[11]; 而树冠相互磨损的加剧也会造成林分叶面积的减少^[17]。同时随着林龄的增加, 树木个体死亡引起的叶面积减少由于不能被弥补, 也造成了林分叶面积的减少。但是林分郁闭后树木生长效率和叶面积的变化并不同步, 说明叶面积的降低不是林分净初级生产量降低的唯一原因^[2]。

随着林龄的增加, 树木叶片的光合能力降低。Schoettle^[18]对 *Pinus aristata* 的研究表明, 老龄树的光合能力、气孔导度和叶氮含量都低于幼龄树。对于 *Sequoiadendron giganteum*, Grulke 和 Miller^[19]发现, 随着树龄增

加叶片最大净光合速率、呼吸速率和气孔导度等逐渐降低。光合能力的降低使得林分碳固定效率降低,枯落物的质量降低。高的碳氮比使更多的氮被固定,而氮可利用性降低则加速叶片氮含量的减少,进一步使光合能力降低^[2]。

叶片光合性能与光合能力变化不完全同步。老龄林和幼龄林的叶片可能有着相似的光合能力,但光合速率日变化却不同,这主要是由于老龄树的气孔导度在日变化过程中比幼树降低的早,使得日总碳同化量较低,光合性能降低^[4]。Yoder 等人^[4]推测这可能是由于随着树高和枝条长度增加,树木的水力阻力增加引起的。有证据表明,随着树高^[4]和枝条长度^[20]的增加,水力阻力增加。树木为了维持叶片水势在某一阈值之上,避免发生木质部气穴现象,通常降低叶片气孔导度。气孔的关闭在一定程度上起到了维持叶片水势的作用^[21],但限制了 CO₂ 的扩散,造成了日光合产物的降低^[22]。Delzon 和 Loustau^[23]认为,随着林龄的增加,林冠蒸腾速率的降低也与树木高度增加引起的水力导度降低相关。

总结树木光合生理随着树高或年龄的变化规律,Ryan 和 Yoder 提出了水力限制假说。水力限制假说认为随着树木高度增加,水分运输距离增加,造成了树木叶片比导率降低。如果高的树木通过气孔关闭来保持一个恒定的午间最小叶水势,相比矮的树木,需要在一个更低的叶片蒸汽压差下关闭气孔。叶片气孔的关闭降低了光合作用、树木的生长和树木潜在最大高度^[10]。验证水力限制假说的许多研究表明,虽然随着树高/年龄增加气孔导度降低,但不能完全解释林分郁闭后净初级生产量的快速降低^[8-9,24],认为它与植物的补偿机制有关。边材面积与叶面积的比值(A_s/A_l)随着树高的增加而增加,是植物适应水力导度降低的重要机制。对研究过的树种进行总结发现大部分植物 A_s/A_l 都是增加,但也有少数植物降低,其中的原因不是很明确^[25]。这表明在适应水力限制时,并不一定要减少树冠叶面积^[26]。但是 A_s/A_l 的单独增加并不能完全补偿由于运输距离增加引起的水力限制^[27-28]。在对 *Eucalyptus saligna* 的研究中,发现通过增加 A_s/A_l 和降低最小午间叶水势维持导管水流和树冠平均气孔导度^[24]。 A_s/A_l 的增加有可能会增加木质部的呼吸消耗,但这种消耗的增加不足以影响到树木的生长衰退^[6]。最小午间叶水势的降低则会增加木质部导管发生气穴现象的可能,减少运输水分的能力^[29],降低气孔的开放和光合作用^[24,30]。深入研究树木对水力限制的补偿机制,对阐明树木的光合生理随树高/年龄增加的适应机制有着重要意义。

1.2 呼吸作用

树木细胞正常生理的维持和新细胞的生长需要消耗大量的能量,这需要消耗相当部分的光合产物。树木的叶片、细根和木质部边材薄壁组织细胞可以消耗 50%—70% 的光合产物^[31]。由于树木大量的呼吸消耗,使得早期研究认为随着林龄的增加,木材生物量降低主要是由于呼吸增加所致。但是直接测量 *Pinus aristata* 的呼吸速率以及对一些发表的与呼吸速率相关文献的总结,认为木本组织呼吸的增加不足以引起与年龄相关的林分净初级生产量的降低^[6]。这是因为树干含有很少的活细胞,而且边材只占很小的生物量比,因此呼吸速率在木质部组织中很低。随着树木的生长,木本组织的呼吸会逐渐降低^[31],而且只使用了很小一部分全年的光合产物(5%—12%)^[32]。虽然叶片和细根的呼吸速率比木本组织大的多,但是随着林分的发育,这两部分的呼吸速率却不会增加。如果叶面积不变化,则叶呼吸消耗不会增加;而如果叶面积降低,则会降低^[33]。对于细根呼吸的了解目前不够深入,而对根系周转速率或根系分泌物和真菌碳分配的研究可能比细根呼吸的变化更有意义。

2 林分营养元素

随着林分的不断发育,营养元素会逐渐积累在植物体内。Pearson 等人^[34]发现, *Pinus aristata* 体内的氮或其它元素的积累速率达到最大值时与树木干材增长速率达到最大值同步,然后降低。*Eucalyptus grandis* 人工林和 *Eucalyptus pilularis* 人工林都是在林分郁闭时年营养物积累速率达到最大^[35]。对不同林龄的针叶混交林研究发现,氮矿化速率随着林龄的增加不断降低^[36]。但对哥斯达黎加的两块相邻的低地雨林,老龄林与 4 年生幼龄林之间的氮矿化速率没有显著差异^[37]。营养元素累积速率的降低可能与树木利用养分元素的能力降低或者是营养元素供应量减少有关。随着林龄的增加,土壤供给营养元素的降低可能与营养元素在树木体内

大量积累^[12]或者是木材分解过程中被固定下来有关^[13]。

营养元素的供应与林分净初级生产量密切相关。随着林龄的增加, 营养元素供应的减少降低了叶片的光合能力^[9]和林分叶面积^[16], 使得林分碳同化速率降低。树木为了获得更多的营养元素, 增加了对细根的碳分配^[16], 使得根系生物量分配增加, 减少了用于木质部生长的碳分配。因此, 碳同化效率的降低和根系生物量分配的增加造成了木质部生长速度的降低。

随着林龄的增加, 林分营养元素含量有着不同的变化规律, 有的减少^[12], 有的增加^[38], 有的是在中间年龄最小^[6]。营养元素供应(尤其是 N) 在干扰后, 大多数情况下会增加, 但这不是一个普遍的规律。因此, 营养元素供应对老龄林生长衰退有着一定的作用, 但不是普遍的^[2]。最近的研究表明土壤营养元素可利用性的降低不能完全解释年龄相关的生长降低^[7]。但是 Martin 和 Jokela^[39]认为林分生产力的降低在一定程度上是由土壤营养元素限制引起的。

3 林分生物量分配

生物量分配随着林分的不断发育有着不同的变化。在幼龄林阶段, 树木将更多的光合产物分配给叶片, 有利于叶片数的迅速增加。但是随着林冠逐渐郁闭, 分配给叶片的光合产物逐渐降低。由于树木会经历强烈的竞争胁迫, 因此将更多的生物量分配给树干有利于其高生长^[40]。在老龄林阶段, 虽然叶面积降低, 但由于树木数量的降低, 仍使得单株叶面积增加, 引起枝生物量分配的增加^[17]。

随着林分不断发育, 细根生物量的分配增加^[41], 根系的生物量分配也逐渐增加^[42], 这是地上部净初级生产量降低的重要原因。但是对于根系如何控制树木地上部生长的生理机制了解还不够深入^[43], 可能与削弱根系与水分的关系^[43]、降低营养元素吸收能力^[44]、改变从根系到叶片的激素变化^[45]等有关。

对繁殖的分配只占树木年碳同化量很小的一部分。但在一定程度上也会影响到植物的生长^[46]。对于随着林分发育如何变化研究则很少, 对发表文献的总结认为对繁殖的分配不能解释林分生长的衰退^[8]。

4 林分结构

动物和 1 年生植物存在着与年龄相关不可逆转的衰老过程。但对于多年生植物, 其分生组织不存在衰老现象^[8, 47-48]。通过嫁接试验, 发现从 *Pseudotsuga menziesii* 老树上截取的枝条嫁接到幼树的砧木上的幼苗仍然有着高的生长速率^[48]。而老龄林在疏伐之后, 老树的生长效率明显增加。这些都表明树龄增加不是生长衰退的主要原因^[49]。虽然 Day 等人^[14]认为随着分裂组织年龄的增加引起的基因变化对树木的生长衰退有着显著影响, 但是更多的研究表明树木的生长衰退与其大小更加相关, 而不是与年龄^[8-9, 48, 50]。

随着林分年龄的增加, 树木死亡将会增加。但是在这方面的研究较少。虽然老龄林的生长速率低于幼龄林^[6], 但是活着的树木生长可以抵消死亡树木造成的生产量的减少^[51]。因此, 增加的树木个体死亡不是引起年龄相关木材产量降低的主要原因^[2]。但是, 在最近的研究中, Berger 等人^[52]认为, 在林分生产力降低的开始阶段, 树木之间的竞争引起的树木个体死亡起到了主要作用, 而在随后的发育过程中, 由于树木死亡不断增加, 树木的生长不能抵消林分生产力的降低, 最终造成了林分生产力的降低。

林分结构的变化与林分生产力的降低密切相关。随着林分的不断发育, 树木的优势度发生变化^[15, 53-54]。树木优势度的变化与林分生产力的降低密切相关^[15, 54]。根据林分发育过程, Binkley 等人^[15]将林分优势度划分为 4 个阶段: 很小、强烈增加、下降和反向增加, 认为林分生产力的降低是在优势度产生的阶段出现的。优势树木使用了林分大量的资源, 资源使用效率低, 降低了木材生长效率, 与个体树木生理过程关系不大^[55]。但 Binkley 等人^[56]认为优势树木增加资源获得, 提高了资源使用效率, 保持高的生长速率; 而非优势树木生长速率降低, 主要由于低的资源获得和使用效率; 这两方面的结合使得林分生长速率降低。在生理上, 可能是非优势木低的光合能力和光合性能造成了其较低资源使用效率。对桉树无性系人工林的研究表明, 优势木比非优势木有着高的树干生长速率、光截获效率和光使用效率^[57], 支持 Binkley 等人^[56]的观点。桉树个体大小差异小的林分有着高的光使用效率, 但不能降低与年龄相关的生长衰退^[57]。这些研究表明树木个体大小差异是林分生产力衰退重要原因, 但还存在着其它的作用因子。

5 研究展望

人工林生产力衰退是一个复杂的过程。Ryan 等人^[7]总结认为,人工林生产力的降低除与林冠光合作用的降低密切相关,如林分叶面积减少、叶片光合能力降低以及水力限制等,还与随林龄的增加树木对地下部生物量分配、叶片呼吸的增加有关;而与林地营养元素限制关系不大。Woodruff 等人^[11]研究表明,随着树高的增加,叶片细胞膨压的降低,限制了树木叶片和分枝的生长。渗透调节作用的增强,增加了对光合产物的消耗,进一步加剧了树木生长的降低。Ryan 等人^[58]指出,水力限制假说应该考虑补偿机制缓解水力导度限制的因素。

随着研究的深入,逐渐认识到衰退机理很复杂很难从单方面进行解释^[50]。大量相关文献支持随林分年龄增加叶面积降低是林分生产力降低的主要原因,但造成叶面积降低原因(如林分营养元素的变化、树冠之间的磨损、死亡树木个体增加等)的多样性增加了问题的复杂性;随着树木个体高度的增加,水分在体内的运输距离和高度增加,水力导度降低,叶片光合能力和光合性能降低是个必然出现的年龄过程,是人工林生产力衰退的重要原因;气孔在较低的蒸气压差下开始关闭、树木对根系生物量的分配增加,进一步加剧了叶片的数量和光合能力的变化,是人工林生产力衰退的间接因子。

事实上,人工林生产力的变化是个复杂的生理生态过程,许多内容包括影响林分郁闭后叶面积降低的主导因子、水力限制对光合能力的影响及其补偿机制、树木根系及林地养分随林分发育的变化规律、树木个体地上地下部分相关性 & 生物量分配格局、优势木与非优势木的资源使用效率差异等都有着这样或那样的影响;而逆境下林分生长衰退与逆境性质、强度、作用时间及其动态变化密切相关,衰退机理更为复杂,弄清这些问题有助于从根本上揭示林分生产力衰退的实质。

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