



碳供给与碳利用对树木生长的限制机制

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摘要 树木生长固碳过程使森林生态系统成为减缓大气CO₂浓度升高的一个巨大而持续的碳汇。根据树木可利用碳的状况, 限制树木生长的机制可分为碳供给限制和碳利用限制。许多环境因子交互作用, 共同影响树木的碳供给与碳利用, 因而很难量化碳供给和碳利用活动及其对环境变化敏感性对树木生长的影响。因此, 从碳供给与碳利用角度揭示环境变化对树木生长影响的生理机制, 对于预测全球变化背景下树木生长及森林碳汇功能至关重要。为此, 该文介绍了树木生长碳供给与碳利用限制争议的相关背景; 从碳供给与碳利用角度探讨了叶损失、干旱和低温等胁迫条件限制树木生长的生理机制; 提出该领域今后应优先研究的3个问题: (1)探索非结构性碳水化合物(NSC)储存形成的调控机制, 确定什么情况下以及多大程度上树木通过主动降低生长而将光合产物优先分配给NSC储存; (2)加强碳利用活动研究, 系统测定光合产物在其碳利用组分的分配(特别是根系及其共生微生物活动); (3)开展树木碳代谢、矿质营养与水分生理的互作研究, 充分认识树木碳、水和养分耦合关系及对树木生长的影响。

关键词 碳利用; 碳供给; 非结构性碳水化合物; 胁迫; 树木生长

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Mechanisms of carbon source-sink limitations to tree growth

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Abstract

Forests are large and persistent carbon (C) sink mainly through the C sequestration of tree growth, which can mitigate the rising rate of CO₂ concentration in the atmosphere. According to C availability in trees, two mechanisms involved in controlling tree growth are attributed to limitations to C input and C utilities. Since many environmental factors influence the activities of C-source and C-sink of trees interdependently, it is difficult to quantify how the sensitivity of C-source or C-sink activity to environmental changes affects tree growth. Therefore, it is of significance to understand physiological mechanisms underlying potential limitations to tree growth in order to predict tree growth and forest C sink under global change scenarios. In this review, the debates on the C-source and C-sink limitations to tree growth were firstly introduced. Second, we discussed responses of tree growth to biotic and abiotic stresses, such as defoliation, drought and low temperature from the perspective of C-source/sink limitations. Finally, we proposed three priorities for future studies in this field: (1) to explore the regulating mechanisms on the allocation of non-structural carbohydrates (NSC) in trees, and to determine what conditions and what extent trees actively allocate the photosynthates to NSC storage at the expense of growth; (2) to strengthen studies on the tree C-sink, and determine the photosynthates allocated to all components of tree C-sink, especially the missing C-sinks such as the activities of roots and related microorganisms; and (3) to implement studies on interactions among C metabolism, mineral nutrition and hydraulics physiology, and fully understand the C-water-nutrient coupling and its effects on tree growth.

Key words carbon sink; carbon source; non-structural carbohydrates; stress; tree growth

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植物生长使森林生态系统产生巨大而持续的碳汇, 从而可减缓大气 CO_2 浓度($[\text{CO}_2]$)升高速度(Dymond *et al.*, 2016)。森林每年固碳60 Pg, 占陆地总初级生产力的1/2 (Beer *et al.*, 2010)。树木生长, 尤其是木质组织的生长能够持续固碳长达数百年。不断加剧的全球变化(大气 $[\text{CO}_2]$ 升高、气候暖化、降雨格局改变等)通过影响树木生长、改变森林结构等(Aber *et al.*, 2001), 进而影响森林的碳汇功能(Chapin *et al.*, 2000), 但树木生长对全球变化的响应适应机制尚不明确。因此, 揭示限制树木生长的生理机制, 对评估和预测全球变化情景下森林碳汇功能具有重要意义。

根据树木可利用碳状况, 限制树木生长的生理机制可分为碳供给限制和碳利用限制。前者指树木生长受碳可利用性的限制(图1 a-b-c路径); 后者指环境条件(养分、水分匮乏)或发育限制降低树木碳利用活动, 进而限制其生长, 即树木对体内非结构性碳水化合物(NSC)的利用能力降低, 导致NSC浓

度升高(Wiley & Helliker, 2012), 进而通过反馈作用下调光合作用(图1 f-h-i路径; Paul & Foyer, 2001)。然而, 有研究显示NSC对树木具有更积极、主动的生理作用(Smith & Stitt, 2007; Wiley & Helliker, 2012; Dietze *et al.*, 2014)。树木增加碳储备导致可利用碳减少, 这样即使NSC充足, 树木生长也可能受碳供给限制(图1 d-e-c路径; Sala *et al.*, 2012; Wiley & Helliker, 2012; Hartmann *et al.*, 2015)。在当前大气 $[\text{CO}_2]$ 下, 大多数陆生植物的净光合速率并未达到饱和状态(Körner, 2006), 因此 $[\text{CO}_2]$ 升高会加快光合速率, 增加植物的可利用碳(Kirschbaum, 2011)。当树木生长受碳供给限制时, 大气 $[\text{CO}_2]$ 升高将促进树木生长, 增强森林的固碳功能; 而当树木生长受碳利用限制时, 大气 $[\text{CO}_2]$ 升高对树木生长和森林固碳功能则影响不显著。因此, 阐明树木生长在何时、何种情况以及多大程度上受碳供给或碳利用限制, 对于预测全球变化情景下树木生长及森林碳汇功能至关重要。为此, 本文首先介绍了树木生长碳供给与碳利用限制机制争议的背景; 接着从碳供给与碳利用角度探讨了叶损失、干旱和低温等胁迫条件下限制树木生长的生理机制; 最后提出树木生长和碳供给与碳利用活动的3个优先研究问题。

1 树木生长的碳供给与碳利用限制机制

树木体内的碳既是其生物量主要组分, 也是其生命活动的能量源泉。植物通过调节碳供给-碳利用活动, 改变其生长速率和光合产物分配, 从而适应不断变化的环境条件(White *et al.*, 2016)。因此, 碳供给与碳利用活动是影响树木生长的重要生理机制(Burnett *et al.*, 2016; White *et al.*, 2016), 也是树木生理生态学和全球变化研究的热点和争议焦点之一。

1.1 碳供给限制

树木生长是其体内碳供给与碳利用活动相互作用的结果。碳供给包括一切为树木生长和生命活动提供碳的过程, 如光合作用、树木体内NSC转化与分配等过程。树木通过反馈调节完成碳在生命活动过程之间的分配, 如呼吸、生长、繁殖、储存、防御等, 从而影响树木碳供给活动。然而, 由于碳分配特别是地下碳分配过程很难测定, 因而多数研究仅关注叶片净同化(Ainsworth & Rogers, 2007)。例如: Evans (1972)提出: 植物相对生长速率(RGR)取决于叶质量分数(LMF)、比叶面积(SLA)和净同化速率

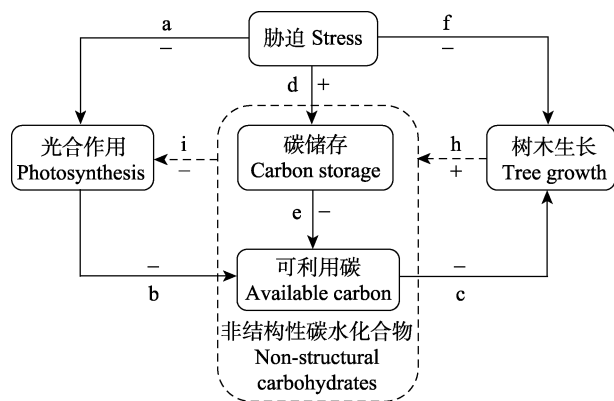


图1 树木生长的碳供给与碳利用限制机制概念框架。a-b-c路径, 生物和非生物胁迫(如叶损失、干旱或低温等)减少光合作用碳固定, 非结构性碳水化合物(NSC)浓度降低, 从而降低树木生长(碳供给限制); d-e-c路径, 面对胁迫, 树木主动储备NSC, 减少可利用碳, 从而降低树木生长(碳供给限制); f-h-i路径, 生物和非生物胁迫直接限制树木生长(碳利用限制), 过剩的NSC通过反馈作用抑制光合作用。实线指直接作用, 虚线指反馈作用; +指正效应, -指负效应。

Fig. 1 A conceptual framework of the mechanisms of carbon source-sink limitations to tree growth. From a-b-c pathway, carbon assimilation is reduced by biotic and abiotic stresses (such as defoliation, drought and low temperature), hence tree growth is limited by available carbon (i.e. carbon source limitation). From d-e-c pathway, the storage of non-structural carbohydrates (NSC) is an active process, which decreases available carbon for tree growth (carbon source limitation). From f-h-i pathway, tree growth is constrained by biotic and abiotic stresses directly, leading to NSC accumulation and thus limitation to photosynthesis (i.e. carbon sink limitation). Solid lines represent direct effects, and dotted lines represent feedbacks. + and - represent positive and negative effects, respectively.

(NAR), 即 $RGR = LMF \times SLA \times NAR$ 。Farquhar等(1980)提出的光合作用机理模型使光合作用成为很多植物生长理论和模型的核心, 并且使基于此模型研发的便携式叶片气体交换测定在植物碳收支研究中更加重要(Körner, 2015)。Stevens和Fox (1991)提出: 光合效率低和(或)生长季较短导致的碳供给限制是高山林线形成的主要原因。进一步研究表明, 光合作用对不同时空尺度上的植物生长和呼吸均有调控作用(Litton *et al.*, 2007)。Huang等(2018)利用微生长芯技术监测了马尾松(*Pinus massoniana*)木质部形成的年内动态, 并利用线性或混合模型分析了气候对木材形成的影响, 发现马尾松在干旱季节的生长速率比在湿润季节快, 认为这是由于干旱季节光合有效辐射高, 马尾松针叶光合能力强。因而, 光合产物增多, 分配给树干生长的碳亦增加(Yan *et al.*, 2013)。近期, 很多全球植被动态模型(Dynamic Global Vegetation Model)仍然根据光合作用与呼吸作用的差异计算植物生长量(Friend *et al.*, 2019), 并将陆地碳汇增加的原因归咎于大气[CO₂]升高导致光合速率加快, 从而对植物生长产生“施肥效应”。

除了光合作用之外, 树木体内NSC的积累与转化也会导致树木生长受碳供给限制。可溶性糖参与植物渗透调节、运输和信号传达, 树木优先将光合产物分配于可溶性糖, 使其浓度维持在一定阈值之上(Sala *et al.*, 2010; Hartmann & Trumbore, 2016; Martínez-Vilalta *et al.*, 2016)。正在生长和分化的细胞中糖的多少直接限制木材形成(Michelot *et al.*, 2012; Simard *et al.*, 2013)。例如: 欧洲云杉(*Picea abies*)和欧洲落叶松(*Larix decidua*)树干形成层可溶性糖浓度变化与木材形成过程存在耦合关系, 即次生壁形成过程和木质化阶段的细胞最多时, 其可溶性糖浓度最高(Simard *et al.*, 2013)。

另外, 树木生长、呼吸、繁殖、储存、防御等不同生命活动过程之间的碳分配格局变化, 通过反馈调节机制可使树木生长受碳供给限制。地下根呼吸对碳的消耗会影响树木地上组织的生长; 同样, 繁殖生长与营养生长对碳的竞争会互相制约(Ryan *et al.*, 2018)。例如: Rosati等(2018)对两种油橄榄(*Olea europaea*)栽培种(速生与慢生)进行摘花处理后发现, 处理之间总生物量差异不显著, 但繁殖组织生物量增加导致营养组织生物量成比例减少。在环境胁迫下, 为提高生存机率, 树木是否会主动降

低生长速率增加碳储存, 也引发关注和讨论(Wiley & Helliker, 2012)。已有研究证实拟南芥(*Arabidopsis* spp.)可采取这种保守的碳分配策略(Smith & Stitt, 2007; Gibon *et al.*, 2009; MacNeill *et al.*, 2017)。例如: Gibon等(2009)将拟南芥置于不同光照时间下(12、8、4和3 h), 结果显示随光照时间缩短, 拟南芥逐渐抑制生长和淀粉降解, 促进淀粉合成。这表明当碳同化减少时, 植物可以调整碳在储存与生长之间的分配(Smith & Stitt, 2007; Gibon *et al.*, 2009)。遮阴、降低大气[CO₂]等模拟碳限制的控制实验也显示, 树木亦可改变碳分配策略, 主动降低生长, 增加碳储存(Sala *et al.*, 2012), 形成树木生长、碳储存和防御的权衡关系, 以提升在胁迫环境中的生存机率(Huang *et al.*, 2019)。例如: Weber等(2019)将10种温带树种置于6%自然光照下3年, 发现遮阴显著降低了树木的生长, 但其NSC浓度表现为先降低后复原的格局。Huang等(2019)测定了生长于低[CO₂]中欧洲云杉幼树的生长、气体交换特征、NSC和次生代谢产物浓度, 以及新同化碳的分配, 发现碳限制强烈导致幼树生长速率降低, 但因新同化碳持续供给而使可溶性糖和次生代谢产物的浓度得以稳定。这些研究结果均表明树木通过改变碳分配策略, 减少分配给生长的碳, 增加碳储存(Sala *et al.*, 2012), 形成树木生长、碳储存和防御的权衡关系(Huang *et al.*, 2019); Wiley和Helliker (2012)认为这是一种不论是否面对环境胁迫都会频繁发生的保守生存策略。但以上研究均基于控制实验, 判定自然条件下植物是否会采取这种保守的碳分配策略十分困难, 但值得深入研究。

1.2 碳利用限制

NSC是树木体内的可移动碳库, 在一定情况下可能意味着碳收入的增加, 且可在任何天然林开展相关研究(Körner, 2003)。因而可根据NSC浓度判定树木生长是否受碳供给限制。判定标准为: NSC浓度持续降低, 表明碳供应无法满足树木对碳的需要或者树木碳供给与碳利用活动均不活跃; 而稳定、较高的NSC浓度则表明光合同化的碳能够满足甚至超过生长对碳的需求(Körner, 2003)。Hoch等(2002)对*Pinus cembra* NSC浓度季节动态的研究结果显示: NSC浓度常年维持在较高水平, 从未显著消耗, 因而林线树木生长的限制机制极有可能是低温直接抑制组织形成, 而非因为碳同化减少。即使完全落叶,

树木体内储存的NSC足够树冠重新长叶4次(Hoch *et al.*, 2003)。Körner (2003)综合分析了高海拔林线、温带山地森林、地中海硬阔叶林、半落叶热带森林等4个不同气候区1993–2002年生长季与非生长季的大树不同器官NSC储量动态, 结果显示: 除了地中海仲夏旱季之外, 所有调查地区树木的碳均处于满负荷状态, 全年NSC储量都很高, 由此提出: 在当前大气[CO₂]下, 限制树木生长的不是碳供给, 而是环境因子(如低温、干旱)或发育限制引发的碳利用活动限制。

[CO₂]加富实验(FACE)也在一定程度上支持了碳利用限制假说。例如, 在瑞士成熟落叶森林8年的FACE实验发现, 尽管将[CO₂]升高到550 $\mu\text{mol}\cdot\text{mol}^{-1}$ 使叶片净光合速率提升了40% (Bader *et al.*, 2010), 但树木的生物量生产并未持续增加(Bader *et al.*, 2013)。在美国田纳西 Oak Ridge 的10年生 *Liquidambar styraciflua* 幼龄林的一个FACE实验(550 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO₂)显示, 最初6年的净初级生产力增加了24%, 但随后5年又下降到对照组水平(Norby *et al.*, 2010)。究其原因可能是[CO₂]升高促进了植物和微生物生物量增加, 减少了环境中可利用氮, 从而导致渐进性氮限制(Luo *et al.*, 2004)。这一现象也符合生态化学计量学原理, 即碳、氮、磷等元素之间具有一定比例, 其中某一种元素的增加, 不一定会影响植物的生长(Ågren, 2008)。因此, 在养分添加情况下, [CO₂]升高可促进欧洲云杉的生长(Sigurdsson *et al.*, 2013)。然而, Klein等(2016)报道, 在瑞士西北部的温带针阔混交林中, 虽然土壤不受氮限制, 但5年的[CO₂]加富(550 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO₂), 110年生欧洲云杉树干径向生长、枝生长和针叶凋落物产量均无显著效应, 这表明还有其他因素限制该树木生长。McCarthy等(2010)发现杜克FACE实验中[CO₂]加富10年使得火炬松(*Pinus taeda*)生物量持续增加是受土壤有效氮和水分共同驱动。然而, 树轮数据分析显示在过去100多年[CO₂]升高对热带树木(van der Sleen *et al.*, 2015)和北方亚高山树木(Hararuk *et al.*, 2019)的径向生长均无促进作用。上述研究结果均支持碳利用限制机制; 而且这些学者认为: 在当前大气[CO₂]下, 树木生长不受碳供给限制, [CO₂]升高不会促进或不会持续促进树木生长。

树木生长碳供给与碳利用限制假说的另一焦点是, 随树高增加, 树木高生长停滞是因为水力限制

减少碳同化, 对树木生长造成碳供给限制, 还是水力限制导致树木顶端水分供应不足, 而使树木生长受碳利用限制? Ryan和Yoder (1997)提出了水力限制假说, 即: 随树高增加, 水分传输路径增长、重力势增大, 水分运输阻力增大, 造成水力导度下降; 树木为减少蒸腾失水、维持叶片水势, 其叶片气孔会提前关闭, 进而导致光合速率降低、碳同化量减少、树木生长潜力降低。Ryan等(2006)进一步指出, 随树高增加, 尽管树木在形态、解剖结构、生理机制等方面的调整可在一定程度上缓解树高增加对水力导度的负效应, 但水力限制阻碍气体交换的现象依然十分普遍。Liu等(2018)也报道, 樟子松(*Pinus sylvestris* var. *mongolica*)的叶面积与边材面积之比随树高增加而减小, 可在一定程度上缓解大树的水分胁迫, 但同时也可导致碳失衡, 进而限制树木生长。然而, Sala和Hoch (2009)发现, 西黄松(*Pinus ponderosa*)边材和针叶NSC浓度以及枝条木质部储存的脂质均随树高增加而升高, 而且干旱立地该趋势比湿润立地更明显。这说明虽然树高增加可使气孔关闭, 但并未引发碳供给限制, 而是其他因素限制了细胞生长及其对碳的需求(Bond *et al.*, 2007; Greenwood *et al.*, 2008)。Piper和Fajardo (2011)报道 *Nothofagus pumilio* 的NSC浓度不随树高和树龄增加而降低, 即使夏季干旱导致碳同化减少, 这种格局也没有改变。Bauerle等(1999)指出, 在没有蒸腾的情况下, 树高每增加1 m, 树木木质部水势梯度中的重力势也会增加0.01 MPa; 而蒸腾作用会进一步降低叶片水势。在渗透势不变的情况下, 叶片和顶芽细胞的膨压随着叶片水势的降低而成比例降低, 从而直接影响细胞形成、扩大和代谢等生长过程(Hsiao *et al.*, 1976)。当因水分不足而使膨压低于某一阈值时, 细胞扩张和生长将停滞(Steppe *et al.*, 2015)。由此推测, 高大树木的顶端细胞生长受限可能是由膨压降低引起的(Bond *et al.*, 2007; Greenwood *et al.*, 2008; Ishii *et al.*, 2008; Meinzer *et al.*, 2008), 即碳利用限制。

综上所述, 大多数实验证据支持树木碳利用活动对环境变化的响应比碳供给活动更敏感, 在多数情况下树木生长受碳利用限制(Millard *et al.*, 2007; Körner, 2015; Fatichi *et al.*, 2019)。例如: 为适应低温环境, 林线树木叶片能提升其光合能力(Wang *et al.*, 2017), 而组织生长等碳利用活动则不能(Alvarez-Uria

& Körner, 2007; Rossi *et al.*, 2008)。尽管目前关于树木碳储存形成是被动或主动的问题仍没有明确答案(Sala *et al.*, 2012)。但如果树木能够主动增加碳储存, 减少用于生长的碳, 则这个过程仍可以导致树木生长受碳供给限制。因此, 碳供给与碳利用活动影响树木生长的机制仍需深入探索。

2 胁迫环境下树木生长的碳供给与碳利用限制

环境胁迫可减少树木光合作用的碳收入, 但树木体内储存的NSC可为树木呼吸、生长、防御等碳利用活动提供一定的碳。

2.1 叶损失

以往研究显示, 叶损失可导致树木生长降低(Jacquet *et al.*, 2014; Piper & Fajardo, 2014; Wiley *et al.*, 2017), 可能原因包括: (1)叶损失导致树木的可利用碳供应不足, 引发树木生长碳供给限制。例如: 100%人工摘叶后3年以后, *Quercus velutina*径向生长与NSC浓度始终低于对照树(Wiley *et al.*, 2017)。(2)树木为提高生存机率, 调整碳分配策略, 将光合产物优先分配给储存, 减少分配给生长的碳。例如, 海岸松(*Pinus pinaster*)叶损失后枝干生长降低, 但NSC浓度在一个生长季内恢复到与对照树木相同, 甚至超过对照树木(Puri *et al.*, 2015)。(3)叶损失影响树木维管组织对水分和糖的运输, 进而限制树木的碳利用活动。摘叶减少树冠总叶面积, 蒸腾作用降低, 进而抑制形成层产生木质部(Zimmermann & Brown, 1974; Palacio *et al.*, 2014), 树木碳利用活动降低(Schmid *et al.*, 2017)。最近, Hillabrand等(2019)对2年生*Populus balsamifera*人工摘叶后发现, 叶损失增加木质部栓塞脆弱性, 降低水分运输效率, 同时还减小韧皮部筛管直径。然而, 值得注意的是, 叶损失可能导致树木生长同时受碳供给限制和碳利用限制。例如, Schmid等(2017)对生长于不同 $[\text{CO}_2]$ (160、280和560 $\mu\text{mol}\cdot\text{mol}^{-1}$)中的*Quercus petraea*和*Quercus ilex*幼苗摘叶后发现, 摘叶降低幼苗生长速率, 但生长降低的相对速率不受 $[\text{CO}_2]$ 影响, 表明生长速率降低不是碳供给限制; 但生长季末树冠总叶面积与树干断面积增长显著相关, 暗示着碳利用限制。

另外, 树木应对叶损失而产生一种补偿机制, 即叶损失使树木碳供给活动降低, 而碳利用活动维

持不变, 重新展叶过程增加对碳的需求会进一步降低树木的碳供给与碳利用比; 为了维持碳供给与碳利用的平衡, 叶片光合速率会加快(Pinkard *et al.*, 2011; Barry & Pinkard, 2013)。因而叶损失不一定降低树木生长, 也可能对树木生长影响不显著(Quentin *et al.*, 2012), 甚至促进树木生长(Collett & Neumann, 2002)。这与叶损失的程度与叶损失后的恢复时间有关。因而叶损失是否会导致树木生长下降, 在什么条件下、什么阶段、以哪种碳限制机制为主等问题尚需深入研究。

2.2 干旱

在水分胁迫下, 树木为了减少蒸腾失水会关闭气孔, 从而减少气体交换, 降低光合速率(Chaves *et al.*, 2009)。当叶片新合成的光合产物无法满足树木对碳的需求时, 由于树木生长、呼吸(Poyatos *et al.*, 2013)、修复、维持(包括水力完整性)、防御(Bréda *et al.*, 2006)等生理活动不断消耗树木储存的碳而可能使其NSC浓度持续降低, 导致树木生长受碳供给限制。然而, 大量研究显示, 干旱条件下, 树木体内NSC浓度可维持不变甚至升高, 其可能原因之一是: 水分胁迫先降低细胞膨压, 后降低气体交换量(Muller *et al.*, 2011; Tardieu *et al.*, 2011), 即水分胁迫对树木碳利用活动的限制早于碳供给活动, 树木生长受碳利用限制, 树木碳利用活动对碳的消耗少于碳的供应, 进而导致NSC积累。例如: Gričar等(2019)报道, 土壤可利用水减少显著降低*Quercus pubescens*次级生长, 但对NSC浓度没有显著影响。Piper等(2017)比较不同水分立地上*Pinus contorta*和西黄松的生长和NSC浓度发现, 干旱立地上树木径向生长较慢, 但其木质组织NSC浓度较高。

干旱胁迫使树木NSC浓度不变或升高的第二个原因是: 适应干旱的树木具有“干旱记忆效应”(Galiano *et al.*, 2017)。为了避免下一个生长季冠层更严重的枯梢(Bréda *et al.*, 2006)或产生碳饥饿(Galiano *et al.*, 2011), 树木会主动将光合产物优先分配给NSC储存, 从而与生长产生对光合产物的竞争, 最终导致树木生长受碳供给限制。在这种情况下, 干旱虽然降低了树木生长速率, 但其NSC浓度升高(Galiano *et al.*, 2017)。例如: von Arx等(2017)在瑞士干旱地区对欧洲赤松(*Pinus sylvestris*)的10年灌溉试验发现, 灌溉组和对照组均呈现年轮越窄、NSC浓度越高的格局; 这表明树木适应了长期的干旱环境

之后,即使干旱停止,树木依然会主动储备NSC,从而减少用于生长的NSC,使树木生长受碳供给限制。Duan等(2013)研究干旱对不同 $[\text{CO}_2]$ 中*Eucalyptus globulus*幼苗生长、NSC浓度和碳平衡的影响发现,在中度干旱时, $[\text{CO}_2]$ 升高可同时促进生长和NSC储存。而当干旱加剧时,这种促进作用消失。这表明树木是否采取这种主动储备NSC的策略可能与干旱的持续时间和强度有关。

第三,干旱降低韧皮部运输速度也会导致NSC积累(Sala *et al.*, 2010)。从周围细胞进入韧皮部筛管的水是韧皮部运输的主要驱动因子(Jensen *et al.*, 2009)。干旱减少韧皮部的可利用水,使韧皮部汁液黏性增高(Epron *et al.*, 2016),运输速度下降。Hesse等(2019)采用 $^{13}\text{CO}_2$ 方法发现,经过3年的控雨处理,由于从周围组织中吸收的水分减少,*Fagus sylvatica*韧皮部汁液黏性增高,运输速度下降。如果干旱发生时间与韧皮部生长同步,韧皮部解剖结构可能会受到影响(Salmon *et al.*, 2019)。Dannoura等(2019)的干旱对8年生*Fagus sylvatica*碳运输和韧皮部运输能力影响的研究结果也显示,干旱处理的树木韧皮部筛管直径较小、活跃的韧皮部较窄,从而使其韧皮部运输能力较低。然而,Kiorapostolou和Petit (2019)研究土壤水对*Fraxinus ornus*韧皮部的影响发现,干旱使其产生了更大的管腔面积,可能是为了抵消其韧皮部汁液黏性的增加,其韧皮部对干旱表现出一定的适应能力。但该研究没有测定韧皮部的运输速度。总之,干旱可能会降低韧皮部的运输速度(Dannoura *et al.*, 2019),阻碍NSC的运输,使叶片积累的NSC反馈于光合作用(Nikinmaa *et al.*, 2013)和树木生长(Sevanto, 2014),在严重干旱时甚至会导致韧皮部失调,引发碳饥饿,造成树木死亡(Sala *et al.*, 2010; Hartmann *et al.*, 2018)。

也有研究报道,树木可能在持续的严重干旱中存活,但干旱结束后树木生长会逐渐降低,最终死亡(Berdanier & Clark, 2016)。这种树木生长对干旱的滞后效应可能与碳供给限制有关。一方面,干旱对芽的伤害可能阻碍树木长出新的光合组织和枝条(Power, 1994; Stribley & Ashmore, 2002),从而导致树木在干旱之后逐渐耗尽边材中储存的NSC (Galiano *et al.*, 2011); 另一方面,干旱造成树木木质部导管栓塞,而储存的NSC可为栓塞修复提供能量,参与渗透调节(Nardini *et al.*, 2011),从而在干旱过

后引发碳饥饿,造成树木死亡(Trugman *et al.*, 2018)。综上所述,干旱限制树木生长的机制包括: (1)水分亏缺可直接限制细胞分裂与扩大等树木碳利用活动,引发碳利用限制; (2)干旱可减少碳同化、改变碳分配等,导致树木可利用的碳减少,造成碳供给限制; (3)干旱可使韧皮部运输速度下降,影响NSC的运输,导致韧皮部运输限制; (4)干旱可对树木生理活动产生滞后影响,导致树木生长受碳供给限制。至于在何种情况下哪种机制起主导作用或多种机制联动,值得深入研究。

2.3 低温

低温是中高纬度和高海拔林线树木生长的主要限制因子(Rossi *et al.*, 2007),但低温限制林线树木生长的生理机制仍存在争议,主要包括碳供给限制和碳利用限制两个假说(Körner, 2003; Li *et al.*, 2008; Fajardo & Piper, 2017)。碳供给限制假说认为,气温降低,光合速率降低或光合季节缩短(Susiluoto *et al.*, 2010),造成光合产物供应不足(Stevens & Fox, 1991),表现为树木NSC浓度降低(Li *et al.*, 2008),生长速率降低(Li & Yang, 2004)。例如: Fajardo和Piper (2017)研究发现,4个不同气候和土壤条件下,随着海拔升高,林线*Nothofagus pumilio*枝条NSC浓度降低,树干生长降低,表明其生长受碳供给限制。林线FACE实验也发现, $[\text{CO}_2]$ 增加促进林线欧洲落叶松针叶、芽(Handa *et al.*, 2005)和地上木质组织生长(Dawes *et al.*, 2011, 2013),进一步证明林线树木生长受碳供给限制。

然而,有研究发现植物木质部(Rossi *et al.*, 2008)、根(Alvarez-Uria & Körner, 2007)等组织生长对5℃以下寒冷环境的适应能力微乎其微;叶片光合速率在0℃和5℃时分别是其光合能力的30%–50%和50%–70%(Körner, 2012)。Wang等(2017)借助“最低消耗假说”和“共同限制假说”验证了随海拔升高,叶片胞间与大气 $[\text{CO}_2]$ 比降低,最大羧化速率提高,从而实现光合速率的最大化。林线树种通常有较强的光合作用调节能力,以确保树木碳同化能提供足够的光合产物(Cavieres *et al.*, 2000; Wang *et al.*, 2017)。碳利用限制假说认为: 低温对碳利用活动的限制早于对碳供给活动的限制(Körner, 2003),树木生长降低,NSC浓度不变或者升高(Hoch & Körner, 2009),这是最为认可的林线形成机制。例如: Dolezal等(2019)报道,随海拔升高秀丽水柏枝

(*Myricaria elegans*)的早材和晚材宽度均降低,而叶、枝和树干边材的NSC浓度无显著变化,支持了假说。Dawes等(2011, 2013)的FACE实验发现: 尽管*Pinus uncinata*针叶NSC浓度增加,其生长无显著变化。表明[CO₂]升高加快光合速率,但是由于生长受碳利用限制,导致NSC在针叶中的积累。

Li等(2018)对11个高山林线树木的NSC研究发现: 在生长季,树木地上组织淀粉和可溶性糖浓度均随海拔升高而升高。通常,可溶性糖是呼吸、生长等碳利用活动的底物,而淀粉的主要功能是储存。如果淀粉和可溶性糖浓度同时升高,表明过剩的可溶性糖在树木体内以淀粉形式积累,即碳供应充足。如果可溶性糖浓度降低,为满足生理活动需要,通常淀粉应转化为可溶性糖以供应树木对碳的需求,因而淀粉浓度降低。但Li等(2018)发现尽管根系可溶性糖浓度降低,淀粉浓度却升高;这表明即使在碳供给限制下,可溶性糖仍然可转化为淀粉,即树木存储碳的过程不仅是碳供应过剩时的被动积累,也可能是优先于生长等其他碳利用活动的主动储备(Chapin *et al.*, 1990; MacNeill *et al.*, 2017)。而地上木质组织与根系响应的差异可能是因为根系位于树木碳运输路径的末端,光合产物先供给靠近树冠的碳利用活动,后供给根的活动(Wardlaw, 1990; Minchin, 2007)。因而,碳限制的负效应对根系的影响最久(Landhäusser & Lieffers, 2012)。因此,为避免碳饥饿,根系会主动将可溶性糖转化为淀粉,以增加碳的储存。

面对低温,不同树种可能有不同的限制机制。例如: 在智利南部林线(海拔1 300 m)和林线以上(海拔1 350 m), Fajardo和Piper (2014)将*Nothofagus pumilio*和*Pinus contorta*幼苗置于离地面2–3 m高处,*Nothofagus pumilio*生物量和NSC浓度均显著降低(碳供给限制),但*Pinus contorta*生物量和NSC浓度均无显著变化。这项研究支持,不同树种对低温的响应有差异,该差异可能源于生长以外的其他碳利用活动对碳的利用。通常,被子植物的抗栓塞能力比裸子植物弱(Field & Brodribb, 2001; Maherali *et al.*, 2004),其木质部修复会消耗更多的碳(Johnson *et al.*, 2012); 常绿树种枝生长为有限型,仅在春季进行一次生长(Palacio *et al.*, 2018),而落叶树种枝生长为无限型,如果环境条件允许,其枝条可以在生长季后期不定期生长(Deppong & Cline, 2000),

因而落叶树种需要消耗更多的碳(Dawes *et al.*, 2011)。

综上所述,低温限制树木生长的机制有3种: (1)低温降低光合作用,使树木生长受碳供给限制; (2)低温直接抑制碳利用活动,使树木生长受碳利用限制; (3)低温改变光合产物分配格局,对碳储存的分配减少树木生长可利用碳,使树木生长受碳供给限制。至今为止,对于上述机制是否有树种分异、同一树种阶段性以及共存性等问题的研究还不多。

3 优先研究问题

许多环境因子交互作用,共同影响树木的碳供给与碳利用活动,而且碳供给与碳利用在一定条件下可以相互转化,因而很难区分和量化碳供给和碳利用活动及其环境变化敏感性对树木生长影响的相对贡献(Fatichi *et al.*, 2014)。关于碳供给和碳利用如何限制树木生长至今为止已有一些探索。例如: Deslauriers等(2016)报道: 在不同温度和水分处理下,水分是*Picea mariana*幼苗树干形成层分裂活动的主要限制因子,而碳是其木质部细胞壁增厚过程的主要限制因子。为了从碳供给与碳利用角度揭示环境变化对树木生长影响的生理机制,更精确地预测全球变化情景下树木生长及森林碳汇功能,提出如下优先研究问题:

(1)探索NSC储存形成的调控机制,确定什么情况下以及多大程度上树木通过主动降低生长而将光合产物优先分配于NSC储存。在不同时间尺度上和胁迫环境中,光合产物的分配、NSC动态变化、糖和淀粉的相互转化,反映着树木生长、生存与繁殖的权衡关系,其中的调控因子尚不清楚。利用同位素等手段,区分追踪NSC合成、转化、分配、储存及利用,有助于阐明NSC库及其组分的动态,确定在碳限制下NSC库储存过程是否能持续,进而深入认识树木生长、生存与繁殖的权衡机制。

(2)加强树木碳利用活动研究,系统测定光合产物在其碳利用组分的分配(特别是根系及共生微生物的活动)。在森林生态系统,冠层光合作用固定的碳有25%–75%用于根系及其共生菌的生长和呼吸(Litton & Giardina, 2008),特别是在土壤养分、水分等资源匮乏时,树木可能减少地上部分生长,而将更多的碳分配到地下器官,更多地用于细根周转、菌根真菌、根际微生物等。例如: 干旱胁迫解除后,地下碳利用活动的增强对*Fagus sylvatica*幼苗的恢

复起积极作用(Hagedorn *et al.*, 2016)。由于地下碳利用活动短暂、季节变化大, 测定困难, 因而研究较少, 有必要强化地下碳利用活动研究, 阐明其对树木碳平衡和树木生长的影响。

(3)开展树木碳代谢、矿质营养与水分生理的互作研究, 充分认识树木的碳、水和养分耦合关系及对树木生长的影响。碳、水、养分相互作用、相互依存, 共同驱动树木的生命活动和生长发育过程。然而, 目前的研究大多是关注分离的、相对孤立的过程。即使以碳限制为背景的研究, 也很少重视碳对水分运输、碳参与木质部栓塞修复等的作用, 进而影响树木的生长。最近研究显示: 碳限制影响树木木质部和韧皮部结构和功能, 可能导致水力失调(Hillabrand *et al.*, 2019), 最终导致树木死亡。因此, 在气候变暖、降水格局变化、旱涝频发、害虫爆发加剧的全球变化情景下, 开展碳-水-养分联合驱动的树木生长、存活和繁殖过程机制研究, 显得尤为重要。

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