

虫害叶损失造成的树木非结构性碳减少与树木生长、死亡的关系研究进展

陈志成 万贤崇*

中国林业科学研究院林业新技术研究所, 北京 100091

摘 要 大规模虫害爆发可造成区域森林死亡, 近年的气候变化进一步增加了虫害的频度和危害程度。森林和林地植物死亡会导致植被生产力降低, 改变生态系统结构和功能, 使森林由一个净的碳汇转变为一个碳源。因此, 加深虫害对树木危害机制的认识有重要意义。虫害造成的叶损失(虫害叶损失)降低树木光合作用能力, 增加非结构性碳(NSC)消耗, 使得树木体内碳储备降低, NSC降低到一定程度会导致树木因碳饥饿而死亡。外部环境和树木自身的补偿性机制也会对这个过程产生正或负的影响。在近年气候变化背景下, 树木死亡在全球尺度上增多, 重新激起了人们对碳饥饿的重视, 碳饥饿被视为解释树木死亡的主要生理机制之一。该文介绍了碳饥饿的定义, 综述了虫害叶损失减少树木NSC储备与树木生长、死亡的关系, 以及树木虫害和叶损失与气候变化之间的关系, 并对今后的研究进行了展望。

关键词 碳饥饿; 非结构性碳; 树木死亡; 气候变化; 干旱; 昆虫; 防御

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The relationship between the reduction of nonstructural carbohydrate induced by defoliator and the growth and mortality of trees

CHEN Zhi-Cheng and WAN Xian-Chong*

Institute of New Forestry Technology, Chinese Academy of Forestry, Beijing 100091, China

Abstract

Large scale herbivorous insect outbreaks can cause death of regional forests, and the events are expected to be exacerbated with climate change. Mortality of forest and woodland plants would cause a series of serious consequences, such as decrease in vegetation production, shifts in ecosystem structure and function, and transformation of forest function from a net carbon sink into a net carbon source. There is thus a need to better understand the impact of insects on trees. Defoliation by insect pests mainly reduces photosynthesis (source decrease) and increases carbon consumption (sink increase), and hence causes reduction of nonstructural carbohydrate (NSC). When the reduction in NSC reaches to a certain level, trees would die of carbon starvation. External environment and internal compensatory mechanisms can also positively or negatively influence the process of tree death. At present, the research of carbon starvation is a hotspot because the increase of tree mortality globally with climate change, and carbon starvation is considered as one of the dominating physiological mechanisms for explaining tree death. In this study, we reviewed the definition of carbon starvation, and the relationships between the reduction of NSC induced by defoliation and the growth and death of trees, and the relationships among insect outbreaks, leaf loss and climate change. We also presented the potential directions of future studies on insect-caused defoliation and tree mortality.

Key words carbon starvation; nonstructural carbohydrate; tree mortality; climate change; drought; insect; defense

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虫害或虫害与其他环境胁迫(如干旱)结合造成的叶损失可导致树木死亡(Kosola *et al.*, 2001; Gaylord *et al.*, 2013; Jacquet *et al.*, 2014)。气候变暖提高昆虫的生长速率和繁殖能力(Ayres & Lombardero, 2000; Tran *et al.*, 2007), 增加虫害爆发和其他极端事件的频率(Allen *et al.*, 2010)。因此, 虫害爆发造成区域森林死亡被认为与气候变化有关(Kurz *et al.*, 2008)。森林系统覆盖着30%的陆地面积, 储存着地球陆地生态系统45%的碳(Bonan, 2008), 森林和林地植物死亡会导致生态系统结构和功能改变(Allen & Breshears, 1998; Breshears *et al.*, 2005), 还会导致森林碳通量速率增加, 使森林由一个净的碳汇转变为一个碳源(Kurz *et al.*, 2008)。即使虫害没有导致树木死亡, 虫害叶损失也会造成生产力严重下降(May & Carlyle, 2003)。因此, 探索虫害叶损失导致树木死亡的机制、了解叶损失发生后树木的响应过程, 对加深理解虫害对树木的影响有重要意义。

虫害叶损失会减少树木光合作用产物, 增加非结构性碳(nonstructural carbohydrate, NSC)消耗, 从而使树木体内碳储备降低(Anderegg & Callaway, 2012; Anderegg *et al.*, 2015), 生长减弱, 当NSC储备降低到一定阈值时树木会由于碳饥饿(carbon starvation)而死亡。外部环境和树木自身的补偿性机制也会对这个过程产生或正或负的影响。本文介绍了碳饥饿假说的定义和虫害叶损失对树木NSC和生长的影响。通过综述虫害叶损失后内外因素对树木的影响、树木对虫害的防御和恢复, 以及树木虫害和叶损失与气候变化的关系, 来探讨虫害叶损失所造成的树木NSC减少与树木生长、死亡的关系。

1 碳饥饿假说与树木死亡

1.1 碳饥饿假说

碳水化合物是植物光合作用的主要产物, 按其存在形式可分为结构性碳水化合物和NSC两类。结构性碳水化合物包括木质素、纤维素等, 主要用于植物体的形态建成, 而NSC是树木可移动性碳库的主要储存形式, 为植物新陈代谢提供能量, 其总量的90%以上是可溶性糖和淀粉(Hoch *et al.*, 2003)。

碳饥饿假说最早在1975年被提出(Parker & Patton, 1975), 但长期以来, 碳饥饿多用来解释干旱胁迫造成的树木死亡。Bossel (1986)和Mueller-Dumbois (1987)认为长期的干旱胁迫会打破植物碳摄取与碳

支出的平衡, 使植物死亡。McDowell等(2008)认为干旱导致气孔关闭阻止了水分进一步散失, 但是同时也导致了光合作用的碳摄取减少, 而植物新陈代谢对NSC的继续消耗就导致了碳饥饿的产生。

当光合作用、可动员NSC和液泡内蛋白质水解NSC的供应量小于包括呼吸、生长和防御的NSC使用量时, 树木体内NSC含量必然降低。碳饥饿可泛指为当NSC降低到一定阈值时树木新陈代谢不足或终止而导致树木死亡(McDowell, 2011)。叶片是光合作用器官, 所以虫害叶损失会降低光合作用(碳源减少), 而叶损失后新叶萌发会增加NSC消耗(碳汇增加)。这个过程必然会降低树木体内NSC含量(Anderegg & Callaway, 2012; Atkinson *et al.*, 2014)。若虫害爆发导致树木叶损失严重, 或虫害连续爆发, 树木就会因NSC严重降低而死亡(Hogg *et al.*, 2002; Anderegg *et al.*, 2015)。

1.2 对碳饥饿假说的质疑与证据

对于碳饥饿假说定义, 树木死亡时的NSC不一定是0, 但是任何剩余的NSC对于新陈代谢来说都是不可利用的(McDowell, 2011), 而现实情况中植物死亡时体内也确实仍保留了相当一部分的NSC(Chaves *et al.*, 2003; McDowell & Sevanto, 2010), 这是质疑碳饥饿假说的重要一点。甚至在干旱胁迫后存在NSC升高的情况(Sala & Hoch, 2009)。碳饥饿假说存在争议(Sala, 2009), 但争议主要围绕在干旱对树木的致死上。

对于树木死亡时不能利用剩余的碳, 有很多解释。Millard等(2007)指出即使在根上环剥韧皮部, 也不能完全消耗掉NSC。树木可能会划分出某些组织把难利用的碳储存起来(Millard *et al.*, 2007), 或限制酶活性, 比如限制酶进入淀粉颗粒(Srichuwong & Jane, 2007); 并且有一部分可溶性糖是用来维持细胞渗透势的, 其不能用于呼吸代谢(Chaves *et al.*, 2003)。Marshall和Waring (1985)发现遮阴的树会消耗掉全部的淀粉之后死亡, 但是可溶性糖无法完全消耗。干旱初期常出现NSC浓度升高, 这是因为树木生长对胁迫的灵敏度大于光合, 导致在胁迫发生的一段时间内NSC还在积累(McDowell, 2011)。另外在所有的NSC储备消耗之前, 碳饥饿可能因筛管功能丧失而发生(Sala *et al.*, 2010)。Sevanto等(2014)用干旱和遮阴控制试验为碳饥饿导致树木死亡提供了确凿证据。

对于虫害叶损失导致树木碳饥饿死亡, 因为机理更为简单, 所以更容易接受(Landhäusser & Liefers, 2012)。Landhäusser和Liefers (2012)发现重复的叶损失导致树木碳储备显著减少, 最终使树木衰败死亡。在虫害叶损失后, 树的恢复被认为与碳储备相关(Galiano *et al.*, 2011); 而在连续几年重复虫害叶损失后, 成年杨树显示出生长减缓, 对疾病、死亡的敏感性升高(Hogg *et al.*, 2002)。Piper和Fajardo (2014)用实验证明了叶片全部损失后的碳饥饿直接导致了树木死亡。

2 虫害叶损失对树木NSC和生长的影响

2.1 虫害叶损失对树木NSC的影响

大部分情况下, 昆虫啃食叶片导致树木光合作用减少(碳源减少)和NSC消耗增加(碳汇增加), 使树木体内NSC含量降低(Vanderklein & Reich, 1999; Anderegg & Callaway, 2012; Atkinson *et al.*, 2014)。如Vanderklein和Reich (1999)发现两个研究树种叶损失后整株的淀粉水平都下降了50%。只有在某些很轻微的叶损失研究中, 树木的NSC浓度没有降低(van der Heyden & Stock, 1995)。但是树种之间对叶损失的响应存在差异, 并且树木各个器官对叶损失的响应也不同。

Trumble等(1993)提出假说认为相比落叶树种, 常绿树种对虫害叶损失更敏感, 因为常绿树种叶片的初始投资更高, 叶片中存储的NSC占整株的比例更高, 且单位投资的周转率低(Mooney & Gulmon, 1982); 而落叶树种更多的NSC储存在茎中, 有助于叶损失之后树的恢复(Tuomi *et al.*, 1984)。有些研究支持这个假说, 认为落叶树种对叶损失的忍耐性高于常绿树种(Krause & Raffa, 1996); 但也有研究不支持这个假说(Vanderklein & Reich, 1999), 即不能确定叶损失之后常绿树种的情况比落叶树种更糟; 也有某些常绿树种在叶损失之后碳储备恢复得很快(Li *et al.*, 2002; Roitto *et al.*, 2003)。

另外, 从树种的生长快慢来讲, 一般长得慢的树种显示更保守的生存策略, 例如器官的组织密度更大、周转时间更长, 根中的NSC库比长得快的树种更大(Atkinson *et al.*, 2014)。Atkinson等(2014)发现生长慢的树种的根NSC浓度在叶损失后没有马上改变, 而生长速度快的树种NSC浓度下降迅速, 但恢复得也快, 即生长快的树种比生长慢的树种响应叶

损失更快。Rose等(2009)也发现在虫害叶损失之后, 生长快的树开花率更低、死亡更高。

虫害叶损失之后, 树木会萌发新叶, 并同时采取其他的修复策略, 如快速调动碳储存(Li *et al.*, 2002)或限制某些部位的生长(Honkanen *et al.*, 1994), 这就导致了树木各个器官的响应规律不同。一般在虫害叶损失后, 根、茎、叶3个器官的NSC含量都会降低, 但叶和根系统NSC的降低更明显(Jactel *et al.*, 2012)。根是储备器官, 叶损失后根系NSC减少, 暗示树木依赖其碳储备克服由叶损失造成的碳失衡(Eyles *et al.*, 2009)。在植物体的源汇关系中, 叶片是碳源器官, 无论是对于幼树(Tschapinski & Blake, 1994)还是成年大树(Parker & Patton, 1975), 新的光合产物会优先分配给源附近的器官(新叶和茎), 而分配到根的光合产物会减少。高大的树木表现得更明显(Landhäusser & Liefers, 2012)。茎的碳恢复更快(Jactel *et al.*, 2012), 所以根与枝的NSC比率会降低(Eyles *et al.*, 2009)。

2.2 虫害叶损失对树木生长的影响

虫害叶损失往往会显著减弱树木的生长。叶损失后枝条生长减缓(Eyles *et al.*, 2009; Jactel *et al.*, 2012), 高生长减慢(Dormann *et al.*, 2000), 在相当长的时间内木材组织生长放慢(Wiley *et al.*, 2013), 根的生长停止或减弱(Willaume & Pagès, 2006)。其中树木径向生长对叶损失的敏感性高于树高生长(Alcorn *et al.*, 2008)。而新长出的叶片数量减少(Anderegg & Callaway, 2012), 单叶叶面积下降(Anderegg & Callaway, 2012; Wiley *et al.*, 2013), 比叶面积增加(Wiley *et al.*, 2013)。但在叶损失后树顶端叶片与枝条数量的比例(Eyles *et al.*, 2009)、整株树水平上叶片与木材干物质量的比(Pinkard *et al.*, 2004; Eyles *et al.*, 2009)升高。叶片比例的增加有利于碳固定和碳恢复(Causton, 1985)。虫害叶损失对树木生长的影响也受树种、损失程度的不同而存在差异(Anttonen *et al.*, 2002), 如Krause和Raffa (1996)发现严重的叶损失对*Larix decidua*这个落叶树种生长的影响是快速的、暂时的, 而对*Pinus resinosa*这个常绿树种的影响是延迟的和长期的。

3 虫害叶损失后内外因素对树木的影响

3.1 树木自身对叶损失的补偿性机制

虫害叶损失后, 树木自身可能会采取某些重要

的修复策略,即补偿或超补偿机制(Vanderklein & Reich, 1999; Eyles *et al.*, 2011)。对虫害叶损失后这种补偿机制的发现大约最早可追溯到1966年(Sweet & Wareing, 1966),他们发现了叶损失之后光合作用能力上调。Wareing和Patrick (1975)认为叶损失后源汇比减小,树冠重新长叶导致了更大的碳需求,刺激了剩余叶片的光合作用,使得剩余叶片的光合作用能力上调。剩余叶片的光合作用能力上调可能也是叶损失后最常见、最重要的一种树木补偿方式。Eyles等(2011)发现*Pinus radiata*就是通过补偿性的上调光合作用能力,抵消了叶损失的部分损害。*P. radiata*在叶损失3周后光合速率显著升高,直到16周后才与对照树木差异不显著(Eyles *et al.*, 2011)。其他树种在叶损失后光合作用能力也发生了上调(Pinkard *et al.*, 2007; Turnbull *et al.*, 2007; Eyles *et al.*, 2009; Quentin *et al.*, 2012)。

叶损失后光合作用能力上调被认为主要与树木体内NSC水平、叶龄(Wingler *et al.*, 1998)和光合酶(Jordi *et al.*, 2000)的变化有关。也有研究认为与氮分配的改变有关,因为氮分配的改变有可能增强光合酶和色素的活性(Lavigne *et al.*, 2001)。氮的位移是一个重要的营养物质保守机制(Nambiar & Fife, 1991),Hopmans等(2008)认为蚜虫损害叶片要经过大约几周甚至上月的时间,因此怀疑树木有机会重新转移损害叶片中的氮。还有研究认为叶损失减少了总的蒸腾面积,改善了剩余叶片的水分状况,使得剩余叶片的蒸腾和水力导度升高,从而光合作用能力上调(Quentin *et al.*, 2011)。

叶损失后其他的补偿性机制还有改变生长模式和改变内部资源的分配模式,比如优先生长叶面积(Medienne *et al.*, 2002)、地上和地下器官中资源分配的改变(Pinkard *et al.*, 2004)等。

3.2 虫害叶损失与干旱的交互对树木水分与NSC的影响

因为干旱是全球范围内最严重最广泛的自然灾害,气候模型也预测未来干旱会更频繁和严重(Seager *et al.*, 2007),而且有证据表明干旱后昆虫活性增强,树木死亡增多,所以加深干旱对树木抵抗昆虫攻击能力的影响的认知是很重要的(Mattson & Haack, 1987; Gaylord *et al.*, 2013)。在这里,有两个问题值得我们深入探讨:一是在虫害叶损失中水分对树木NSC起到什么作用,干旱会不会加重碳饥

饿?二是虫害与干旱同时发生时,叶损失是缓解还是加重干旱?因为叶损失减少了树木的蒸腾面积,有利于缓解干旱对树木的影响,但是NSC是木质部导管栓塞修复的基础物质,叶损失造成NSC减少也可能会加重干旱对树木的影响。

一般认为干旱对树木NSC的影响依赖于干旱的强度和持续时间。如果干旱强度很大,土壤水分对树木供应不足,持续的蒸腾需求可能导致木质部导管和根系产生空穴化,使树木产生水力失衡(hydraulic failure),直接导致树木组织干化死亡(McDowell *et al.*, 2008),而这时可能还来不及对树木的NSC产生大的影响。对于某些树种,在干旱胁迫初期,膨压降低,不足以驱动细胞分裂或扩展,树木生长减弱或停止,而此时光合作用还在正常进行,所以在这个期间NSC会盈余(Woodruff & Meinzer, 2011)。而随着干旱时间的延长,光合作用也降低,但呼吸作用还在进行,这时会导致NSC储存的消耗(Galiano *et al.*, 2011)。

在虫害叶损失中干旱往往加重树木的碳饥饿,因为干旱会通过限制新陈代谢对NSC的利用(McDowell & Sevanto, 2010)和NSC的运输(Chaves *et al.*, 2003)来扩大碳饥饿。细胞新陈代谢的限制假说认为在干旱时低的组织水势可能限制细胞水平上的新陈代谢(Sala & Hoch, 2009)。另外,在干旱时筛管碳运输的失败也会扩大碳饥饿(McDowell & Sevanto, 2010)。干旱对筛管功能的负影响不但会降低碳从叶片输出的速率(Quick *et al.*, 1992),还会使防御物质不能运输到遭受攻击的部位(Guérard *et al.*, 2007)。即使长期干旱后环境变得湿润,死亡也可能小概率地发生,因为作为前期干旱的结果,一些树依然遭受着碳饥饿,最终因虫害的叶损失而死亡(McDowell *et al.*, 2008)。

轻微的干旱胁迫可能使树木防御虫害的能力更强,如生长分异平衡假说(growth-differentiation-balance hypothesis)认为,轻微的干旱胁迫对生长的限制更大,而防御物质生产得更多(Dunn & Lorio, 1993; Stamp, 2003)。即以碳为基础的虫害防御与水分之间的关系是钟形的(bell-shaped relationship) (Stamp, 2003),当水分状况好时,树木会优先把光合产物分配到生长而不是防御上;而干旱严重时树木不能提供足够的用来生产防御物质的光合产物。Gaylord等(2013)的研究证明了这个理论,其减

水和增水处理的树木产生的树脂更少,而中度水分胁迫(来自自然环境中季节性的水分胁迫)的树木产生的树脂量最大,生长也呈现中间状态。

因为干旱本身就能使树木发生水力失衡而死亡(McDowell *et al.*, 2008),所以虫害叶损失对树木水分的影响也非常引人注目,但其影响没有一致结论。有的研究发现叶损失后树木遭受的水分胁迫并不严重,更易维持水分状态的内稳性(Quentin *et al.*, 2012)。因为不但叶损失开始时总叶面积减少,而且之后新长出的叶片面积也会变小,导致树木整体的蒸腾量减弱(Hart *et al.*, 2000),单叶蒸腾强度(Quentin *et al.*, 2011)和叶片水势升高(Wiley *et al.*, 2013);树木边材面积与叶片面积比值也会发生改变,导致土壤到叶片的整树水力导度升高(Quentin *et al.*, 2012)。但也有研究认为叶损失诱导的NSC减少(碳胁迫)对树木水力性状的负影响很大(Anderegg & Callaway, 2012)。比如有的研究发现叶损失1年后可能抑制了新木质部的形成,从而显著降低了枝条的水力导度(Anderegg & Callaway, 2012)。虫害叶损失可能会放大干旱效应也因为树木在栓塞修复过程中需要NSC的参与,这个过程依赖淀粉转化为糖,并在栓塞的导管中产生渗透梯度(Bucci *et al.*, 2003; Zwieniecki & Holbrook, 2009)。并且叶损失后NSC的减少还会限制碳向根供给,从而限制根的生产力和吸收水分的能力(Gieger & Thomas, 2002)。

3.3 氮与虫害叶损失的交互影响

叶损失不止降低树木光合能力和NSC储存,还可能减少树木其他的重要资源,比如氮元素。碳-营养平衡假说认为叶损失后很多树木发生变化是因为氮的损失(Bryant *et al.*, 1993)。氮与Rubisco酶浓度相关,因此关系到光合羧化效率(Field & Mooney, 1986);氮施肥常常能刺激光合和生长(Huttunen *et al.*, 2007),提升植物忍受重复的昆虫取食的能力(Maschinski & Whitham, 1989);而氮限制会影响化学计量(碳氮比)和新陈代谢中NSC的利用(Millard *et al.*, 2007)。在NSC储备不受限制时,如果氮素足够,即使由于叶损失导致的碳同化减少,树木的生长速率依然可以很高,维持或接近叶损失之前的生长速率(Gleason & Ares, 2004)。

有的研究发现叶损失不但减少树木氮含量,而且还可能影响树木氮吸收(Kosola *et al.*, 2001)。叶损

失后树木吸收氮的能力降低可能与根对叶损失的响应有关(Bryant *et al.*, 1993)。特别是当根的碳储备比较低时(Tuomi *et al.*, 1990),可导致根的生长减弱、死亡率升高(Kosola *et al.*, 2001)。所以有研究认为叶损失后根吸收氮的能力下降和根死亡升高是由同样的信号驱动的,即NSC含量或其有效性的下降(Tuomi *et al.*, 1990; Kosola *et al.*, 2001)。也有研究认为叶损失后树木的氮损失可以由氮施肥逆转,甚至在根吸收氮能力下降的情况下(Tuomi *et al.*, 1990)。

但很多研究发现叶损失对氮吸收的影响是短暂的。Mediene等(2002)对一年生的*Prunus persica*进行60%的叶损失后,树体内的氮浓度在两个半月后就恢复了。Kosola等(2001)也发现叶损失后树木的氮吸收能力在第二年春季就恢复到了对照水平。也有研究发现叶损失后树木氮浓度(Eyles *et al.*, 2009; Wiley *et al.*, 2013)或氮吸收能力(Lovett & Tobiessen, 1993)没有显著变化。甚至Turnbull等(2007)发现*Eucalyptus globulus*幼树叶损失5周后叶片的氮浓度存在短暂升高。这种叶损失后树木氮响应的差异可能是叶损失的程度不同造成的(Kosola *et al.*, 2001)。

3.4 CO₂和温度对叶损失后树木的影响

温度和大气CO₂浓度升高是气候变化的重要内容,二者的升高有可能增强虫害叶损失后树木的补偿效应。Handa等(2005)发现*Pinus uncinata*在严重的叶损失之后,CO₂浓度升高提高了其碳的有效性,减轻了其叶损失的负效应,加快了恢复。Huttunen等(2007)也发现施肥的桦树幼苗叶片损失25%后,在温度和CO₂共同升高的处理下,表现出了极端的超补偿效应:超补偿了树高和总的叶面积,甚至在生长季结束时树高比对照还要高10%,根和枝的生物量也变得更高。Petit等(2011)发现对枝条尖端的芽加热也会显著增加枝条生长,可能是增温使树木的碳从保守的储存模式中释放了出来,从而促进了生长。温度和CO₂浓度升高还会提高树木呼吸(Lee *et al.*, 1998)和化感物质产量(Lindroth *et al.*, 1993),有利于植物忍受或防御昆虫取食。温度和CO₂浓度升高还可能会延长生长季和加速土壤枯落物分解,对木本植物产生间接作用,提高其养分的有效性(Mäkipää *et al.*, 1999)。但在Adams等(2009)的增温试验中(升高约4.3℃),温度升高使得呼吸加速,NSC

消耗更快, 缩短了干旱诱导树木死亡的时间。

4 树木对虫害叶损失的防御和恢复

4.1 碳和树木防御虫害的关系

树木中萜类、酚醛、树脂、单宁等防御虫害的物质都是从NSC转化而来, 足够的碳储备有利于树木生存(Gleason & Ares, 2004)或抵抗生物攻击(Dunn *et al.*, 1987)。Gaylord等(2013)在不同水分情景下对*Pinus edulis*的成年大树的树脂进行碳同位素研究, 发现碳同化与树脂的合成之间存在滞后性, 大部分树干上的树脂是由先前同化的碳合成的。防御物质多是由早前的碳合成, 这一发现解释了为什么足够的碳储备有利于树木生存和对生物攻击的防御。相反, NSC不足不利于树木对虫害进行防御, 如Anderegg和Callaway (2012)发现*Populus tremuloides*在其叶损失1年之后受到的虫害攻击更多。根部的碳储存多更有利于防御, 因为相对于地上部分, 根部难以被虫食。所以对根储存更高的初始投资, 相当于在地下维持了相对安全的储备(Atkinson *et al.*, 2014)。Vanderklein和Reich (1999)也发现*Pinus resinosa*和*Larix leptolepis*以根部作为最大的NSC库是很重要的, 好的年份在根部储存大量的碳可以维持不好年份的碳需求(Landhäusser & Lieffers, 2012)。

但是碳固定多不代表树木的碳储备多, 更不代表转化为树木的防御物质多, 因为碳还要分配到生长或生殖上(Wiley *et al.*, 2013), 即碳分配在防御和生长之间存在权衡, 如先前提到的生长分异平衡假说。

4.2 虫害叶损失后碳与生长的恢复

在虫害叶损失之后的早期, 由于NSC减少, 供给生长的碳不足, 树木生长受碳限制(carbon limitation) (Wiley *et al.*, 2013)。此后随着固定的碳逐渐增多, 树木体内总的NSC含量升高, 但这些碳往往优先分配给碳储备(即碳储备相对于生长来说是一种更主动的汇), 所以NSC用于生长的能力仍然不足(Lacointe *et al.*, 2004), 这时树木的生长受到汇限制(sink limitation)。

碳限制和碳饥饿都是树木体内NSC相对不足, 但碳限制没有碳饥饿的程度严重; 且在文献中一般碳限制侧重于对生长的影响, 而碳饥饿侧重于对树木死亡的影响。Wiley等(2013)认为判断是碳限制导

致生长减弱必须满足两个条件: 1) 碳获取降低; 2) 生长的减弱是因为碳有效性的减弱, 而不是汇限制。汇限制经常被认为是因为营养供给、环境条件等引起树木利用碳生长的能力不足(Sala & Hoch, 2009; Wiley *et al.*, 2013), 类似于解释高山树线的生长限制假说(growth-limitation hypothesis), 即细胞分裂减慢的速度大于光合减慢的速度, 导致碳在树体内积累(Körner, 2003)。但叶损失后树木倾向于储存而抑制生长的策略可能是植物长期适应环境和进化的结果(Smith & Stitt, 2007), 是一种保守的碳利用的策略, 这样更有利于减轻不利条件的影响(包含抵抗再次虫害叶损失) (Smith & Stitt, 2007)。这种叶损失后改变碳分配的证据很多, 例如Wiley等(2013)发现*Quercus velutina*的叶片全部损失后, 即使淀粉恢复到了对照水平, 树木的生长依然很低; Jacquet等(2014)也发现*Pinus pinaster*在50%和100%两种叶损失处理后, 茎的NSC都显著高于对照, 而茎生长很弱; 其他的叶损失研究中同样是NSC的恢复早于生长(Susiluoto *et al.*, 2010)。

虫害叶损失前碳储备(特别是根的碳储备)多有利于叶损失后树木碳和生长的恢复。很久之前人们就认识到NSC对叶损失后重新生长的重要性(Sullivan & Sprague, 1943), 在虫害叶损失发生后, 植物的剩余部分会大范围地动员NSC来生长(Volenec *et al.*, 1996)。储存, 特别是地下的储存, 有利于在虫害爆发或其他干扰(干旱、火)之后树木再次萌发(Wiley *et al.*, 2013)。如果储存的NSC足够, 叶损失后树的生长能维持或接近叶损失之前的生长速率(Gleason & Ares, 2004)。

根的碳储备很重要的另外一个原因是叶损失后树木往往优先恢复地上部分(Eyles *et al.*, 2009), 所以根只能主要依靠之前的碳储备来继续维持获取水分、养分的功能(Canham *et al.*, 1999)。Dickmann等(1996)和Kosola等(2001)发现叶损失后分配到根中的碳下降; Frost和Hunter (2008)对二年生的*Quercus rubra*幼苗研究发现, 叶损失7天后分配到地下细根的碳减少了63%; 而Jactel等(2012)发现茎的NSC在叶损失后只是短暂地降低。汇分层理论(sink hierarchy)认为树体的碳运输路径一端是树冠, 另一端是根, 根虽然是一个大的汇, 但树冠这一端将首先从功能叶的光合作用中获取碳, 根的这一端只能在其他的汇不能马上获取或已经获取完成的时候再获

得碳(Landhäusser & Lieffers, 2012)。因此, 叶损失后树木根的NSC储备往往会显著低于叶损失之前, 并且相比树冠碳的恢复, 根碳储备恢复所用的时间更长(Landhäusser & Lieffers, 2012)。例如山杨根碳储备的恢复用了两个生长季(Landhäusser & Lieffers, 2012)。如果根本身的NSC储备不足, 叶损失将导致根吸收水分、养分的能力降低, 反过来会限制碳同化或加重木质部栓塞的危险, 导致更严重的碳饥饿或防御降低(Bryant *et al.*, 1993; Landhäusser & Lieffers, 2012)。

5 树木虫害及叶损失与气候变化的关系

5.1 虫害爆发与气候变化的关系

气候变化对森林的影响既有积极的一面, 如大气CO₂浓度升高和氮沉降增加所引起的施肥效应, 增强了森林活力和水分利用效率, 也有气候变化和其驱动的病虫害动态变化引起的森林树木生长减弱和胁迫、死亡增多等消极的一面(Ayres & Lombardero, 2000; Scholze *et al.*, 2006)。

干旱和高温可诱导虫害爆发。基于干旱后昆虫活性增强和树木死亡增多的证据, 干旱与虫害之间的内在联系被广泛接受(Mattson & Haack, 1987); Gaylord等(2013)也证明干旱过后树木更容易遭受虫害攻击。温度升高也可能增加病虫害发生, 特别是在北方温带地区(Ayres & Lombardero, 2000)。温暖的气候还容易扩大昆虫的分布, 因为相对于寄主树木, 昆虫具有较高的移动性, 而现在的昆虫种群多被地理因素限制(MacLean, 1983)。

干旱、高温与昆虫种群之间的关系也常常因昆虫自身状态和干旱、高温的强度、发生时间而不同(Huberty & Denno, 2004; Jactel *et al.*, 2012)。在美国西南部, 伴随着温度升高, 干旱容易增强当地甲虫的繁殖力和扩大其地理范围(Ayres & Lombardero, 2000; Tran *et al.*, 2007)。而Hicke等(2006)发现温度升高对低海拔虫害种群生长起负作用, 但是对高海拔的虫害种群生长起到正作用。黄忠良(2000)对鼎湖山樟翠尺蛾(*Thalassodes quadraria*)种群动态的研究发现降雨是卵期和幼虫期昆虫死亡的重要因子, 特别是二月和四月的降雨, 所以降雨量对樟翠尺蛾的存活率和繁殖力具有极端的负影响; 而温度具有正影响(黄忠良, 2000)。Zhou等(2011)的研究指出鼎湖山干季、湿季的温度和年平均气温在1954年以后显

著升高, 而在1980年以后年平均无雨天数显著增多。鼎湖山的这种气候变化趋势有利于樟翠尺蛾的爆发, 与鼎湖山近几年虫害爆发的情况一致, 而在20世纪80年代之前, 鼎湖山从未爆发过虫害(黄忠良, 2000)。

5.2 叶损失及树木死亡对气候变化的正反馈

虫害叶损失不仅导致全球植被生产力严重下降(May & Carlyle, 2003), 而且因为森林中储存着大量的碳, 森林死亡会使这些碳释放到大气中, 再在生态系统中重新分布(Allen *et al.*, 2010)。许多学者认为森林死亡和相关的扰动将在较短的时间内增加森林碳通量速率, 改变局地、区域或全球的碳平衡, 潜在地破坏森林作为碳汇的能力(Breshears & Allen, 2002; Allen *et al.*, 2010)。加拿大British Columbia这个地区的大量树木由于虫害爆发而死亡, 模型模拟发现这种昆虫的扰动使这个地区的森林由一个净的碳汇转变为一个碳源(Kurz *et al.*, 2008)。因此, 虫害爆发造成森林严重的叶损失或森林大面积死亡应该引起足够的重视。

6 问题与展望

未来虫害叶损失与树木死亡的研究可以在以下几个方面进行: (1)加强在细胞、组织、器官和个体等不同水平上研究NSC与新陈代谢之间的关系, 以加深认知碳饥饿导致植物死亡更深层次的原因。目前国外对碳饥饿理论的研究取得了一定的进展, 但国内对这方面的研究还很少, 更未见到实例报道。目前国外新的研究提供了确凿的碳饥饿导致树木死亡的证据, 但碳饥饿理论的研究还远未停止, 甚至现在只是处于起步阶段。(2)植物物候本身就会导致植物体内NSC波动, 探索不同物候时间和不同生存策略的树种应对虫害叶损失的差异响应, 揭示在虫害干扰之后为什么有的树种能够存活, 而有的树种容易死亡, 有助于预测虫害干扰后森林结构的变化或为营造人工林的种间搭配提供理论依据。(3)进一步研究虫害种群动态与气象因子之间的关系, 为气候变化背景下的虫害爆发预警提供依据。

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