

植物光合产物分配及其影响因子研究进展

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摘 要 植物光合产物分配受环境因子和生物因子的共同影响。为增进对植物对全球变化响应的理解, 从植物个体水平与群落/生态系统水平综述了植物光合产物分配的影响因子与影响机理的最新研究进展。植物个体在光照增强及受水分和养分胁迫时, 会将光合产物更多地分配到根系; CO₂浓度升高对植物光合产物分配的影响受土壤氮素的制约, 植物受氮素胁迫时, CO₂浓度升高会促进光合产物更多地分配到根系; 反之, 对植物光合产物分配没有影响。植物群落/生态系统的光合产物分配对环境因子的响应不敏感; 光合产物向根系的分配比例随其生长阶段逐渐降低。功能平衡假说、源汇关系假说和相关生长关系假说分别从环境因子、个体发育和环境因子与个体发育协同作用方面阐述了植物光合产物分配的影响机理。在此基础上, 指出了未来拟重点加强的研究方向: 1) 生态系统尺度的光合产物向呼吸部分的分配研究; 2) 地下净初级生产力(belowground net primary productivity, BNPP)研究; 3) 温室和野外条件下及幼苗和成熟林光合产物分配对环境因子响应的比较研究; 4) 生态系统尺度的多因子控制试验; 5) 整合环境因子和个体发育对植物光合产物分配格局的影响研究。

关键词 分配模型, 相关生长关系假说, 影响因子, 功能平衡假说, 植物光合产物分配, 源汇关系假说

Advances in the study of photosynthate allocation and its controls

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Abstract

Photosynthate allocation is influenced by both environmental and biological factors. This paper reviews recent advances in the mechanism of photosynthate allocation and its controls at individual and community/ecosystem levels in order to improve understanding of plant responses to global change. At the individual level, more photosynthate will be allocated to roots under conditions of high light, low water and low nutrient availabilities. The effect of increased atmospheric carbon dioxide concentration on photosynthate allocation depends on soil nitrogen availability. The root mass fraction (RMF) will increase under low nitrogen and is unchanged under high nitrogen. At the community/ecosystem levels, photosynthate allocation is insensitive to environmental change. The RMF decreases with increasing stand age. The functional equilibrium hypothesis (optimal partitioning) can explain the regulation of photosynthate allocation in response to environmental change, the source-sink relationship can reflect the effect of ontogeny on photosynthate allocation and the allometric relationship provides an important theoretical baseline prediction to disentangle the effects of plant size and environmental variation on photosynthate allocation. Research is needed on 1) the fraction of photosynthate allocated to respiration at the ecosystem level, 2) accurate estimation of belowground biomass and belowground net primary productivity (BNPP), 3) comparative study of photosynthate allocations between young and mature forests and between field and greenhouse experiments, 4) effects of multiple factors and their interactions on photosynthate allocation at the ecosystem level and 5) cooperative effects of ontogeny and environmental factors on the regulation of photosynthate allocation.

Key words allocation model, allometric relationship, controlling factors, functional equilibrium hypothesis (optimal partitioning), photosynthate allocation, source-sink relationship hypothesis

植物光合产物分配是陆地生态系统模型中一个重要的中间变量, 其分配过程不仅受环境因子如光照、水分、养分、温度和CO₂浓度等的影响(Müller

et al., 2000; Zak et al., 2000; Domisch et al., 2001; Hale et al., 2005; Rachmilevitch et al., 2006; Sigee et al., 2007), 还受到生物因子如遗传特性、生长阶段

和密度竞争等因素的制约(Litton *et al.*, 2004, 2007; Day *et al.*, 2005; Vanninen & Makela, 2005; Feng *et al.*, 2007)。光合产物向植物器官分配比例的变化及其对植物生长的反馈作用会对植物的生活史对策、群落结构和进化策略产生重要影响(Niklas & Enquist, 2002)。短时间尺度上, 光合产物向各个器官的分配比例发生变化将影响各个器官的相对生长速率(Lacointe, 2000); 长时间尺度上, 光合产物分配格局的变化将改变植物的叶面积指数、根系吸收养分和水分的速率、根系碳周转及群落的物种组成等, 进而对植物的生长产生深远影响(Jackson *et al.*, 2000; Malhi *et al.*, 2004)。正因如此, 植物光合产物分配已成为植物生态学和遗传学研究中的热点问题(Lacointe, 2000)。然而, 植物光合产物分配机理的研究远落后于光合、呼吸及叶片生长等方面的研究(Cannell & Dewar, 1994; Grechi *et al.*, 2007), 目前仍未形成统一的结论, 限制了对光合产物分配的准确模拟, 影响了陆地生态系统生产力与碳收支的准确评估(Friedlingstein *et al.*, 1999; Litton *et al.*, 2007)。为此, 本文试图对近年来国内外有关植物光合产物分配的最新研究进展进行综述, 着重从个体和生态系统水平分析植物光合产物分配的影响因子, 并探讨植物光合产物分配的影响机制和定量模拟, 为陆地生态系统生产力和碳收支的准确评估提供依据。

1 植物光合产物分配常用术语

植物的光合产物分配(photosynthate allocation)也称同化物分配(assimilate allocation), 包括两个时间尺度的分配过程: 1)在秒或小时尺度上, 光合作用生成的碳水化合物(包括蔗糖、淀粉和非结构性碳水化合物)在植物体内的分配(carbohydrate allocation), 通常用稳定同位素法研究叶片中固定的 ^{14}C 向植物体内不同库的分配(Cairney & Alexander, 1992; Domisch *et al.*, 2001); 2)在月或年尺度上, 短时间分配对各个器官光合产物积累量的影响(Tilman, 1988; Dewar, 1993), 包括碳分配和生物量分配两种形式。碳分配(carbon allocation)指植被总第一性生产力(gross primary production, *GPP*)以碳(C)的形式向呼吸、根、茎和叶等部分的分配, 通常采用碳平衡法(carbon balance approach)估算*GPP*向地下部分的分配(Litton *et al.*, 2007)。生物量分配(biomass allocation), 也称干物质分配(dry matter

allocation), 指一定时间内积累的干物质向植物体各个器官的分配, 干物质分配多用于繁殖器官占重要作用的植物的研究, 如农作物及果树等(Marcelis *et al.*, 1998; Andrews *et al.*, 2001), 通常采用测定一段时期内植物体各器官生物量的增量来计算生物量向各部分的分配比例(Domisch *et al.*, 2001; Glynn *et al.*, 2003; Ngugi *et al.*, 2003)。

在研究中通常采用根冠比表征光合产物分配格局的变化, 但由于根冠比忽视了茎和叶在生态系统中的功能区分(草原生态系统除外), 并且夸大了环境因子对光合产物分配的影响(光合产物向根系分配比例的减少必然伴随着地上部分分配比例的增加), 所以不提倡使用。为此, 提倡使用根分配比例(root mass fraction, *RMF*)、茎分配比例(stem mass fraction, *SMF*)和叶分配比例(leaf mass ratio, *LMF*), 分别表示光合产物向根、茎和叶的分配量占总分配量的比例(VanderWerf & Nagel, 1996; Poorter & Nagel, 2000)。

2 植物光合产物分配的影响因子

影响植物光合产物分配格局改变的原因主要包括: 1)表面上的分配可塑性。由于植物不同器官的相对生长速率随生长阶段的不同发生变化, 导致光合产物分配格局发生改变, 这种变化与环境因子的改变没有关系, 主要受植物个体发育的影响(Müller *et al.*, 2000)。2)真正的分配可塑性。当植物各个器官都处于平衡状态时, 环境因子的变化才会真正改变植物的光合产物分配格局, 这种改变是真正的分配可塑性(McConnaughay & Coleman, 1999)。因此, 植物光合产物分配格局受个体发育和环境因子的共同影响(Gedroc *et al.*, 1996; McConnaughay & Coleman, 1999; Harmens *et al.*, 2000; Poorter & Nagel, 2000; Cahill Jr, 2003)。

2.1 环境因子

2.1.1 光照

高光强下, 植物会增加光合产物向根系的分配比例, 减少向叶片的分配比例(Poorter & Nagel, 2000; Kotowski *et al.*, 2001; Ammer, 2003; Grechi *et al.*, 2007; 陈亚军等, 2008; 孙晓方等, 2008)。遮阴时, 植物光合产物向叶片的分配比例增加, 向根系的分配比例降低, 向茎的分配比例则没有明显的变化(Welander & Ottosson, 1998; Day *et al.*, 2005;

Feng *et al.*, 2007; Lockhart *et al.*, 2008); 但也有研究表明, 光照减弱时光合产物向茎的分配比例增加, 向叶的分配比例不变甚至降低, 但比叶面积增加, 表明植物通过改变其形态学特征来最大程度地获取光照(de Groot *et al.*, 2002; 陈亚军等, 2008)。

描述光照对植物光合产物分配的影响机理主要有两个假说: 1)通过影响植物体内的N含量对光合产物分配进行调节。研究表明, 遮阴增加了植物体的N含量, 降低了淀粉含量, 而植物体的淀粉含量和光合产物向根系的分配比例呈正比, 导致植物光合产物向根系的分配比例降低(de Pinheiro Henriques & Marcelis, 2000; de Groot *et al.*, 2002)。2)在高光强下, 温度升高, 相对湿度降低, 叶片受到的水分胁迫增加, 导致气孔关闭和光合作用减弱, 进而引起植物的反馈调节, 使光合产物向根系的分配比例增加, 促进根系吸水(Lockhart *et al.*, 2008)。研究表明, 光照通过影响植物体内的C、N平衡来调节光合产物的分配(Cronin & Lodge, 2003; Grechi *et al.*, 2007)。

2.1.2 养分

个体水平上, 土壤养分(主要是N)的减少会促使光合产物向根系的分配比例增加, 而养分充足时, 光合产物将更多地向叶片分配, 这种分配格局的改变对不同的植被类型(灌木、草本或木本植物)和植物生活型(一年生或多年生)都是一致的(Balachandran *et al.*, 1997; Müller *et al.*, 2000; Warembourg & Estelrich, 2001; Cronin & Lodge, 2003; Glynn *et al.*, 2003; Vanninen & Makela, 2005; Grechi *et al.*, 2007)。但不同的元素对植物光合产物分配的影响差异很大。土壤中N、P和S含量的降低会导致光合产物向根系的分配比例增加, K、Mg和Mn的缺失却会降低光合产物向根系的分配比例(Ericsson *et al.*, 1996; Balachandran *et al.*, 1997; Nielsen *et al.*, 2001), 而植物在受Ca、Fe或Zn胁迫时光合产物分配格局不变(Ericsson *et al.*, 1996)。植物受N素胁迫时, 根系向茎部输送的细胞分裂素含量减少, 茎部细胞分裂速度变慢, 导致从韧皮部向茎部输送的蔗糖减少, 使韧皮部周围的蔗糖含量增加, 引起叶片膨压的升高; 而根系细胞分裂继续进行, 细胞膨压没有发生变化, 从而使源(叶片)和汇(根部)之间产生膨压梯度, 促使光合产物相对较多地向根系分配。植物受P胁迫时, 各个器官对光合产物的需求减弱, 光合产物更多地积累到叶片, 植物

通过增加光合产物向根系的分配来吸收养分(Dingkuhn *et al.*, 2007)。K作为调节气孔开闭的重要因子, Mg参与光能的获取, K和Mg影响光合作用酶的活性, 因此这些元素的缺失会导致光合作用的降低, 从而减少光合产物向根系的分配(Ericsson *et al.*, 1996)。

群落或生态系统水平上, 有关植物光合产物分配对土壤养分变化的响应研究还较少。研究指出, 养分胁迫促使森林和草原生态系统光合产物向根系的分配比例增加(Dukes *et al.*, 2005; Litton *et al.*, 2007)。也有研究表明, 根冠比对土壤N素含量的变化不敏感(Yang *et al.*, 2009)。LeBauer和Treseder (2008)指出, 全球绝大多数生态系统都受到N素胁迫。在全球变化背景下, 未来人为N沉降将会覆盖北美、欧洲以及东南亚等温带和热带地区, 研究这些地区植物的光合产物分配对N素添加的响应会对理解陆地生态系统碳循环产生重要的影响(Dentener *et al.*, 2006)。

2.1.3 水分

个体水平上, 水分和养分对植物光合产物分配的影响是相同的。植物受水分胁迫时, 光合产物会更多地分配到根系来促进根系吸水(McConnaughay & Coleman, 1999; Huang & Fu, 2000; Ngugi *et al.*, 2003; 肖冬梅等, 2004; Coyle & Coleman, 2005; Xu & Zhou, 2005; 贺海波和李彦, 2008)。水分胁迫对植物光合产物分配的影响要小于养分胁迫(Balachandran *et al.*, 1997; Hale *et al.*, 2005)。水分胁迫会导致植物体内蛋白质合成的减弱, 降低了植物体内的N含量, 但并不增加淀粉含量, 促使光合产物较多地分配到根系(Poorter & Nagel, 2000; Andrews *et al.*, 2001)。

生态系统水平上, Mokany等(2006)研究表明森林、灌木和草原生态系统的根冠比均随年降水量的增加而降低。Wang等(2003)研究发现羊草草原生态系统光合产物分配格局受东北样带水分梯度的影响。随经度由东向西, 降水逐渐减少, 光合产物向地上的分配比例逐渐降低, 向地下的分配比例增加。这与中国北方林和全球尺度森林生态系统上得出的结果相似(Litton *et al.*, 2007; Wang *et al.*, 2008)。同时, 也有研究表明草原生态系统光合产物分配对年降水量或土壤含水量的增加响应不敏感(Fan *et al.*, 2009; Yang *et al.*, 2009)。

2.1.4 温度

个体水平上, 温度升高对植物光合产物分配的影响还没有得到一致的结论。空气温度升高会降低叶片同化产物的积累, 增加光合产物向叶片的分配比例, 降低根冠比(Farrar & Williams, 1991; Andrews *et al.*, 2001), 但也有研究发现在一定的阈值内土壤温度升高会降低光合产物向根系的分配比例, 当温度高于或低于这一阈值时光合产物向根系的分配比例都会增加(Lambers *et al.*, 1995; Peng & Dang, 2003)。温度对植物光合产物分配的影响机理有两种假说: 1) 温度通过影响植物的生长来改变光合产物分配格局, 当植物处于极端高温或低温情况下, 植物的生长尤其是地上部分受到抑制, 导致根冠比增加。当植物处于适宜的生长温度时, 温度升高促使植物的生长速度增加, 尤其是地上部分的增加更快, 导致根冠比降低(Farrar & Williams, 1991; Peng & Dang, 2003)。2) 温度升高后, 植物体内的N含量增加, 同时土壤养分的供应能力提高, 导致植物根冠比降低(Andrews *et al.*, 2001; Vogel *et al.*, 2008), 未来的研究热点将集中于区分光合产物分配格局的改变是由植物各部分生长速率不同引起的表型可塑性还是真正的分配可塑性。

生态系统水平上, 温度对植物光合产物分配的影响也不确定。温度升高会降低草原生态系统光合产物向根系的分配比例(Mokany *et al.*, 2006; Fan *et al.*, 2009)。Litton和Giardina (2008)研究了全球尺度下植物光合产物分配对温度的响应, 结果表明在温带和热带地区, 光合产物向地下的分配比例随年平均温度的升高而增加。在北方林中, 地下部分分配比例随年平均温度的升高而降低, 这可能是由于年平均温度升高使土壤养分的供应能力提高, 导致光合产物向地下的分配变少(Vogel *et al.*, 2008)。也有研究表明, 温度对植物光合产物分配的影响不显著(Gorissen *et al.*, 2004; Dukes *et al.*, 2005; Hawkes *et al.*, 2008)。

2.1.5 CO₂

个体水平上, 植物光合产物分配对CO₂浓度升高的响应的研究已经很多(Farrar & Williams, 1991; Poorter, 1993; Ceulemans & Mousseau, 1994; Norby *et al.*, 1995; Rogers *et al.*, 1996)。总体而言, 植物光合产物向根系的分配比例随CO₂浓度升高而增加(Ceulemans & Mousseau, 1994; Johnson & Lincoln,

2000; Niklaus *et al.*, 2001; Xu *et al.*, 2007), 也有研究表明植物光合产物分配格局对CO₂浓度升高不敏感(Farrar & Williams, 1991; Poorter, 1993; Rogers *et al.*, 1996)。Rogers等(1996)综述了农作物光合产物分配对CO₂浓度升高的响应, 结果发现59.5%的结论支持根冠比增加, 37.5%的结果表明根冠比下降, 另有3%的研究表明根冠比对CO₂浓度升高没有反应。CO₂浓度升高对光合产物分配的影响受植物体内N素和非结构性碳水化合物含量的共同控制(Poorter & Nagel, 2000; Andrews *et al.*, 2001)。CO₂浓度升高会降低植物各个器官的N含量, 植物为确保养分的供应将增加光合产物向根系的分配比例。同时, CO₂浓度升高会增加植物叶片的淀粉含量, 使叶片和根系之间产生膨压梯度, 导致相对较多的光合产物向根系分配(Farrar & Williams, 1991; Zak *et al.*, 2000; Liu *et al.*, 2002; Suter *et al.*, 2002; Xu *et al.*, 2007)。这种影响在养分匮乏下较为明显, 在养分充足的环境中, CO₂浓度升高不会改变植物的光合产物分配格局(Liu *et al.*, 2002)。

生态系统水平上, 当受到养分和水分胁迫时, CO₂浓度升高会促使大多数生态系统的光合产物更多地分配到根系(Bazzaz, 1990; Hyvonen *et al.*, 2007)。资源充足时, CO₂浓度升高对生态系统光合产物分配没有显著的影响(Norby & Jackson, 2000; Dukes *et al.*, 2005; Milchunas *et al.*, 2005)。

2.1.6 因子交互作用

群落或生态系统水平上, 植物光合产物分配对环境因子的响应不如个体水平上明显, 原因是个体水平上, 环境因子对植物光合产物分配的影响是通过控制试验得到的。在群落或生态系统水平上, 对环境因子的控制较为困难, 环境因子间的交互作用导致植物光合产物分配规律不明显(Hyvonen *et al.*, 2007)。

降水及养分胁迫对植物光合产物分配的影响受CO₂浓度升高的制约, CO₂浓度升高提高了植物的水分利用效率(water use efficiency, WUE), 降低了植物体N素水平, 从而制约了降水及N沉降对植物光合产物分配的影响(Poorter & Nagel, 2000; Coviella *et al.*, 2002; Shaw *et al.*, 2002)。光照与N素之间、水分与光照之间的交互作用也显著影响植物光合产物分配格局(Kotowskil *et al.*, 2001; de Groot *et al.*, 2002)。生态系统水平上, 光合产物分配对土壤温度变化不敏感, 但土壤温度与降水增加的协同作用显著增加

了黑云杉(*Picea mariana*)林生态系统光合产物向地上部分的分配比例(Vogel *et al.*, 2008)。

2.2 生物因子

2.2.1 生长阶段

植物光合产物向根系的分配比例会随生长阶段逐渐降低, 光合产物向茎的分配比例随林龄的增加而增加(McConnaughay & Coleman, 1999; Suter *et al.*, 2002; Mokany *et al.*, 2006; Litton *et al.*, 2007; Wang *et al.*, 2008)。多年生黑麦草(*Lolium perenn*)的根冠比从生长初期的0.94下降到收获前的0.46(Suter *et al.*, 2002)。相比幼林, 美国黄松(*Pinus ponderosa*)和湿地松(*P. elliottii*)成熟林的SMF分别增长了48%和58%, RMF分别降低了17%和21%(Litton *et al.*, 2007)。植物在生长初期更多地将光合产物向根系和菌根分配来保证水分和养分的充足供应, 随着植物的生长, 光合产物向叶片的分配比例增加来最大程度地增加光合作用, 同时木本植物增加光合产物向茎的分配来获取光照和提供支持(Litton *et al.*, 2004; Weiner, 2004)。

2.2.2 竞争

竞争对植物光合产物分配的影响受环境因子的制约。在土壤养分和水分匮乏的环境中, 植物的竞争主要集中在根系(Schenk, 2006), 竞争导致光合产物向根系的分配比例增加(Cronin & Lodge, 2003; Weigelt *et al.*, 2005; Wang *et al.*, 2008; Berendse & Möller, 2009)。当土壤养分和水分充足时, 整株竞争使植物对光照和养分的需求同时增加, 不会引起植物的光合产物分配格局发生变化(Berendse & Möller, 2009)。当只有地上竞争时, 植物通过增加光合产物向叶片的分配以获得更多的光照(Bloor *et al.*, 2008)。在考虑竞争对植物光合产物分配的影响时, 要特别分清分配格局的改变是竞争直接引起的, 还是由竞争导致的植株体积的减小所引起的(Weigelt *et al.*, 2005)。

3 植物光合产物分配机理

植物光合产物分配受光合作用、同化物传输、呼吸作用和同化物的存储等一系列时间尺度不同的生理过程的共同影响, 而环境因子和植物个体发育对光合产物分配的调控作用, 进一步增加了过程的复杂性, 使得植物光合产物的分配机制存在很大争议, 没有一个合理的解释(Atkinson & Farrar,

1983; Vander Werf & Nagel, 1996; Vivin *et al.*, 2002; Grechi *et al.*, 2007)。目前, 植物光合产物的分配机制主要有以下3个假说: 功能平衡假说、源汇关系假说和相关生长关系假说。

3.1 功能平衡假说

功能平衡假说(functional equilibrium hypothesis)由Brouwer于1962年提出。该假说将植物分为根和冠两部分, 根的生长受冠部光合作用碳供应速率的限制, 而冠的生长受根系对养分和水分吸收速率的限制。因此, 植物受到水分和养分胁迫时将增加光合产物向根系的分配以保证水分和养分的供应; 当植物受到光照胁迫时通过增加光合产物向冠部的分配来促进光合作用(Marcelis *et al.*, 1998)。

在此基础上, 一些研究者对功能平衡假说进行了改进, 提出了最优分配理论(optimal partitioning theory)和协调理论(coordination theory)。最优分配理论认为, 植物通过对光合产物的分配来获取光照、养分、水分和CO₂等资源以达到最大的生长速率(Bloom *et al.*, 1985)。协调理论认为, 叶片对C的供应及根系对养分和水分的吸收二者之间的协调和平衡决定了植物光合产物的分配, 环境因子发生变化后, 植物会通过改变光合产物的分配来调整体内C和N的供应以达到平衡(Reynolds & Chen, 1996; Chen & Reynolds, 1997)。

许多研究表明, 功能平衡假说与最优分配理论能较好地反映环境因子(光照、CO₂、水分、N和P等)对植物光合产物分配的影响(Poorter & Nagel, 2000; de Groot *et al.*, 2002; Grechi *et al.*, 2007; McCarthy & Enquist, 2007)。因此, 很多研究者基于功能平衡假说构建植物光合产物分配模型, 如普遍用于植物生长模型中的目的模型(teleonomic model)和传输阻力模型(transport resistance model)等(Thornley, 1972; Johnson & Thornley, 1987; Hunt *et al.*, 1998; Agren & Franklin, 2003; Makela *et al.*, 2008)。Arora和Boer (2005)基于功能平衡假说建立了区域尺度的光合产物分配模型。Friedlingstein等(1999)构建了全球尺度光合产物分配模型, 目前该模型已被耦合到很多陆地生态系统模型中(Fung *et al.*, 2005; Krinner *et al.*, 2005)。

3.2 源汇关系假说

源汇关系假说(source-sink relationship hypothesis)认为, 植株是由相互作用的源(主要是叶片)和汇

(茎、根和果实)组成的系统, 源通过韧皮部运输提供同化物, 汇通过相互之间的竞争获得同化物(Wardlaw, 1990; Dewar, 1993)。植物光合产物分配由源的供应能力、汇的竞争能力及韧皮部对光合产物的传输能力等三方面所决定。同化物的供应遵循就近供给原则, Palit (1985)利用 ^{14}C 同位素技术研究发现, 顶部叶片会将光合产物分配给顶芽和幼叶, 中部叶片将光合产物分配给茎, 基部叶片将光合产物分配给基茎和根系, 繁殖器官会从就近的叶片获取光合产物。各个汇的竞争强度可以量化为没有资源限制条件下的潜在生长速率。各个器官的潜在生长速率随生长阶段和温度的变化而改变(Marcelis & Heuvelink, 2007)。

源汇关系假说可以通过测定各个器官在没有资源限制条件下的潜在生长速率来描述植物的个体发育特征(Génard *et al.*, 2008)。环境因子与竞争都通过影响汇的竞争能力来改变植物的光合产物分配格局。植物在面临 CO_2 浓度升高及水分和养分胁迫时, 汇的强度都会减弱, 导致光合产物向根系的分配比例增加(Poorter, 1993; Rogers *et al.*, 1996; Grechi *et al.*, 2007)。

源汇关系假说能从机理上解释植物光合产物向各个器官的分配, 同时可以模拟光合产物向繁殖器官的分配, 因此常被用于果树和农作物光合产物分配的模拟(Wermelinger *et al.*, 1991; Vivin *et al.*, 2002; Marcelis & Heuvelink, 2007; Génard *et al.*, 2008)。近年来源汇关系假说主要用于构建功能结构模型(functional-structural models), 如GREENLAB和GRAAL模型已在果树和农田生态系统中得到了应用(Drouet & Pagès, 2003, 2007; Yan *et al.*, 2004; Cournede *et al.*, 2008)。

3.3 相关生长关系假说

相关生长关系假说(allometric relationship)由Kleiber于1932年提出, 认为植物体内生长速率和个体大小之间符合相关生长方程:

$$B = B_0 M^{3/4} \quad (1)$$

式中, B 代表相对生长速率, M 为个体大小, B_0 为系数(West *et al.*, 1997; Farrell-Gray & Gotelli, 2005)。相关生长关系假说反映了生物个体大小对其身体结构和生理过程的影响, 进而反映种群、群落甚至更大尺度上的许多生态特征(韩文轩和方精云, 2003)。

Enquist和Niklas (2002)基于该假说提出了相关

生长关系模型, 该模型是建立在代谢理论基础上的(Niklas & Enquist, 2002)。它认为植物体内存在一个“普遍”的生物量分配模式, 并假定植物是由根、茎和叶3个功能部分组成, 同时满足以下3个假设: 1)茎和根的容重在个体发育过程中保持不变; 2)茎和根的有效截水面积相同; 3)根的长度和茎的长度成正比。由此推出植物的根、茎和叶之间的生物量分配模式:

$$M_{\text{stem}} \propto M_{\text{root}}; M_{\text{leaf}} \propto M_{\text{stem}}^{3/4} \propto M_{\text{root}}^{3/4} \propto M_{\text{tot}}^{3/4}; M_{\text{leaf}} + M_{\text{stem}} \propto M_{\text{tot}} \quad (2)$$

式中, M_{root} 、 M_{stem} 、 M_{leaf} 和 M_{tot} 分别代表根、茎、叶的生物量和总生物量。

相关生长关系体现了生物量在植物体各器官之间的分配关系, 并且相关指数与群落组成或环境条件等关系不大。这表明, 尽管在进化中出现了物种和生活型等方面的多样性分化, 但由于植物个体都遵循相似的最优化设计原则, 使得生物量的基本分配模式并没有发生根本变化(Niklas, 2006)。程栋梁(2007)对我国西北5个干旱、半干旱区域的天然植被群落地上和地下生物量进行了研究, 其结论支持存在一个“标准”的地上-地下生物量分配模式, 并且证明地上-地下生物量关系可以从个体水平上推到群落水平上(Cheng & Niklas, 2007; 程栋梁, 2007), Yang等(2009)在高寒草原生态系统上得到的结论也支持相关生长关系假说。

基于相关生长关系假说建立的模型由于模式简单, 参数较少, 并且模型模拟的效果也较好, 因此成为近年来植物光合产物分配的研究热点。但同时有很多研究结果不支持这一假说(Li *et al.*, 2005; Grechi *et al.*, 2007), 如Li等(2005)搜集了中国17个森林类型的生物量数据, 发现并不存在统一的相关生长关系, 同时在热带森林中也没有发现这一规律(Muller-Landau *et al.*, 2006)。

3.4 3个假说的相关性及其优缺点分析

功能平衡假说认为, 植物通过调整光合产物向茎部和根系的分配来保证资源的最优化利用(Bloom *et al.*, 1985), 这种策略被应用于植物生长的不同阶段并被逐渐保留, 从而体现出植物的相关生长关系(Niklas & Enquist, 2002; Cheng & Niklas, 2007)。功能平衡假说认为, 植物光合产物向茎和根系这两个汇的分配由各自功能之间的相互平衡达到, 而相关生长关系中的分配指数代表了该器官汇的强度, 体现了源汇关系假说(Génard *et al.*, 2008)。

虽然功能平衡假说、源汇关系假说和相关生长关系假说都包含了环境因子和个体发育对植物光合产物分配的影响,但3种假说各有其优缺点:1)功能平衡假说能较好地解释环境因子变化对植物光合产物分配的影响,但没有考虑植物个体大小对光合产物分配的影响,环境因子可能通过影响器官的生长来改变植物光合产物分配格局(McCarthy & Enquist, 2007)。同时,该假说只能对营养生长阶段进行模拟,难以模拟植物光合产物向繁殖器官的分配(Thornley, 1972; 刘颖慧等, 2006);并且植物体各个器官之间功能平衡过程的机理非常复杂,目前对其缺乏深入的认识(Marcelis & Heuvelink, 2007)。2)源汇关系假说能很好地解释个体发育或遗传特性对植物光合产物分配的影响,在植物萌发阶段根系是主要的汇,植物接受光照后叶片成为主要的碳源,之后根系的主导作用丧失,茎部成为主要的汇。在植物生长的不同阶段各个汇的强度也不同,从而导致植物光合产物的分配格局发生变化(Marcelis & Heuvelink, 2007)。源汇关系假说作为一个半机理假说,能较好地模拟植物繁殖器官的分配,因此已被用于很多研究中。但是不同种类植物各个器官的汇的强度是不同的,建立统一的光合产物分配模型较为困难(Génard *et al.*, 2008)。3)相关生长关系假说的优点在于能很好地区分环境因子及个体发育对植物光合产物分配的影响,通过观测生长关系系数和指数的改变就能给出光合产物分配是环境因子引起的还是植物个体发育或个体大小的改变引起的(Cheng & Niklas, 2007; McCarthy & Enquist, 2007)。同时,相关生长关系假说可以进行尺度扩展,这有助于建立各个层次上的生物量分配模型。因此,将相关生长关系模型扩展到其他植被类型从而建立全球植被生物量分配模型将是未来的研究方向(程栋梁, 2007)。但该假说不能定量地描述环境因子对植物光合产物分配的影响,并且不能从机理上解释光合产物向不同器官的分配规律(李妍等, 2007; Génard *et al.*, 2008),另外,不同的生态系统类型是否具有统一的生物量分配模式目前还存在着很大的争议(韩文轩和方精云, 2008),这些因素限制了相关生长关系模型的发展。

4 结论和展望

植物光合产物分配在全球陆地生态系统碳循

环中具有重要的作用,对光合产物分配的影响机制和过程模拟等方面已经开展了大量的研究,但是植物光合产物分配的影响机制仍存在着很大争议,对光合产物分配的定量模拟还存在着很多不足,未来应加强以下方面的研究:

1)生态系统尺度的光合产物向呼吸部分的分配研究:生态系统水平上,光合产物的分配包括向根、茎、叶生长的分配和呼吸作用的分配,目前的研究大多只针对生长的分配,关于光合产物向呼吸部分分配的影响因子及其控制机理的研究还较少(Poorter, 1993; VanderWerf & Nagel, 1996; Nadelhoffer *et al.*, 1998; Vivin *et al.*, 2002; Agren & Franklin, 2003; Litton *et al.*, 2007)。未来在研究环境因子对光合产物分配的影响时应该考虑呼吸部分所占比例的变化,这将是光合产物分配影响机制研究中的一个关键问题。

2)地下净初级生产力(belowground net primary productivity, *BNPP*)研究:由于根系生物量测量的不准确性,死根和活根区分的困难性,以及*BNPP*估算方法的多样性,导致不同研究者得到的*BNPP*结果之间没有可比性(Woodward & Osborne, 2000; Tierney & Fahey, 2007)。准确估算*BNPP*对于更好地理解植物光合产物分配具有重要意义。

3)温室和野外条件下及幼苗和成熟林光合产物分配对环境因子响应的比较研究:个体水平上,由于幼苗试验的环境条件比较容易控制且操作简单,因此被普遍用于研究植物光合产物分配对环境因子的响应。但温室试验往往处理时间较短且植物生长受到样地的限制,同时幼苗对环境因子的响应能否推广到成熟林还存在着很大的争议(Ceulemans & Mousseau, 1994; Kolb & Matyssek, 2001)。因此,未来要关注温室和野外条件下环境因子对植物光合产物分配影响的比较研究。

4)生态系统尺度的多因子控制试验:群落或生态系统尺度上植物光合产物分配对环境因子的响应规律还不明确,并且目前全球变化对光合产物分配的影响大都是进行单因子控制试验,关于长期的、多因子控制的光合产物分配试验研究还较少,环境因子之间交互作用的研究更少(Shaw *et al.*, 2002),这限制了生态系统水平上植物光合产物分配对全球变化的准确评估,进而影响陆地生态系统碳收支的准确估算。因此在群落或生态系统水平上

进行长期的多因子控制试验来研究植物光合产物分配对环境因子的响应必将成为以后的研究热点。

5)整合环境因子和个体发育对植物光合产物分配格局的影响研究: 目前还没有假说能解释植物的个体发育与环境因子的协同作用对光合产物分配的影响。功能平衡假说或最优理论能很好地解释环境因子对植物光合产物分配的影响, 源汇关系假说和相关生长关系假说可以解释个体发育对植物光合产物分配的影响。因此未来的研究需要整合现有的假说, 进一步从机理上探讨环境因子和个体发育对植物光合产物分配格局的影响(McCarthy & Enquist, 2007)。

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