

林木细根寿命及其影响因子研究进展

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摘要 细根周转要消耗大量的 C, 它影响森林生态系统 C 分配格局与过程和养分循环, 对生态系统生产力具有重要意义。细根的周转取决于细根的寿命, 细根寿命越短, 周转越快, 根系对 C 的消耗也越多。大量研究表明, 细根的寿命与地上部分 C 向根系供应的多少有密切关系, 同时也与细根直径大小、土壤中 N 和水分的有效性、土壤温度以及根际周围的土壤动物和微生物的活动有关。本文综述了国外近年来在该领域里的研究进展, 特别是对控制细根寿命的机理和主要影响因子进行了评述, 目的是引起国内研究者的关注, 促进我国根系生态学的研究与发展。

关键词 森林 细根寿命 细根周转 根系 C 和 N 根系结构

A REVIEW : FACTORS INFLUENCING FINE ROOT LONGEVITY IN FOREST ECOSYSTEMS

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Abstract Fine root longevity is an essential component of root ecology and physiology. It is also a critical determinant of root turnover and therefore carbon (C) and nutrient flow in terrestrial ecosystems. Despite the ecological importance of fine root longevity and the tremendous research efforts devoted to it, the understanding of fine root longevity and turnover is still rudimentary. This article reviews some of the most important factors that control fine root longevity, including carbon allocation, fine root structure, soil nitrogen (N) and water availability, soil temperature, and soil biota in forest ecosystems, with the purpose of providing a brief summary of recent advances in fine root longevity research and to point out the gaps of understanding and directions for future root longevity research in China.

The most important function of fine roots is resource acquisition from the soil. To perform this function, C fixed in leaves must be used to build the fine root biomass and to supply energy needed for root growth, resource uptake, and maintenance of the fine roots. Consequently, C availability to roots may exert strong control over root longevity, and the interactions between C source (leaves) and C sink (roots) has been postulated as a mechanism through which root longevity may be explained. However, due to the lack of experimental evidence, the mechanisms by which C is allocated to roots and how C availability in roots controls root longevity remains poorly understood. Detailed studies on C allocation and utilization in processes such as root growth and root respiration (in growth and maintenance) are needed.

In addition to physiological controls of root longevity (e.g., C availability), structural characteristics of root systems also have a strong influence over root longevity. Recent studies showed that both root diameter and branching order were important regulators having shorter lifespans and turn over more rapidly than larger diameter, higher order roots. These findings are likely to contribute greatly to a more accurate quantification and prediction of C and nutrient flow via root turnover.

The efficiency model, which suggests that the mortality of fine roots may occur when the C costs of plant roots exceed the benefits (e.g., nutrient acquisition) they provide, also has been invoked to explain root mortality and longevity. This model necessitates that root longevity is closely related to resource availability in the soil. Some evidence suggests that roots in resource rich sites live longer, while others suggest the opposite. Much of the controversy may result from different methods used in estimating fine root longevity and turnover, and differences in C sink-source relationships among different species, stand development, as well as the length of the experiments in which the influence of resource levels on root longevity are tested.

Climatic factors also influence root longevity. Fine root longevity appears to be the longest in cold environments with marked seasonal variations in seasonal environments. However, most recent evidence suggests that root longevity may be more dependent on root structure than on root environment, with first order roots having similar longevity regardless of differences in species and the root environment.

Finally, ecosystem-scale processes, such as environmental stresses and pathogen and herbivory pressure, may also influence root longevity. Drought and high temperatures may shorten root longevity. However, because soil moisture, temperature, leaf C fixation, and soil resource availability are tightly linked, independent tests of moisture and temperature influences on root longevity are difficult to conduct. Evaluating the regulation of herbivores and pathogens on root longevity is also difficult, in part because little quantitative information is available on the populations of root pathogens and herbivores in different ecosystems and the responses of root systems to different levels of pathogen and herbivory pressure.

In sum, root longevity is a critical but difficult research subject. There are many opportunities as well as challenges for future root longevity research in China, of which we list only a few: 1) C allocation and C utilization in fine roots may be a primary mechanism controlling root longevity, but, to understand this mechanism fully, the methods for accurately estimating C allocation and utilization in roots of different structural and functional characteristics must be developed first; 2) Root longevity is clearly related to soil resource availability (e.g., N and moisture) and environmental factors (e.g., soil temperature and moisture), and further studies on the impact of these factors on the longevity of individual roots and root systems as a whole may prove fruitful. Studies in this area should be large-scale and long-term to encompass large environmental variability frequently observed in natural ecosystems and to provide relevant information for a better understanding of the belowground aspect of global environment change; and, 3) Linking root structure, function, and longevity is likely to be one of the most promising areas of root longevity research in the near future. Current technologies seem to be reasonably reliable for making estimates of root longevity on roots of different structural and functional features; the main challenge lies in the time and effort needed to collect such information, particularly in a country as vast and diverse as China.

Key words Forests, Fine root longevity, Fine root turnover, Root carbon and nitrogen, Root structure

细根(直径 ≤ 2 mm)是植物吸收养分和水分的主要器官,其寿命是指从出生到死亡的这段时间,是细根重要的生理生态学特性。细根的生长、衰老、死亡、脱落和再生长过程称为细根周转(Vogt *et al.*, 1986),该过程要消耗大量的 C(Hendricks *et al.*, 1993; Bloomfield *et al.*, 1996; Eissenstat & Yanai, 1997)和释放出养分(Vogt *et al.*, 1986)。在大多数陆地生态系统中,细根的生物量虽然只占地下总生物量的 3%~30%左右,但由于细根处于周转过程之中,维持这个动态过程要消耗净初级生产力的 10%~75%左右(Vogt *et al.*, 1986; Raich & Nadelhoffer, 1989; Gill & Jackson, 2000)。因此,细根周转与生态系统生产力有密切关系(Hendricks *et al.*, 2000; Nadelhoffer, 2000)。通过细根周转而归还到土壤中的 C 和养分超过地上凋落物(Raich & Nadelhoffer, 1989; 黄建辉等, 1999; 张小全等, 2000),是生态系统物质循环和能量流动的重要组成部分,近年来已成为生态系统 C 分配格局与过程研究的核心环节(Nadelhoffer, 2000; Gill & Jackson, 2000)。

细根周转归根结底是由细根寿命决定的(Schoettle & Fahey, 1994)。细根的寿命越短,周转越迅速(Bloomfield *et al.*, 1996; Eissenstat & Yanai, 1997),对 C 的消耗也越大(Hendrick & Pregitzer, 1993; Steele *et al.*, 1997; Gill & Jackson, 2000);从另一方面来讲,归还到林地的养分越多,养分及 C 的循环也加速(Jackson *et al.*, 1997; 李凌浩等,

1998)。细根的寿命长则几年或数月,短则几天,生长在不同的立地上的同一树种的细根寿命有较大的差异,甚至不同季节长出的细根寿命也不相同(Eissenstat & Yanai, 1997; 张小全等, 2001)。究竟哪些因素控制着细根的寿命?这个问题一直是细根寿命研究的重点(Eissenstat *et al.*, 2000)。为此,近些年来国内外生态学者分别从影响根系的生物因素和非生物因素,如光合产物的分配过程(Farrar & Jones, 2000)、细根直径大小和分枝方式(Wells & Eissenstat, 2001; Pregitzer *et al.*, 1997; 2002)、土壤 N 和水分的有效性(Norby & Jackson, 2000)、土壤温度(Pregitzer *et al.*, 2000)、根际微生物(Bloomfield *et al.*, 1996)以及研究方法(Eissenstat & Yanai, 1997)等方面进行了深入研究。本文对影响细根寿命的几个重要因素的研究概况和进展进行介绍,以便引起我国相关研究人员的重视,促进我国根系研究的深入。

1 细根寿命与 C 消耗

根系在树木体内有“源”和“汇”的双重功能,是养分、水分的“源”和“汇”(Farrar & Jones, 2000; Anderson, 2003)。细根与其它器官一样也有其生活史。细根寿命受树木体内 C 源-C 汇分配关系的控制,分配到细根的 C 主要用于 4 个方面,即细根伸长、呼吸及养分吸收与同化、有机物分泌、土壤植食动物(Herbivory)等(Chapin III *et al.*, 2002)。一些证据表明,细根吸收养分和水分越多,分配到细根的 C 也就越多(Bloomfield *et al.*, 1996; Hendricks *et al.*,

1997) ,其寿命也较长。一旦细根周围养分耗尽,吸收能力减弱,C向细根分配立刻减少(Burton *et al.* , 2000) ,细根则衰老(Pregitzer *et al.* , 1993 ; Eissenstat & Yanai , 1997 ; Majdi , 2001)进而死亡。Högberg 等(2001)在欧洲赤松(*Pinus sylvestris*)林分做环割试验,证明C向细根分配减少后,根系呼吸明显降低,其原因可能是细根衰老和死亡增加。

树木体内关于C向细根分配过程并通过该过程控制细根寿命的机理还不清楚,根系研究者分别从细根环境和细根功能方面提出不同假设。针对细根环境方面,Hendricks 等(1993)根据细根养分吸收依赖于C的投入,对其控制机理给出了两种假设: 1) 异化分配(Differential allocation) ,即随N在系统中的有效性的提高,分配给细根的C的相对比例下降,细根的寿命或死亡率保持不变。2) 恒定分配(Constant allocation) ,即随N有效性的提高,分配给细根的C的比例保持不变,根系死亡率增加。在针叶林中连续钻取土芯法的研究结果多支持异化分配假设(Comeau & Kimmins , 1989 ; Gower *et al.* , 1992 ; Haynes & Gower , 1995)。在落叶林中使用C-N平衡法的研究结果多支持恒定分配假设(Nadelhoffer *et al.* , 1985 ; Raich & Nadelhoffer , 1989 ; Hendricks *et al.* , 1993)。在细根功能方面,Farrar 和 Jones(2000)给出了4种假说: 1) 功能平衡假说,即根系得到的C量取决于根系与叶之间的功能平衡关系; 2) 推力假说(Push) ,即根系的C取决于地上部分C的输入; 3) 拉力假说(Pull) ,即根系的C获取是自身的一种功能,分配到根系中C的多少受根内对C需求所控制; 4) 共同控制假说,即分配到根系的C受地上部分和地下部分因子的共同控制。C的减少引起细根衰老和生命终结是一个复杂的生理生态过程(Farrar & Jones , 2000 ; Anderson , 2003) ,难点在于影响光合产物C分配的内部和外部因素还不清楚,目前仅是通过“源-汇”关系去解释。野外实验研究表明,上述理论和假说并不能完全解释C控制细根寿命的机理,主要是树种与环境的多样性(Farrar & Jones , 2000 ; Nadelhoffer , 2000)。一些假说都是针对某一具体的生态系统提出的,是否具有普适性,还有待于检验。尽管如此,我们认为C向地下分配的多少是影响细根寿命的重要因素。

2 细根的寿命与细根形态

直径是根系形态的重要指标之一,对寿命有很

大的影响(Eissenstat & Yanai , 1997)。直径越细的根,N的浓度较高(Gordon & Jackson , 2000) ,非木质化程度高(Hendricks *et al.* , 2000) ,寿命较短(Eissenstat & Yanai , 1997)。在60年生的欧亚槭(*Acer pseudoplatanus*)林中,直径<0.25 mm细根的(N浓度24.4 mg·g⁻¹)平均寿命<300 d,而直径>0.25 mm细根的(N浓度13.0 mg·g⁻¹)平均寿命则>600 d(Pregitzer *et al.* , 1997)。Wells 等(2002)对15年生的碧桃(*Prunus persica*)细根存活分析表明,直径≤0.25 mm的细根寿命140 d,直径为0.25~0.5 mm的细根寿命262 d,而直径>0.5 mm的细根寿命426 d左右。我国鼎湖山南亚热带森林直径≤2 mm的细根平均寿命630 d,直径2~5 mm的细根寿命1 050 d左右(温达志等 , 1999)。

根系生长过程中产生复杂分枝系统,形成不同等级的根序(Pregitzer *et al.* , 1997)。根序的分级依赖于根系分枝的起源(Fitter , 1985) ,根系最先端的细根为一级根(起源于二级细根) ,上推二级细根(起源于三级细根) ,三级细根(起源于四级细根) 等(Pregitzer *et al.* , 2002)。根序对细根寿命的影响与直径类似,N的浓度随根序降低而增加,C的浓度则不同程度的减少(Pregitzer *et al.* , 1997 ; Majdi , 2001 ; Wells *et al.* , 2002)。因此,一级细根(常常非木质化) 其寿命较短,根序较高的细根寿命较长。Pregitzer 等(2002)对北美4种阔叶树和5种针叶树研究表明,直径小于0.5 mm的细根根长占直径小于1.5 mm根长的80%左右。根序等级与直径正相关,与N浓度负相关(Pregitzer *et al.* , 1997 ; 2002)。基于Pregitzer 等(1997 ; 2002)发现,细根死亡的顺序可能与发育顺序相反,一级根可能先死,随后是二级根,再后是三级根、四级根等。Wells 等(2002)用两年的时间对15年生碧桃的研究表明,二级和三级细根平均寿命452 d,而一级细根的平均寿命为190 d左右。我们认为从根系发育的角度来讲,研究不同根序的寿命问题可能更合理,因为对于某些树种,在直径小于0.5 mm的细根中,既包括一级细根又包括二级和三级细根,但是它们的寿命是不同的。然而,一些研究数据表明,在最细的前三个根序当中,长叶松(*Pinus palustris*)同一级根序的细根在直径方面的变异往往大于0.3 mm¹⁾。最近的研究表明,在木本植物中,无论种类和根系环境如何,根系的结构(尤其是分枝方式) 可能是与寿命有关的一个最基本

1) 郭大立, R. J. Mitchell 和 J. J. Hendricks. 2003. 长叶松(*Pinus palustris*) C源和C汇的改变对不同根序的细根C和N含量影响(未发表数据)

特征(Ruess *et al.*, 2003)。但是,直径和根序如何独立地影响细根寿命还是一个尚待解决的问题,主要是细根死亡的过程和顺序不清楚。我们认为随着估计根系寿命方法的可靠性相对提高,如微根管法(Minirhizotron)、同位素法(Isotope),尤其是各种方法联合使用等,这为揭示根系结构对根系寿命调控机理的研究提供了保障。

3 细根寿命与土壤 N 的有效性

N 是林木生长需求量最多的限制性养分,根系获取 N 包括吸收、运输及同化 3 个过程。吸收 N 需要消耗大量的 C(Eissenstat *et al.*, 2000; Norby & Jackson, 2000)。投入到细根中 C 的多少依赖于根系吸收 N 的数量,可能遵循“投入-产出”(Cost-benefit)规律(Eissenstat & Yanai, 1997)。土壤中有有效 N 的含量是有限的,根系统中一些分枝细根因吸收作用很快耗尽根际周围的有效 N,致使向这些根系投入的 C 减少,细根出现衰老而死亡(Bloomfield *et al.*, 1996; Eissenstat & Yanai, 1997)。根系只有不断生长,才能伸展到新的土壤空间去吸收有效 N(Burton *et al.*, 2000)。因此,土壤中的有效 N 与细根寿命有密切关系(King *et al.*, 1999; Burton *et al.*, 2000)。

一些野外林地试验表明,随着土壤有效 N 的增加,细根寿命缩短,如栎树(*Quercus ilex*)林土壤有效 N 在 $143 \text{ kg} \cdot \text{hm}^{-2} \cdot \text{a}^{-1}$ 时,平均寿命 167 d,有效 N 在 $133 \text{ kg} \cdot \text{hm}^{-2} \cdot \text{a}^{-1}$ 和 $107 \text{ kg} \cdot \text{hm}^{-2} \cdot \text{a}^{-1}$ 时,平均寿命分别为 188 d 和 301 d(Aber *et al.*, 1985)。另一些试验结果显示细根寿命随 N 有效性提高而延长,如花旗松(*Pseudotsuga taxifolia*)林(Keyes & Grier, 1981)、糖槭(*Acer saccharum*)林(Pregitzer *et al.*, 1993; Burton *et al.*, 2000)。这些相悖结果引出细根寿命与 N 有效性关系的一些假说(Hendricks *et al.*, 1993; Eissenstat & Yanai, 1997; Burton *et al.*, 2000)。对于第一种情况,认为在有效性养分比较充足的土壤斑块,细根组织中 N 浓度较高、呼吸增大,如果 C 的投入不能满足呼吸消耗,导致细根寿命缩短(Burton *et al.*, 1996; Black *et al.*, 1998),周转加速,而贫瘠土壤有利于延长细根的寿命(Pregitzer *et al.*, 1995)。后一种情况, Burton 等(2000)认为土壤有效 N 增加,能够较长时间地提供生长所需养分,只要有足够的 C 投入到具有吸收功能的细根中去,就可使细根寿命延长。Hendrick 和 Pregitzer(1996)认为细根寿命与土壤养分有效性可能呈正相关,也可能呈负相关,取决于植物种类、器官或整个植物 C 平衡、有效养分在土壤中分布的空间异质性等。他们还认为野外林地几年的施肥

试验导致细根寿命的延长或缩短仅是暂时现象,不能代表肥沃土壤中 N 有效性对细根寿命的长期反应。因此, Burton 等(2000)提出:不同树种或不同林分类型中,每一个树种都有自身有效 N 的适应范围,在这个范围内,细根寿命与土壤有效 N 的关系可能呈正相关或负相关,但把这些对 N 有效性反应的不同树种放在一起考察,总的规律是随着土壤有效 N 的增加,细根寿命缩短。这个假设目前还没有被试验证明。如果该假设成立,则对全球变化条件下预测陆地生态系统的生产力具有重要意义,因为土壤 N 的有效性受全球变化的影响而发生变化,将引起生态系统 C 分配格局的改变。

4 细根寿命与土壤水分的有效性

当土壤水分充足的时候,细根直径增粗,而干旱条件下,细根直径减小,寿命可能降低(Vogt & Persson, 1991)。由于水分还影响土壤养分的有效性,因此,水分对细根寿命的影响很难与养分的相互作用分开(Pregitzer *et al.*, 2000)。在干旱的立地上,细根现存量较高,周转率较快,加速细根的死亡(Santantonio & Hermann, 1985)。C 的投入主要是促进细根的生长,维持细根吸收水分的功能,尤其是促进细根向深层发展(Hendrick & Pregitzer, 1996; Joslin *et al.*, 2000)。但是,长时间的干旱会引起树冠 C 同化率降低,常常不能满足细根生长的需要,细根因 C 的供应不足而死亡。北美杨树(*Populus grandidentata*)、红槲栎(*Quercus rubra*)和北美红枫(*Acer rubrum*)等林分经过 20~40 d 灌溉后,细根寿命长达 82~90 d,而不灌溉的对照林分细根寿命仅为 40 d 左右(Pregitzer *et al.*, 1993)。Comeau 和 Kimmins(1989)对湿润立地和干旱立地生长的 70 年生小干松(*Pinus contorta* var. *latifolia*)研究表明,干旱立地上细根(直径 < 2 mm)和小根(直径 < 5 mm)生物量为 $6.4 \text{ t} \cdot \text{hm}^{-2} \cdot \text{a}^{-1}$,年净初级生产力为 $4.3 \sim 6.3 \text{ t} \cdot \text{hm}^{-2} \cdot \text{a}^{-1}$ (占总净初级生产力的 55%~66%),而湿润立地上生物量为 $5.1 \text{ t} \cdot \text{hm}^{-2} \cdot \text{a}^{-1}$,年净初级生产力为 $4.5 \sim 5.5 \text{ t} \cdot \text{hm}^{-2} \cdot \text{a}^{-1}$ (占总净初级生产力的 38%~46%)。热带森林和蓝桉(*Eucalyptus globulus*)人工林研究表明,细根生长与水分季节动态关系密切,细根生长高峰出现在雨季,旱季生长减慢,死根量提高(Kaetterer *et al.*, 1995)。

对于土壤有效水分长期下降的影响, Joslin 等(2000)认为该作用能够导致:1)细根生物量、细根密度、总伸长和净伸长增加;2)地下/地上比率,特别是细根生物量/叶生物量的比率增加;3)改变细根周转速率;4)促进根系向下生长或增加深层细根密度。

这些假设在一些野外林分微根管的 4 年试验中得到验证(Hendrick & Pregitzer, 1996 ; Joslin *et al.* , 2000)。但是也有一些试验表明水分对细根生物量的现存影响不大(Tomlinson & Anderson, 1998),但对地下/地上比率影响显著,干旱导致细根周转速率增加、引起细根寿命缩短的假设在野外水分试验中都得到证实(Joslin *et al.* , 2000)。但是水分对细根寿命的影响与 N 的影响一样,也具有两方面的特点,不同树种细根寿命对水分的反映存在明显差别,需要多树种在控制水分条件下试验,才能得出准确的结论。

5 细根寿命与土壤温度

Ryan(1991)认为根系的寿命对土壤温度非常敏感。Steele 等(1997)认为较高的土壤温度可增加细根生产,促进细根的衰老和周转,缩短细根寿命。在温带地区, Hendrick 和 Pregitzer(1993)对密歇根州糖槭林研究表明,北部林分比南部林分细根寿命平均延长 75 d。不同年均温的立地上细根的寿命差异与土壤温度有关,而同一立地上细根寿命的季节变化也可能与土壤温度有关(Burke & Raynal, 1994)。在温带气候条件下,晚春产生的细根寿命最短。如糖槭从 6 月到 9 月产生的细根寿命从 125 d 增加到 200 d(Hendrick & Pregitzer, 1993)。Kosola 等(1995)对亚热带树种的研究结果则与温带树种相反,亚热带树种秋天生产的细根寿命最短。在同一土壤剖面,随着土层加深,温度下降,土壤有效 N 降低,细根的寿命延长(Burton *et al.* , 2000)。Gill 和 Jackson(2000)总结了 190 个已发表资料的结果表明,草地、灌木和森林细根寿命与年均温具有明显的负相关,从北方到热带地区,细根周转提高,细根寿命显著降低,并对这种关系给出 3 种可能的解释: 1) 高温能够提高土壤养分(尤其是 N)的矿化速率; 2) 维持根系的呼吸随温度升高呈指数增长; 3) 高温地区或非冻土区,细根受病原菌侵染的可能性较大。Pregitzer 等(2000)也认为,温度是限制土壤 N 有效性、根系呼吸、C 消耗和土壤微生物活动的主要因子,并由此解释为什么热带地区森林细根周转较快,温带和北方森林细根周转较慢。

6 细根寿命与土壤生物

真菌、病原菌和土壤植食性动物是影响细根寿命的主要土壤生物(Eissenstat & Yanai, 1997)。多数树木的细根在不同程度上被菌根侵染。菌根的产生不仅扩大细根的吸收表面积,增加对 C 的消耗(Peng *et al.* , 1993),而且对细根具有保护作用(Black *et*

al. , 1998),如内生菌根(VA)和外生菌根(EM)通过产生化学防御物质或对根尖的保护抵御病原菌对细根的侵害(Linderman, 1994),减少土壤动物的伤害(Eissenstat *et al.* , 2000),增强忍受干旱胁迫的能力(Espeleta & Eissenstat, 1998)等。大量实验证明菌根能够延长根系的寿命,降低根系的死亡率和周转速率(Tierney & Fahey, 2001)。例如,没有菌根的细根寿命仅有几周,而侵染菌根的山毛榉(*Fagus grandifolia*)细根寿命接近 9 个月、太平洋银冷杉(*Abies amabilis*)10 ~ 14 个月、欧洲云杉(*Picea excelsa*)48 个月(Bloomfield *et al.* , 1996)。病原微生物也是影响细根寿命的重要因子之一,如根腐真菌可直接伤害根组织和引起贮存的碳水化合物损失,从而促进细根衰亡,缩短了细根的寿命(Shigo, 1984)。

土壤植食性动物主要是地下昆虫和线虫(Nematodes),它们主要取食新生细根,目的是获取碳水化合物(Eissenstat & Yanai, 1997)。Stevens 等(2002)对美国东南部 65 年生长叶松林的研究结果表明,由土壤植食性动物引起的细根死亡占死亡细根总量的 21% ~ 37% ,导致一些新生细根很快消失。如果不考虑土壤植食性动物的影响,净生产力将被低估 5% ~ 10% 左右。在干旱和低温的条件下,细根的寿命较长,除了维持需要的 C 较少外,另一个原因是与同样的环境下土壤植食性动物较少有关(Eissenstat & Yanai, 1997)。此外,植食性动物消耗少量的细根,也能刺激细根生长,但这取决于细根分布密度和地下昆虫的种类(Wardle, 2002),土壤植食性动物对根系的影响程度也决定了林木本身能在多大程度上控制细根的寿命(Yanai & Eissenstat, 2002)。应当指出的是,土壤植食性动物对树木细根寿命和净初级生产力的影响近几年才引起生态学界的注意,目前还没有结论性的解释,但是作为影响细根周转和 C 消耗的重要因子之一,有必要进行深入研究(Eissenstat *et al.* , 2000 ; Murray *et al.* , 2002)。

7 结 语

国外关于细根的研究有近 30 年的历史,对林木细根寿命与细根周转的研究已经广泛开展,尤其是近 10 年来微根管的应用使得细根寿命与周转的研究取得重要进展。但是,关于细根寿命的控制机理了解还很少,其影响因素方面的研究仍然存在很多争议。以往我国根系的研究主要包含在林分或群落生物量研究之内,近年来在细根生物量和周转方面开展了一些研究(单建平等, 1993 ;廖利平等, 1995 ;李凌浩等, 1998 ;温达志等, 1999),但涉及影响细根周转

和寿命的因素研究较少。无论在国内还是国外, 细根研究最大问题是结果的不确定性(黄建辉等, 1999, 张小全等, 2000), 主要原因是研究方法缺乏一致性与可比性、树种的多样性、立地条件差异、长期试验与短期试验、单株树木研究结果到林分或生态系统水平上尺度转换等问题。由此, 建议我国对细根寿命的研究应集中于以下几个方面: 1) C 的地下分配可能是控制细根寿命的主要机理之一, 应着重细根的周转过程与 C 分配的关系。2) 土壤养分、水分和温度对细根寿命有重要影响, 某一根段、整个根系和林分水平上细根寿命与这些因子有何种关系? 需要大尺度和长期(包括不同气候区的)研究。3) 细根的寿命对资源有效性反应的研究得出不同的结果, 这些研究多是短期试验。因此, 这种反应是否只是暂时的现象, 它与资源供应持续的时间有何关系? 需要进行长期的研究去验证。4) 细根本身的结构特征(如直径、分枝位置等)与 C 的消耗有关, 应进一步了解 C 分配、有效资源获取与这些特征的关系。5) 由于细根的动态和土壤的空间异质性, 导致细根研究结果的许多不确定性, 需要探讨有效和准确的方法对细根寿命进行估计。

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