

树线波动与气候变化研究进展

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摘要:作为直立树木分布的高海拔上限和高纬度北界,树线对气候变化具有潜在的敏感性,是全球变化研究的热点内容之一。树线变化不仅包含树线位置(本文中指树线上边界位置)的进退,还涉及到林分结构、空间格局和树木的生长变化等方面。尽管学者们利用不同的假说来解释树线和林线形成机理,但普遍认为温度是影响树线变化的最重要的环境因子。因此,全球变暖背景下,树线位置和种群密度变化趋势的研究备受关注。然而,树线位置的变化对气候变化会有几十年至几百年的滞后性,在全球变暖的背景下树线位置有可能仅发生微小的变化。相对于树线位置,森林种群密度的变化是更敏感的生态指标。国际上多处树线研究(包括藏东南一带)都揭示了近100~200年来树线过渡带内种群密度的显著增加。但是,国际上已经报道的大多数树线样点不同程度地受到人为活动的干扰,难以区分气候变化和人为干扰对树线波动的影响。值得提出的是,青藏高原具有全球最高海拔的天然树线,且受人类活动干扰少,是研究气候变化对树线动态与格局影响的理想地点之一。

关键词:树轮;树线;树线位置;种群密度;气候变化

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A review on progresses in treeline dynamics and climate change

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Abstract: As the elevational and northern limit of erect trees and forest, the treeline and timberline are potentially sensitive to climate change, being one of the hotspots in the study of global change. Treeline dynamics not only include changes in upper treeline position but also in stand density, spatial pattern and tree growth. Although several hypotheses were proposed to explain treeline formation, temperature is considered as the most important environmental factor in controlling treeline dynamics. However, treeline position may have a lag response to climate change from several decades to centuries. In spite of global warming, treeline position may show a little change. In comparison with the treeline position, forest density may be more sensitive to climate change. Several treeline studies (include the studies on the Tibetan Plateau) revealed significant changes in forest density in the past 100 years. It should be mentioned that many reported treeline sites were disturbed to some degree by human activity. As a result, it will be difficult to separate effects of climate change and disturbances on treeline dynamics. On the Tibetan Plateau, there is the world's highest treeine, being ideal to investigate effects of climate change on treeline dynamics.

Key words: Tree ring; treeline; treeline position; forest density; climate change

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树线 (treeline) 作为直立木分布的海拔上限和高纬度北界, 在植被生态学研究备受关注 (Körner, 2003)。由于靠近树木分布的生态阈值极限, 气候条件并不稳定, 因此树线对气候变化具有潜在敏感性, 是探讨植被分布与气候相互关系的理想区域 (Holtmeier, 2003; Körner, 2003; 方精云等, 2004; 崔海亭等, 2005; Nagy and Grabherr, 2009)。

尽管树线受低温、强风、养分不足、种内种间关系等多个生物、非生物因子的影响 (Tranquillini, 1979; Jobbagy and Jackson, 2000; Malanson, 2001; Körner, 2003; Payette, 2007; Wieser and Tausz, 2007; Li et al, 2008; Shi et al, 2008; Smith et al, 2009), 但多数学者认为温度才是影响树线形成和变化的最重要环境因子 (Körner and Paulsen, 2004; Nagy and Grabherr, 2009)。作为反映树线动态的最主要生态指标, 树线位置并非静止, 而会随着气候变化而发生变化 (Kullman, 2001)。此外, 树线的林分结构、空间格局、树木生长也可能因变暖而发生显著变化 (Liu et al, 2002; Camarero and Gutiérrez, 2004; Liang et al, 2010, 2011b; Harper et al, 2011; Kong et al, 2012)。揭示上述生态指标对气候变化的响应是深入理解树线动态的前提与基础。本文综述了近 10 年来国内外树线对气候变化响应方面的研究进展, 旨在强调树线生态学研究的重要性。考虑到已有一系列报告综述了有关树线形成机制的进展, 本文不再赘述。

1 树线的定义及树线类型的划分

树线一般包括高山树线和高纬度树线两种, 严格地讲它并不是一条线, 而是一条生态过渡带。基于任何自然的界限往往是一个逐渐过渡的区域 (Körner, 2003) 这一常识, 学者们将树线定义为林线 (Timberline) 上边界和树种线 (Tree species line) 之间的过渡带 (Körner, 2003)。这里的林线上边界一般指树高大于 5 米, 林冠盖度大于 30% 的森林所能到达的海拔上限 (Holtmeier, 2003), 树种线则是指乔木个体所能达到的最高海拔 (Körner and Paulsen, 2004)。为了更好地描述树线的变化特征, 树线上边界位置一般是指活的、不小于某一高度的单棵直立乔木所能到达的海拔上限。

对于树线位置 (一般指上边界) 所涉及的树高标准学者们存在分歧, 主要有 5 米、3 米、2 米三种判定标准 (Troll, 1973; Wardle, 1974; Körner, 1998)。其中, 3 米和 2 米的标准是最常用的。部分生态学

者认为 3 米可保证树木冠层与周围盛行大气状况保持一致, 且不会被积雪全部覆盖 (Körner, 2003; Nagy and Grabherr, 2009)。另一些学者则认可以 2 米作为基准 (Kullman, 2001; Holtmeier, 2003; Wieser and Tausz, 2007)。由于以上观点的差异, 目前一些研究混淆了树线位置与林线位置的概念, 习惯地把树线上边界位置爬升认为是林线位置上升。事实上, 由于难以重建过去林分盖度的变化, 我们因而无法获取过去林线位置的时空变化特征。另外, 在某一时间尺度内, 如何确定树线位置发生了显著的变化也是一值得关注的问题。最近, Liang et al (2011b) 把一定时期内树线位置变动 (海拔高度的变化) — 树高位置 (以树线过渡带上最大树高作为参考值) 作为标准, 来判定树线位置是否发生了显著变化。

此外, 还可依据不同标准将树线划分为不同的类型。按照外观, 树线可划分为渐变型、急变型、矮曲林和树岛型四种 (Harsch and Bader, 2011)。若按成因划分, 则有山地条件制约型、外界干扰影响型和气候影响型三类树线 (Holtmeier and Broll, 2005; Herrero et al, 2012)。气候影响型树线对气候变化具有潜在敏感性, 是最值得关注的树线类型。但由于全球大部分树线都受到不同程度人为活动的干扰, 因此往往难以区分人为干扰和气候变化对树线波动的影响 (Cairns and Moen, 2004; Holtmeier and Broll, 2005; Wieser and Tausz, 2007; Moen et al, 2008; Smith et al, 2009; Speed et al, 2010)。需要指出的是, 人为干扰会打破树线森林种群与树线之上高密度灌丛间的平衡, 并可能成为促进树线位置上升的重要因素 (Wang et al, 2012a)。

2 树线位置和林分密度变化

一些研究认为, 树线位置是响应气候变化的敏感生态指标。在气候变暖的环境条件下, 树线位置将出现显著的爬升 (Kullman, 2001; Grace et al, 2002; Baker and Moseley, 2007)。但最近的研究并不完全支持这一观点 (Harsch et al, 2009)。在全球已报道的 166 个树线样点中, 过去 100 年来只有 52% 的树线位置出现了显著的爬升, 47% 的树线位置保持相对静止, 还有 1% 的则出现了后退 (Harsch et al, 2009)。与早期的预期相悖, 树线位置对气候变化的响应并未表现出显著的线性响应特征。而其中树线位置出现显著上升的森林样点又不同程度地受到人为活动的干扰, 难以区分气候变化在驱动树

线波动中的贡献 (Cairns and Moen, 2004; Wieser and 2007; Moen et al, 2008; Speed et al, 2010)。

林分密度是树线响应气候变化的又一重要生态指标。与树线位置相比,林分密度对气候变化的响应可能更敏感 (Camarero and Gutiérrez, 2004; Elliott and Kaikuranta, 2011; Liang et al, 2011b)。来自美国科罗拉多州和阿拉斯加州的树线研究显示,林分密度在区域变暖背景下有明显的增加趋势 (Lloyd and Fastie, 2003; Elliott and Baker, 2004)。对于西班牙比利牛斯山树线研究也表明,林分密度的变化趋势与 20 世纪变暖趋势相一致 (Camarero and Gutiérrez, 2004; Peñuelas et al, 2007; Batllori et al, 2009)。此外,基于祁连山区、横断山区和藏东南的树线研究也揭示出,在过去 100 或 200 年时间尺度上,树线种群密度呈持续增加趋势 (Wong et al, 2010; 吕利新, 2011; Liang et al, 2011b; Gou et al, 2012)。然而,也有部分地区的树线研究发现,林分密度在区域气候变化的背景下并没有出现显著变化 (Villalba and Veblen, 1997; Wang et al, 2006),这可能证实了区域响应差异以及人为干扰对种群更新的影响。

树线位置和林分密度对气候变化的非线性响应也暗示了非温度因子对树线过渡带的可能影响 (Moen et al, 2008; Holtmeier and Broll, 2009; Takahashi et al, 2012)。风速和风向被视为影响树线波动的重要环境因子之一。在风力强劲的树线样点,有利的地形可遮挡或减缓强风的侵袭,从而有利于树线位置的显著爬升 (Holtmeier and Broll, 2011)。种子散播距离的局限性和当前树线之上所具有的高密度高山灌丛都可能成为树线大幅爬升的障碍 (Dullinger et al, 2004; Liang et al, 2011b; Wang et al, 2012a)。此外,土壤生境的异质性和种群之间的竞争关系也会影响树木更新,从而阻碍树线的爬升 (Holtmeier and Broll, 2005; Wang et al, 2012a)。考虑到非温度因子在树线变化中的重要作用,揭示树线对气候变化响应时需要慎重评估非温度因子对树线波动的影响,这对于景观尺度或局地尺度上的树线研究尤其必要。

树线位置和林分结构对气候变化的非线性响应也可能存在另一种解释,即树线对气候响应存在一定的时间滞后性 (几十年到几百年) (Lloyd et al, 2003)。基于这一解释,树线所处的海拔应归因于几十年或几百年前的气候状况,而非当前的气候状况 (戴君虎与崔海亭, 1999; 崔海亭等, 2005)。此

外,作为一个顶级群落,树线群落具有相对的稳定性,这也在一定程度上解释了树线位置对气候变化响应的滞后特征 (Liang et al, 2011b)。有模拟研究表明 (Chapin and Starfield, 1997),树线对气候的响应可能滞后 150 ~ 250 年。但该模型所提出的滞后期限尚未得到实测数据的支持和机制研究的验证。

3 树线群落的空间格局动态

群落空间格局主要研究树木的空间分布型、空间关系以及群落特征等内容 (Fortin and Dale, 2005)。树线位置和林分密度的变化势必会引起群落空间格局的变化,因此研究树线群落的空间格局变化已成为揭示树线波动成因的重要途径之一。一般来说,种内或种间的互利关系会随环境胁迫的增强而增强 (Callaway et al, 2002)。树线作为树木分布的海拔上限和高纬度北界 (Körner, 2003),其种内种间关系往往表现为互利关系 (Callaway, 2007),这将有利于缓冲严酷的环境胁迫 (如低温胁迫),从而为树木的更新和生长提供适宜的微生境 (Smith et al, 2003)。此外,种间竞争也可能是制约树线爬升的因素之一。Körner (1998) 的研究指出,树线爬升会受到密集灌木或茂密草被层的阻碍,但并未对其原因作进一步分析。从空间格局的角度来看,这一现象可归因于种间竞争作用,即高密度灌丛抑制了幼苗的更新和存活。这一观点得到了藏东南树线空间格局研究的支持 (Wang et al, 2012a)。此外,群落物种组成也有可能是在气候变化背景下发生显著变化 (Batllori et al, 2009),从而改变种内或种间关系,并最终对树线进退产生影响。

4 树线和林线树木生长动态

树线位置和林分结构的变化反映了树线在种群或群落水平上的变化,而树木生长动态则指示了树线在个体水平上的变化。由于树木生长主要表现为年轮宽度和高度的生长,因此当前树线和林线的生长动态研究主要集中于揭示树木的径向生长和高生长对气候变化的响应。

与高生长相比,树轮宽度的获取相对容易,故有一系列探讨树线、林线树木径向生长对气候响应的研究 (Paulsen et al, 2000; Liu et al, 2005; Liang et al, 2010; Zhang et al, 2011; Zhu et al, 2011)。在湿润、半湿润的高海拔地区,树线树木的径向生长主要受低温限制。而区域增温可缓解低温胁迫,从而促使树木的径向生长增加 (Liang et al, 2010)。同样,

在半干旱地区,降水会随海拔升高而增加,低温仍是树线树木生长的主要限制因子(郑永宏等,2008; Peng et al, 2008; Shao et al, 2010)。但在降水较少的月份,树木生长则受降水限制。在这种情况下,树线树木的径向生长对气候变暖的响应存在季节差异。也有研究认为,半干旱区的树线树木的径向生长同时受温度和降水的限制(Liu et al, 2002)。此外,在半干旱或半湿润地区,树线树木的径向生长对气候变化的响应存在时间上的不一致性(Wilmking et al, 2004; Zhang et al, 2011)。

有关树线过渡带内树木高生长动态的研究则相对较少。Gamache and Payette(2004)在对加拿大魁北克高纬树线研究中指出,在区域增温的背景下,黑云杉的年高生长明显增加,但探讨树线树木的年高生长对气候变化响应的研究仍十分缺乏。近期来自于藏东南的研究指出,在区域增温背景下,急尖长苞冷杉的高生长有可能显著增加(Wang et al, 2012b)。但该研究所使用的年高生长序列较短(多数样点不足60年),尚不能揭示年高生长对长期气候变化的响应情况。植被物候是限制植物分布的重要因子之一(Chuine and Beaubien, 2001),因此,树木春季物候和季节高生长特征在一定程度上决定了树线的分布。研究树线的季节高生长动态有助于阐明树线动态对气候变化的响应机理,对气候变化研究具有重要意义(Wang et al, 2012c)。

5 当前树线研究中的不足

有关树线动态与气候变化关系的研究始于20世纪80年代(Harsch et al, 2009)。随着气候变暖成为生态学研究关注的焦点之一,树线波动及其对气候变化响应的研究也受到日益关注。从样地调查等传统方法到遥感和GIS的引入,从利用树木年轮、孢粉等代用指标重建树线位置和植被格局的变化到利用分子生物学手段推测过去树线波动的历史(Daly and Shankman, 1985; 戴君虎与崔海亭,1999; 刘鸿雁,2002; Gehrig-Fasel et al, 2007; Opgenoorth et al, 2010),树线动态研究已取得了丰硕的成果,但目前的研究仍有以下五点不足:

(1)对树线形成机理和树线波动对气候变化的响应机制的理解仍十分有限。无论是树线位置波动还是种群密度变化,其最核心的问题就是种子的形成和幼苗的更新。然而,目前很少有关树线过渡带上种子发育和传播以及幼苗更新、成活与死亡机制的研究(Hofgaard et al, 2009; Wang et al,

2012a)。

(2)树线过渡带内的实测微环境数据缺乏。尽管温度是影响树线变化的最重要气候因子,但很多树线研究所使用的温度数据却是由低海拔河谷气象站的温度记录推测来的(Richardson and Friedland, 2009);树线处风速和降雨等实测数据更是缺乏(Liang et al, 2011a; Liu et al, 2011; Liu and Luo, 2011)。

(3)对于天然树线研究的较少。需要指出的是,早在1979年Tranquillini就提出:“在探讨森林上限形成时,最好以天然树线作为研究对象”。但从目前所调查的200多个树线样点来看(Harsch and Bader, 2011),多数都曾受过不同程度的人为干扰(如放牧、伐木、旅游、人为火源等)(Cairns and Moen, 2004; Holtmeier and Broll, 2005; 李迈和和 Kräuchi, 2005; Wieser and Tausz, 2007; Moen et al, 2008; Smith et al, 2009; Speed et al, 2010),难以区分人为干扰和气候变化的影响。因此,天然树线成为揭示自然状况下树线变化对气候变化响应机制的理想选择。

(4)缺少不同空间尺度上的树线动态研究。由于树线对气候变化的响应具有明显的空间尺度依赖性(Holtmeier and Broll, 2005; Grafius et al, 2012),所以不同空间尺度上的树线变化可能具有不同的控制因子(Elliott and Kaikuranta, 2011)。目前尚不能证实,树线波动在局地尺度上与区域尺度上是否具有相同控制因子。

(5)作为地球的第三极,青藏高原拥有海拔最高的天然树线和林线(李文华,1985; Schickhoff, 2005; Miede et al, 2007),受人类活动干扰少,是开展树线波动与气候变化研究的理想地点(Liang et al, 2011b)。然而,目前大多数研究都集中于树线过渡带和高山林线的树轮气候学研究(见综述,刘禹等,2010),有关树线结构与动态的研究并没有引起足够的重视(Fang et al, 2009; Wong et al, 2010; Liang et al, 2011b; Gou et al, 2012; Lv and Zhang, 2012),特别是在树线波动驱动机制方面,更有待更深入的研究(Wang et al, 2012a)。

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