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高山林线变化的更新受限机制研究进展

沈　维*,**张　林**,**罗天祥**

中国科学院青藏高原研究所,高寒生态与生物多样性重点实验室,北京　100101

摘要: 全球林线位置对气候变暖的响应表现为上升、无变化或下降等截然不同趋势,表明影响林线位置及动态的因子十分复杂,除了较普遍认为的低温调控机制外,还存在其它控制林线位置变化的机制。林线向上迁移开始于种子向林线以上的传播及幼苗在林线以上的定居,这些过程中的限制因子均会影响林线的位移,因此研究更新过程及其限制因子对理解高山林线对气候变化的响应具有重要的科学意义。主要从种子和幼苗两个关键阶段综述高山林线森林更新的研究进展。在种子阶段,夏季积温不足导致种子产量和活力下降,风速过低和浓密灌丛限制种子向林线以上传播,近地表的霜冻/水分胁迫和灌木释放的化感物质会阻碍种子在林线以上萌发。在幼苗阶段,除冬季低温外,生长季内较大的温度日振幅和偶然出现的冻害事件也是导致幼苗死亡的重要原因,而低温环境下的强烈光照引起的低温光抑制会显著降低生长季的光合作用;土壤低温、由土壤温度昼夜变化引起的冻举事件、夏季土壤干旱可能会导致幼苗光合作用下降和死亡率上升;积雪太浅会导致生长季早期幼苗水分供应的严重缺乏,但积雪太深会导致幼苗感染真菌的可能性增加;浓密的灌木和草本植物以及植食动物的啃食也会降低林线以上的幼苗存活率。气候变暖对林线幼苗定居的影响复杂且具有很大不确定性,需要进一步研究气候变暖导致的环境因子变化对林线更新各关键阶段的影响。未来气候变暖无疑会导致生长季起始日提前,结束日推迟,这很可能会增加生长季期间尤其是早期的低温冻害事件,对高山林线树种幼苗的存活具有重要影响。在未来研究中,需要找出定义生长季冻害事件的温度阈值,利用长期气象观测数据分析增温背景下生长季早期冻害事件特征的变化趋势,并进一步开展野外模拟增温实验以深刻理解林线树种的种子萌发和幼苗定居与生长季冻害事件的关系,加强对不同地区林线树种的繁殖策略研究,这将有助于人们进一步理解不同区域林线的形成机制并预测未来气候变化条件下林线的动态变化趋势。

关键词: 气候变化; 生长季冻害事件; 种子萌发; 幼苗定居; 林线动态

Advances in the study of the limitations of seedling recruitment for alpine timberline forests

SHEN Wei*, ZHANG Lin, LUO Tianxiang

Key Laboratory of Alpine Ecology and Biodiversity, Institute of Tibetan Plateau Research, Chinese Academy of Sciences, Beijing 100101, *China*

Abstract: Advances of alpine timberline forests during last century are not ubiquitous worldwide, suggesting additional factors and mechanisms likely affect the response of alpine timberline forests to climate warming. Upward shifts of treelines begin with seed dispersal and germination, and seedling establishment above the treeline and any limiting factors during these processes may affect treeline migration. Therefore, investigation of mechanisms controlling seedling recruitment at alpine treeline will be helpful to elucidate treeline formation and its response to future climate change. We reviewed recent advances in tree seedling recruitment at alpine treelines from the key seed and seedling stages. For the seed stage, the seed quantity and quality generally decreased with the sum temperature during summer; the seed dispersal to elevations above treeline was impeded by low wind speed, dense dwarf shrub and grass cover; the ability of seed germination above the

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* **通讯作者** Corresponding author.E-mail: shenwei1984@itpcas.ac.cn

treeline was impaired by frost and water stresses near the ground. Also, the allelochemical properties of shrubs had negative effects on seed germination. For the seedling stage, large temperature amplitudes and freezing events during the growing season, as well as the extremely low temperature during winter, were important factors affect seedling mortality. Also the low-temperature photoinhibition resulted from the combination of low temperature and high sunlight significantly decreased seedling photosynthesis during the growing season. Besides, frost-heave activity induced by large soil temperature amplitude and soil water deficits during summer impeded seedling establishment at and above the treeline. Snowpack could keep the seedlings away from the extremely low air temperature during the winter and supply snowmelt water in the early growing season. However, too long duration of the snowpack might increase the possibility of fungal infection that promote seedling mortality. Dense shrub and grass cover above the treeline and the presence of herbivores might decrease seedling survival. In all, the influence of climate warming on seedling establishment across the timberline ecotone is complex and uncertain. Further research is needed to explore the exact effects of warmth-induced environmental changes to seedling recruitment at the alpine treeline. Since the beginning of the growing season might advance under scenarios of climate warming, which in turn led to more early-season freezing events at and above the treeline, it is important to define the temperature threshold of freezing events to analyze the relationship between growing-season freezing events and increasing temperature in the future. Based on this threshold, we can further disclose the effects of growing-season freezing events on seedling establishment at alpine treeline, which will be helpful to elucidate treeline formation and predict treeline dynamics under future climate change.

Key Words: climate change; growing-season freezing events; seed germination; seedling establishment; treeline dynamics

高山林线过渡带(alpine treeline ecotone)是指从山地郁闭森林到树种线之间的生态过渡带[1]。通常认为低温是高海拔地区树木生长的普遍限制因子,因此理论上高山林线应随气候变暖而上升[1-2]。然而,全球林线位置对气候变暖的响应表现为上升、无变化或下降等截然不同的趋势[3-8],表明影响林线位置及动态的因子十分复杂,除较普遍认为的低温调控机制外,还存在其它控制林线位置变化的机制。过去对高山林线形成机理的研究多集中在低温与树木生长限制之间的关系,提出了霜冻胁迫、风雪机械干扰、碳受限、生长受限等众多假说[2,9],而繁殖更新障碍作为林线形成机制的假说之一并未得到足够重视[10-11]。高山林线严酷的环境可能并不足以导致树木死亡或生长受阻,却能强烈地限制种子萌发和幼苗定居等森林更新过程[12-14]。2003年,Smith 等以“Another perspective on altitudinal limits of alpine timberlines”为题对高山林线幼苗定居的生态促进机制进行了综述,提出林线是否向高海拔和高纬度迁移主要取决于幼苗的成功定居和后续的存活[15]。此后,越来越多的研究开始关注森林更新对林线位置及其动态的影响[16-22]。林线向上迁移开始于种子向林线以上的传播及幼苗在林线以上的定居,这些过程中的限制因子均会影响林线的位移。气候变暖对林线环境因子的影响十分复杂,既可能缓解也可能加剧对林线更新的限制。升温对更新的有利影响(如提高种子产量和活力,促进幼苗光合生长等)可能被其它环境限制因子所掩盖。因此,研究森林更新过程及限制因子对理解高山林线的形成及其对气候变化的响应具有重要意义。本文主要从种子和幼苗两个关键阶段综述高山林线森林更新的研究进展,并在此基础上对未来研究方向进行展望。

1　高山林线地区种子的形成、传播和萌发

种子形成是森林更新过程的开始,对更新能否成功具有极其重要的意义[23]。通常认为,高山林线地区的树木产生种子的间隔较长,如在高海拔地区恩格曼云杉(*Picea engelmannii*)和毛果冷杉(*Abies lasiocarpa*)每3—6a、瑞士石松(*Pinus cembra*)每7—10a才出现1个种子丰年[24];且林线的种子产量和质量均低于低海拔地区,如 Sveinbjörnsson 等和 Cuevas 对瑞典和智利的高山林线种子雨调查发现,种子数量、质量和活力都随海拔升高而降低[25-26]。这主要是由于种子成熟与夏季积温密切相关,林线地区较短的生长季和较低的夏季温度

导致产生有效种子的积温不足[27-28]。因此,种子的形成可能是高山林线森林更新的限制因子之一。

种子传播距离决定了该物种能否维持或扩大其分布范围,进而达到延续物种的根本目的,因此种子的传播距离也可能是影响林线森林更新的重要因子。种子传播距离很大程度上取决于传播方式和环境条件。风在林线种子传播过程中具有重要作用,因为大多数林线针叶树的种子以风媒传播为主,其种子传播距离主要取决于风速、风向、种子质量、种翅大小及种子散布时所在高度等[29]。其中,外在的环境条件相对更重要,如与种子重量相比,风速对种子传播距离的影响更大[30]。大多数种子的传播距离只有树高的几倍,而强风和暴风雨可能将种子带到几十公里以外[23,30-31]。此外,高山地区的地形和植被可能会阻止种子向林线以上传播。如澳大利亚 Snowy Mountains 林线位置稳定的原因可能是种子难以克服重力向陡峭的山坡上传播[32]。在厄瓜多尔北部的高山林线,幼苗密度随距林缘的距离增加而显著下降,而移植幼苗的存活率并没有随距离增加而下降,其原因可能主要是浓密的灌丛限制了种子向林线以上的传播[33]。

传播到林线以上的种子必须在适宜的生境中才能萌发[17]。林线以上的严酷环境如近地表的霜冻事件及水分胁迫[34],较厚的凋落物层[35-36]以及灌木释放的化感物质[37-41]等,均有可能阻碍林线树种的种子萌发。此外,种子萌发还与其自身特性有关,如冷杉属植物的种子通常处于不同程度的生理性休眠状态,需要一定时间的低温层积处理才能解除休眠[42-44]。光照对林线种子萌发也有一定的促进作用。Li 等的研究发现,光照显著提高了未经层积处理的巨冷杉(*Abies grandis*)种子的萌发率,但对经过低温层积的种子萌发率没有影响,因此郁闭林冠下极低的光照水平可能会推迟种子的萌发,但未必会降低最终萌发率[45]。

2 影响高山林线树种幼苗定居的主要因子

幼苗定居是林线向上迁移和亚高山森林扩展的必经阶段[15]。然而,在树木生活史中,幼苗生长的早期阶段死亡率最高[46-47]。自然定居的幼苗,第 1 年死亡率就大于 60%,特别是在开阔生境中死亡率可高达 90%以上[48]。在林线进行的人工播种实验中,也只有不到 20%的幼苗能存活到第 2 年[49]。因此,幼苗的低存活率成为林线以上森林更新受限的主要原因之一。在高山林线地区,影响幼苗定居的非生物因子主要包括温度、光照、土壤和积雪等,生物因子包括植被、菌根和植食动物等。

2.1 影响高山林线树种幼苗定居的非生物因子

2.1.1 温度

低温是林线树种幼苗存活和生长的重要限制因子[9]。冬季频繁的冻融事件引起的木质部栓塞和霜冻干旱是导致幼苗死亡的主要原因之一[40,50]。除导致幼苗死亡外,低温对幼苗的生理过程及生长也有着极其不利的影响,包括导致幼苗针叶发育受阻并出现物理性损伤,限制幼苗的光合作用,从而影响其碳获取能力及高生长,并提高幼苗对其它环境限制因子的敏感性[47,51-53]。Tranquillini 发现欧洲云杉(*Picea abies*)的针叶需要至少 50d 连续无霜冻来避免生长过程中的损伤,至少 90d 大于-3℃发育足够的表皮来抵抗冬季干旱[54]。

此外,生长季内较大的昼夜温差和偶然出现的极端温度事件也会导致林线树种幼苗的死亡。在温室实验及林线野外观测中均发现,云杉和冷杉的幼苗在温度日振幅最大时死亡率最高[49,55-56]。与较低的日平均气温相比,极端低温事件对林线幼苗的伤害可能更大。低于 0 ℃的冻害事件通常随海拔升高而增加[57-59]。高海拔地区的空气更加洁净且密度较小,从而导致在静风、晴朗且干燥的夜间辐射冷却效应更强[58],因此生长季各阶段均有可能出现冻害事件[60-61]。特别是在生长季早期,冻害事件对高山林线植物存活的影响更大,因为在该时期内大部分植物在-1.8℃以下就会发生冻结[62]。而与成年树木相比,幼苗受冻害事件的影响更大,这主要是由于夜间风速的下降使得冷空气在地表附近聚集,导致生长在地表的低矮幼苗遭遇更多的冻害事件[63],以及林下幼苗的发芽及展叶时间都要早于成年树木,也会导致其暴露在生长季早期低温环境下的可能性更高[64]。因此,生长季早期不可预测的冻害事件对林线树种幼苗的存活有着极其重要的影响[65-67]。藏东南色季拉山的对坡移植实验显示,生长季早期的冻害事件是导致林线急尖长苞冷杉(*Abies georgei* var. *smithii*)幼苗死亡的主要原因[68]。

2.1.2 光照

生长在高海拔地区的植物通常会在形态和生物化学等方面对强光产生一定的适应特征,如通过增加叶倾角和叶厚度以及叶片中的花青素含量来适应强光环境[69-72]。然而,与多年生草本相比,林线针叶树种的幼苗通常缺乏躲避强光的结构[73]。在热带地区的高山林线,过强的太阳辐射对幼苗定居的影响可能比低温更重要[33]。因此,强光也是林线树种幼苗定居的重要限制因子之一[48,53,74-76]。强光会加剧低温和水分胁迫对幼苗的影响[49],低温环境下的强光引起的低温光抑制会显著降低生长季的光合作用[72,77-78]。例如 Germino 和 Smith 发现夜间霜冻导致冷杉幼苗的同化速率下降 40%,强光导致下降 22%,而这两者联合导致下降 90%[47]。而不同物种对低温光抑制的敏感性存在差异,如与恩格曼云杉(*Picea engelmannii*)相比,毛果冷杉(*Abies lasiocarpa*)幼苗的光合作用受低温光抑制的影响更大[47,73]。

2.1.3 土壤

土壤温度、含水量和质地也会影响林线树种幼苗的存活。有研究显示,根生长所需的最低温度为 4—6℃,土壤温度低于 6℃会强烈抑制根的生长[79],而幼苗对土壤低温更加敏感[80]。Karlsson 和 Nordell 发现,桦树幼苗的氮摄取主要取决于土壤温度[81],而当年幼苗的氮摄取与其冬季存活率密切相关[82]。Karlsson 和 Weih 进一步发现林线地区的土壤低温导致当年幼苗难以渡过首个冬季[83]。除土壤低温的不利影响外,林线幼苗还可能受到由土壤温度昼夜变化引起的冻举事件的威胁。在高海拔地区的无积雪季节内,表层土壤通常会随昼夜节律出现冻结和解冻现象,由此导致的冻举事件能将表层土壤抬高数厘米,将幼苗连根拔起,且这一现象在生长季早期和晚期最为频繁,更易对幼苗造成致命伤害[84]。适宜的土壤含水量对幼苗存活也十分重要[85],夏季土壤干旱可能会导致幼苗光合作用下降和死亡率上升[26,48,53],但过度潮湿的土壤也不利于幼苗存活[86]。质地细腻的土壤通过减缓根生长和降低水分有效性来阻止幼苗定居[87]。此外,质地细腻、潮湿且营养丰富的土壤能促进草本植物的生长,从而加剧其与林线树种幼苗的竞争[88-89]。

2.1.4 积雪

适宜的积雪深度对林线树种幼苗定居非常重要。Hättenschwiler 和 Smith 认为积雪深度与幼苗密度密切相关,积雪太浅或太深幼苗均无法存活,主要表现在树岛向风侧由于积雪过少几乎没有幼苗存在,而背风侧积雪深度为 0.5—1.5 m 之间的位置则幼苗密度最大[90]。雪被可以有效防止幼苗暴露在极端低温条件下[91],防止冬季干旱及其造成的养分缺乏,也可以避免强光对植物休眠组织的伤害[92]。Hu 等在北美西部山区的研究发现,持续的冬季变暖导致积雪减少,进而引起生长季早期植物水分供应的严重缺乏[93]。然而,积雪太深也不利于幼苗存活,除导致生长季缩短外,长期积雪覆盖为真菌提供了适宜的生存条件,从而导致的雪霉病也可能会引起幼苗死亡[94]。

2.2 影响高山林线树种幼苗定居的生物因子

2.2.1 植被

树岛能够改善高山地区恶劣的气候条件(如霜冻、干旱、强光和强风等),提供适宜的微环境,从而有利于幼苗在林线以上的存活[15,47,49]。此外,树岛也能改变土壤的理化特征,并为幼苗提供菌根来源[95-97]。因此,在树岛周围幼苗和幼树的出现频率最高,距树岛近的幼苗存活率较高[49,90]。与树岛相似,高山矮曲林也能够改变微环境条件,促进林线幼苗定居[40,98-99]。高山矮曲林能有效地降低风速,且能在其顺风侧积累更厚的雪盖,因此在高山矮曲林顺风侧幼苗存活率较高[49,90,100]。

灌丛对林线幼苗存活的影响在不同研究中存在差异。有些研究发现,灌丛下的凋落物层和化感物质等不利于幼苗存活[40,101],如 Liang 等对青藏高原东部 14 个云、冷杉林线的研究发现,林线以上的浓密灌丛抑制了幼苗定居,从而减缓了气候变暖条件下林线的上升[102]。而另一些研究则发现,灌丛降低了光照强度并提高土壤湿度,从而有利于幼苗定居[71,103-106]。灌丛对幼苗定居的影响在一定程度上取决于太阳辐射强度和林线树种的耐荫性。在太阳辐射强度较高的热带林线,林线以上的灌丛能为幼苗提供遮荫,从而提高幼苗存活率[33];而对于光合能力较高的光皮桦(*Betula litwinowii*),灌丛的遮荫反而不利于其幼苗的生长和存活[103]。

草本植物对林线树种幼苗定居的影响主要取决于土壤水分条件。在土壤水分比较充足的林线，草本植物提供的遮荫能够提高幼苗的光合速率和存活率[107]；而在相对干旱的林线，草本植物降低了幼苗的光合速率，其对土壤水分的竞争可能比遮荫的保护效应更重要[108]。Germino 等对草本植物和幼苗存活率关系的研究发现，幼苗存活率在有草本覆盖时为 90%，没有地被物时为 44%，被草环绕却不被覆盖时为 19%，因此对当年幼苗来说，温度和水分胁迫导致了 10%的死亡率，强光导致了 56%的死亡率，而这两者的联合导致了 81%的死亡率[49]。

2.2.2 菌根和植食动物

高海拔地区的针叶树种幼苗存在碳同化限制，因此其受菌根的影响可能比其它地区的植物更大[47,73,53]。菌根从寄主植物获取碳，同时改善寄主植物的养分和水分关系，并能阻止根部病原体，其对针叶树种幼苗的存活具有潜在的生态重要性[109–110]。Hasselquist 等对恩格曼云杉（*Picea engelmannii*）和毛果冷杉（*Abies lasiocarpa*）幼苗的研究发现，外生菌根（*Cenococcum geophilum*）能够显著提高幼苗水势，但对光合作用的影响不大[111]。

植食动物的取食和踩踏也会影响高山林线的幼苗存活。驯鹿、驼鹿、松鼠、囊鼠等的啃食会降低林线幼苗的存活率[108,112–115]。然而，中、低强度的家畜踩踏会导致幼苗密度的显著增加[76,116]，这主要是由于动物的踩踏减少凋落物层的厚度，从而促进了幼苗定居[35–36]。

3 问题与展望

综上所述，林线以上严酷的环境条件限制了种子萌发及幼苗存活等更新关键过程。气候变暖可以在一定程度上缓解低温造成的限制，但同时也可能会通过改变其它环境特征而加剧对更新的限制。如增温可能会提高种子的产量和活力[23,117]，但冬季温度升高也可能导致种子因不能经历足够的低温而萌发率降低[42–44]；增温能促进幼苗光合生长[118–120]，但增温也可能会引起生长季提前和积雪减少，导致幼苗在生长季早期遭受冻害和干旱的可能性增加[93,121–122]，从而在一定程度上削减增温对幼苗生长的正效应。因此，气候变暖对林线幼苗定居的影响复杂且具有很大不确定性，需要进一步明确气候变暖导致的环境因子变化对林线更新各关键阶段的影响。

3.1 气候变暖条件下生长季冻害事件对林线位置及动态的影响

与平均温度的升高相比，冻害事件的频率、强度和持续时间的增加对高山林线幼苗定居的影响可能更大[65,123–124]。在全球范围内，长期器测资料及大气环流模型显示未来气候变暖条件下极端温度事件（包括极端高温和冻害事件）具有增加趋势[125–127]。但就高山林线而言，相关数据十分缺乏，且为数不多的几个研究结果并不一致，如，我国川西以及智利安第斯山中部高山林线的模拟增温实验表明，增温使得生长季开始时间提前从而导致生长季早期冻害事件增加[121–122]，而瑞士阿尔卑斯山林线近 35 年的气象数据分析结果表明，尽管温度呈持续增加趋势，生长季期间冻害事件频率并没有显著变化规律[66]。对藏东南色季拉山不同坡向气象数据的分析显示，在更加温暖的阳坡生长季冻害事件更加频繁而剧烈，且生长季早期冻害事件的数量随年平均气温的升高而增加[68]。因此，未来气候变暖虽然能使生长季提前，但也会导致生长季早期冻害事件的显著增加。

在过去 100 年里，全球 47%的林线没有随气候变暖而上升[8]。Harsch 和 Bader 提出，幼苗死亡是决定林线位置和动态的重要机制之一[128]。相对于成年树木，幼苗对环境因子的变化更加敏感，尤其是基于种子繁殖的幼苗具有更高的脆弱性[129–131]。气候变暖可能并没有改善林线以上的严酷环境条件（如强光和极端低温等），甚至还可能加剧其对林线树种幼苗定居的限制，从而导致全球变暖后林线位置相对稳定。已有实验证据显示，在较温暖的气候环境下，基于种子繁殖的冷杉幼苗对生长季早期冻害事件更加敏感和脆弱，从而为冷杉林线位置没有随过去 200 年的气候变暖而上升提供了一种机制上的解释，表明极端气候事件和幼苗死亡在控制林线位置变化方面发挥着更重要的作用[68]。然而，只有通过对长期气象数据的统计分析才能明确冻害

事件特征(如频率、强度和持续时间等)的变化规律，而高山林线地区微环境的长期持续观测记录十分缺乏[58,62]，对高山林线树种繁殖方式的研究也较少，因此目前对于这一机制是否具有普遍意义还不清楚，而这对理解高山林线形成机理及其对气候变化的响应具有重要意义。

此外，前期研究中通常采用 0℃作为定义生长季冻害事件的温度阈值[68,121]，但这一温度阈值是否适用于高山地区，本身存在不确定性。Körner 认为，在生长季期间大部分高山植物在低于-1.8℃时发生冻结[62]。Taschler 和 Neuner 的研究表明奥地利 4 个主要林线树种叶片出现冻害特征时的温度在-8.0 — -4.1℃之间[60]。Rehm 和 Feeley 基于室内模拟冻害实验，发现同一物种在不同生活史阶段出现冻害的温度也存在很大差异，如 *Gynoxys nitida* 幼苗出现冻害时的温度为-6.0℃，而其成年植株则低至-10.3℃[67]。由此可见，不同物种、不同生长阶段植物叶片遭受冻害胁迫时的温度阈值存在很大差异，明确这一温度阈值是量化生长季冻害事件特征的关键。因此，要研究增温背景下生长季冻害事件对林线冷杉幼苗定居的影响，找出定义生长季冻害事件的温度阈值非常关键。通过对林线树种幼苗进行自动、连续拍照观测，确定其开始生长和出现冻害的温度，能够为进一步利用长期气象观测数据分析生长季早期冻害事件特征提供更加合理的温度阈值，从而有助于我们从森林更新的角度理解林线的形成机制，为气候变暖下全球林线位置的相对稳定性提供新解释。

3.2 基于野外环境的种子萌发实验

从种子的形成到萌发是森林更新的关键过程。已有研究显示，种子的形成、传播和萌发均有可能是高山林线森林更新的限制因子[26,32,34]。然而，目前对高山林线森林更新过程中种子阶段的认识还远远不如幼苗阶段，关于林线树种的种子产量和寿命、土壤种子库等方面的研究还相对缺乏，特别是对种子在林线及林线以上的萌发特征的了解还十分有限。目前已有的对种子萌发的认识则大多是来自于不同实验室条件下(如温度、光照、湿度等)的萌发特征[44]，而野外条件下的种子萌发实验十分缺乏[49]。在自然条件下，种子的萌发率远远小于其在实验室理想条件下的萌发率[132]，因此基于室内控制条件下的种子萌发实验结果可能会高估林线树木的更新潜力。目前，由于实验条件的限制，在实验室内通常只能对单一环境因子进行控制，无法模拟气温日振幅或极端温度等因子对种子萌发的影响，并不能反映出林线复杂的气候条件对种子萌发的真实影响，也不利于研究气候变化对种子萌发的影响。因此，未来基于野外模拟增温的种子萌发实验将有助于人们理解种子萌发在高山林线森林更新中的重要作用及未来气候变化对林线种子萌发的影响。

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