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樟子松人工林退化原因及研究展望

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摘要 气候变化对森林可持续性的影响是一个复杂过程, 如何保持人工林长期稳定生长是全球性技术难题. 20世纪50年代以来, 我国北方地区营造了大面积樟子松人工林, 对防风固沙、保持水土发挥了重要作用, 成为我国北方防沙带绿色生态屏障的重要组成部分. 目前“三北”防护林工程区樟子松人工林退化较为严重, 虽然已开展了大量研究, 但对于樟子松人工林退化机制的认识仍然不是非常清楚. 本文梳理了导致樟子松人工林退化的主要因素, 提出樟子松人工林树木退化过程的概念模型, 认为水力学失败和碳饥饿是导致樟子松人工林退化的两种主要生理机制; 水力学失败和碳饥饿降低了樟子松抵抗病虫害的能力, 而病虫害又进一步促进了水力学失败和碳饥饿的发展, 直至樟子松发生严重退化甚至死亡. 今后的研究应该重点关注樟子松退化的生理过程及其与病虫害的相互作用, 应加强以下几个方面的研究: (1) 樟子松人工林退化的多因素协同作用机制; (2) 林分或景观尺度樟子松人工林退化机制; (3) 樟子松人工林对环境胁迫的响应及调控机制; (4) 樟子松适生范围及生态适宜性评价.

关键词 樟子松人工林, 水分亏缺, 水力学失败, 碳饥饿, 病虫害

全球气候正在发生前所未有的变化, 世界范围的森林退化、树木死亡现象逐渐增多, 被认为与全球气温上升、降水格局变化导致的干旱胁迫以及人工林病虫害爆发息息相关[1~6]. 区域尺度上大面积森林退化不仅会影响区域碳平衡, 还会直接导致群落发生逆向演替, 使生态系统服务功能下降[7~9]. 树木退化及死亡率增加已成为全球关注的现象, 涉及生物和非生物因素之间的复杂相互作用, 系统地阐明树木退化的生理生态学机制成为亟待回答的科学问题[4,10~12]. 森林生态系统作为巨大的碳库, 对我国实现“碳中和”战略目标有重要作用. 近几十年来, 我国区域性高温事件、气象干旱事件的增多, 对森林生态系统产生了重要影响, 甚至改变了树木的生理特性[13]. 最新研究表明, 我国人工林退化面积不断增加, 其中“三北”防护林工程区樟子松人工林退化较为严重[14,15]. 樟子松人工林是我国北方防沙带防风固沙林的重要组成部分, 为“三北”地区生态安全及碳增汇做出了重要贡献, 遏制樟子松人工林退化并加快退化林分的改造与修复对构建我国北方生态安全屏障、助力“碳中和”战略具有重要意义. 然而, 现有的研究不足以解释樟子松人工林的退化现象, 简单化的一致性结论越来越站不住脚, 导致退化樟子松人工林修复和经营方案仍存在不足, 限制了樟子松在“三北”地区的推广. 因此, 本文旨在对樟子松人工林退化特征及退化原因进行综述, 在此基础上, 讨论目前樟

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子松人工造林面临的问题和挑战以及今后可能的研究方向，为退化樟子松人工林修复及樟子松人工林合理布局提供科学依据.

1 樟子松人工林退化特征

樟子松是松科常绿乔木，具有耐寒、耐旱、耐贫瘠、适生沙地和速生等优良特性，在中国其天然分布区主要位于大兴安岭北部山地及呼伦贝尔沙地．由于对沙地环境的良好适应性，樟子松在20世纪50年代被引种到荒漠化发展迅速的科尔沁沙地[16]，主要用于营建防风固沙林．1979年我国开始实施“三北”防护林体系建设工程, 樟子松是防护林主要造林树种之一, 辽宁省彰武县章古台镇成为樟子松固沙造林重点试验示范基地. 之后，樟子松引种范围不断向南向西推进，横跨整个“三北”工程区13个省(自治区、直辖市)55个县、旗[17]. 章古台是我国最早引种樟子松的地区, 20世纪末期章古台林龄30~35 a的樟子松人工林开始出现枯枝、黄叶、树势衰弱等退化现象, 同时病虫害加剧, 最终树木死亡. 之后, 类似现象在全国其他樟子松引种地如黑龙江、吉林、内蒙古、河北、陕西、山西等地也相继出现，退化主要表现为生长量下降、生长缓慢、树叶变黄脱落、易被病虫害侵袭、抗寒与抗旱能力减弱、防风固沙效能下降等，许多林带林网出现缺行断带、网格空缺现象, 且天然更新困难[18~23].

根据退化林分的外部特征，将樟子松人工林退化类型分为渐进型退化和突发型退化．渐进型退化表现为林相呈灰绿色，林冠不整；针叶呈灰色，针叶纤细，针叶长度缩短, 百针重下降; 大部分退化林木下部枝条首先变黄枯死, 随后逐渐向树顶发展蔓延, 直至整株死亡[24]．这种退化往往要经过几年、十几年或更长时间, 直至树木死亡樟子松人工林的防护功能才会终止．突发型退化主要表现为在1~2年时间内树木快速枯黄，衰弱(亡)木快速增加．突发型退化又可以分为两种情况: 1) 由松毛虫(*Dendrolimus tabulaeformis*)危害引起的退化, 其特点是树木叶片几乎全被吃光, 树冠、侧枝大量枯死[25]．2) 由松沫蝉(*Aphrophora flavipes*)和松枯梢病(*Sphaeropsis sapinea*)共同危害引起的退化．其特点是, 从单株树木看, 危害程度轻时, 树冠枯黄的嫩枝在绿枝中间呈斑点状分布，通常树冠的向阳面比阴面退化更重, 上部比下部退化更重[26]；从林分的角度看，林缘处的树木比林内退化更重, 越往林内退化越轻, 有时林分从远处看一片枯黄，但在林内看会发现枯黄的程度较轻. 突发型退化发生时, 如果不及时防治松毛虫或松沫蝉, 樟子松人工林的防护功能会快速下降.

2 樟子松人工林退化的过程和影响因素

生物因素和非生物因素都可能对樟子松的生长发育产生影响, 有些因素的作用不明显, 但作用时间很长, 有些因素具有突发性，樟子松人工林在生长过程中由于受到这些因素的综合影响，逐渐退化甚至死亡．图1是樟子松人工林退化过程的概念模型．从森林衰退病学角度来解释和说明樟子松人工林发生退化的原因和机制，可以将导致其退化的主要因素划分为3类，即诱发因素(predisposing factors)、激化因素(inciting factors)和促成因素(contributing factors)[27]．诱发因素是最先开始影响樟子松生长的因素，且在其生命历程中长期起作用，主要包括引种地气候条件不适宜、水分胁迫和养分失衡等；激化因素是第二阶段起作用的因素，它们在较短的时期内起作用且比较剧烈，能够直接损害树木、激化诱发因素对樟子松的影响，使得诱发因素造成的轻度损害经过长期的积累更明显地表现出来. 激化因素主要为食叶虫害和旱灾、雹灾等自然灾害; 促成因素是第三阶段起作用的因素，对樟子松来说主要为松枯梢病，是樟子松林木发生严重退化的重要标志[24,27,28]．诱发因素首先影响樟子松生长，并且可以延续整个生命周期, 激化因素虽然在短期内发生作用, 但可能会多次发生，松枯梢病是最终促成樟子松严重退化甚至死亡的直接原因. 然而, 导致樟子松人工林退化的根本原因还需要进一步具体分析.

2.1 诱发因素

2.1.1 气候条件不适宜

樟子松引种地和原产地之间气候条件存在显著差异. 樟子松自红花尔基引种到章古台, 和天然分布相比, 引种地的降水量、气温、蒸发量、无霜期等均发生变化．与原产地红花尔基相比，章古台在纬度上低5°~6°, 海拔低500~900 m, 年均温9.1°C, ≥10°C年积温1148°C, 生长期加长近77%．年降水量虽然比红花尔基多约100 mm, 但是年蒸发量多约400 mm, 空气湿度降低，干燥度增大, 气候更为暖干, 这种差异可导致树木提前成熟与衰老(表1)[29,30]. 林木的生长状况出现差异, 其中未退化林木生长进程加快，生命周期缩短，成熟期提前；而未能较快适应新环境的林木则呈现出退化趋势，表现出提前衰老或病虫害频发的特征[31~34].

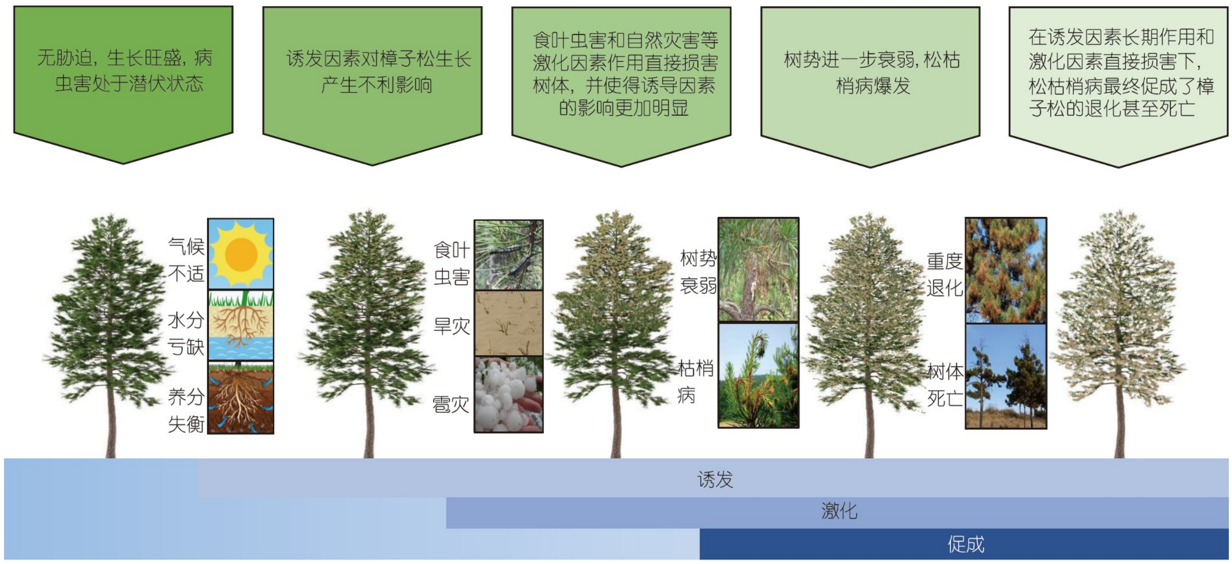

图 1 樟子松人工林树木退化过程的概念模型
Figure 1 The tree decline conceptual model of *P. sylvestris* plantation

表 1 章古台与红花尔基气候因子比较
Table 1 Comparison of climatic factors between Zhanggutai and Honghuaerji

地点	年降水量(mm)	年蒸发量(mm)	相对湿度(%)	干燥度	年均温(°C)	极端最高气温(°C)	极端最低气温(°C)	≥10°C积温(°C)	无霜期(d)
红花尔基	378	1174	70.0	1.33	–3.0	40.1	–49.3	2000	87
章古台	480	1590	60.4	1.45	6.1	43.2	–34.1	3148	154

2.1.2 水分亏缺

水分是干旱、半干旱区植物生长发育的主要限制因子，水分条件是影响林分生产力及其稳定性的重要因素[35~37]. 由于半干旱区降水少且集中, 土壤水分波动剧烈, 加之林分蒸腾输出水量相对较大, 因此经常发生水分亏缺. 同时, 20世纪50~70年代, 人们对生态水文学的认识还不够深入, 且受当时规划设计水平限制, 在章古台地区营造了大面积樟子松纯林. 为了保证造林效果，初植密度多在3300~4400株/hm^2，有些地块甚至达到6600株/hm^2，林分密度过高造成土壤含水量明显降低及地下水位下降，导致樟子松正常生长需要的水分得不到充分供应，这是沙地樟子松人工林退化的主要诱发因素之一[20,24,38~42]. 长期野外林地土壤含水量监测结果表明, 沙地樟子松生长季80%的时间处于严重水分胁迫状态[20]. 朱教君等人[43]对5年生樟子松幼苗进行盆栽控水实验发现，樟子松幼苗的光合作用速率与土壤含水量呈显著正相关关系，当土壤含水量降至一定阈值时，樟子松气孔几乎关闭，不再进行光合作用. 因此，对于沙地樟子松人工林，仅靠自然降水难以满足林木生长的水分需求[44]. 地下水也是维持沙地樟子松存活和生长的重要水源[45~49]. 虽然沙地樟子松大部分根系分布在1.0 m以内土层，但仍有1~3条垂直根系深度能够达到3.0 m以下土层[43,45]. 根据沙地土壤粒级分布调查, 地下水沿毛管上升高度约为1.0 m, 而随着地下水位的不断降低，目前大部分樟子松根系已经难以到达地下水, 因此加剧了水分亏缺[47]. 对樟子松在不同降水条件下水分利用来源的研究发现，在降水量较少的年份, 樟子松树干液流密度在持续干旱过后即使水分条件好转也无法恢复到持续干旱之前的液流密度，说明水分胁迫对沙地樟子松生长的负面影响在一定程度上是不可逆的[50].

2.1.3 养分失衡

“三北”地区气候干旱, 植被稀疏, 土壤贫瘠. 以樟子松引种地章古台为例，章古台与原产地红花尔基之间土壤条件比较相似，都是风沙土，砂粒(粗砂+细砂)占85%以上，粉粒和黏粒较少，养分条件较差[29]. 章古台

地区引种的樟子松人工林土层越深养分含量越少，且林龄较大的樟子松人工林土壤中的有机质、氮和钾的含量较低，土壤有机质随林龄的增大逐渐减少，分析认为林龄超过30 a之后会出现土壤养分含量明显下降的地力衰退现象[51~53]．过多的氮沉降与树木退化密切相关，氮输入量处于一定范围内时对樟子松生长具有促进作用，然而过量的氮沉降对树木的生长产生不利影响，间接造成养分失衡，表现在降低光合速率、影响根系对养分的吸收、使根冠比降低以及减弱树木对干旱、病虫害的抵御能力等方面[54,55]．通过模拟实验分析氮添加对樟子松幼苗生长的影响发现，约30 kg hm^{-2} a^{-1}的氮添加量能够促进地上生物量的积累，对地下生物量没有显著影响，过高的氮输入对总生物量有一定抑制作用[56,57]．

2.2 激化因素

2.2.1 虫害

危害樟子松的害虫主要有油松毛虫(*Dendrolimus tabulaeformis*)、赤松毛虫(*Dendrolimus spectabilis*)、松梢螟(*Dioryctria rubella*)、松果梢斑螟(*Dioryctria mendacella*)、松沫蝉(*Aphrophora flavipes*)和松毒蛾(*Dasychira·axutha*)等．虫害发生时松毛虫幼虫啃食松针，有些林分的针叶70%被吃掉，导致樟子松生长衰弱，进而引发松枯梢病，造成大面积樟子松人工林严重退化．1986~1991、1998~2001和2011~2016年，辽西北地区大面积发生松沫蝉虫害，且连续多年发生，严重地块有虫株率接近100%，这3个时期也是辽西北地区樟子松人工林退化最严重的时期．研究表明，松沫蝉虫害发生时，除其自身对树木的危害外，松沫蝉对松枯梢病的发生还有明显的促进作用，樟子松人工林退化的严重程度与松沫蝉的有无、多少有密切关系[58,59]．

2.2.2 自然灾害

樟子松人工林面临的自然灾害主要为雹灾和旱灾．雹灾对樟子松的直接危害是机械损伤，同时由于冰雹造成的伤口为病菌侵染创造了有利条件，因此雹灾也会对樟子松产生间接危害，即诱发松枯梢病．极端干旱对樟子松人工林是巨大的考验，与天然林相比，樟子松人工林冠层气孔导度更高，蒸腾速率更大，但是气孔导度的调节能力较差，因此在遭遇极端干旱时更容易发生枯梢和退化[18]．与天然林相比，樟子松人工林表现出明显较低的茎水力效率，茎导水率和水力安全范围显著低于天然林，并且随着林龄的增加，往往出现严重的干旱胁迫症状，而在樟子松天然林中没有观察到这种现象[48]．因此，旱灾加重了樟子松所面临的环境压力，激化了诱发因素中水分胁迫的影响，进一步削弱树势，降低了樟子松的抗逆性．

2.3 促成因素

松枯梢病是分布范围最广的林木真菌病害之一，在1999年被列为中国重要的森林病害．导致松枯梢病发生的松枯梢病菌(*Sphaeropsis sapinea*)是一种弱寄生菌，是危害樟子松人工林的主要病菌，对樟子松林木枯梢、死亡起着重要的促成作用[59]．松枯梢病的发生较为隐蔽，病菌在健康的樟子松上存在潜伏侵染现象，但不显露症状，当樟子松生长衰弱时，症状开始显露，表现为顶芽枯死、枯针、枯梢或丛枝等，还可能出现树干溃疡、流脂、坏死、根茎腐烂和木材蓝变等，然而天然林很少发生[24,28]．松沫蝉对松枯梢病的发生与危害有明显的促进作用，樟子松人工林在生命周期内若发生松沫蝉病害，松枯梢病菌便可通过虫口或伤口侵入树体．中老龄(林龄>25 a)的樟子松人工林更易受到松枯梢病菌的侵害，林龄越大，抗病能力越弱，病菌可从当年生新梢的气孔直接侵入，使其表现出染病症状[26]．

3 樟子松人工林退化的生理生态分析

树木生长面临着各种各样的生物和非生物压力，这些压力源发生的顺序、时间和强度存在差异，它们的影响可能是持续的或突发的，具有不同的时间和空间特征．树木退化机制的假说主要有水力学失败假说(Hydraulic Failure)、碳饥饿假说(Carbon Starvation)和生物攻击假说(Biotic Agents)[60~68]．樟子松人工林的退化由外部环境因素诱导，病虫害激化和促进，最终导致出现不同程度的退化甚至死亡．目前针对樟子松人工林退化机制的研究主要围绕以水分平衡为核心的生态机制，但生理机制还不是很清楚．

3.1 樟子松人工林退化的生理生态过程

3.1.1 水力学失败机制导致樟子松人工林退化

前期关于樟子松人工林退化的研究主要集中在环境因子与退化现象之间的联系，初步结论认为水分亏缺是樟子松人工林退化的主要原因[69~72]．对沙丘顶部和底部生长的树龄33 a的樟子松树干木质部水、不同深度土壤水和干湿季地下水中δ^2H和δ^{18}O的分析表明，

在干旱期土壤水分含量较低时，樟子松主要利用40~300 cm深土层中的土壤水，可能还有地下水；当0~100 cm深度土层中的土壤水分含量较高时，土壤水是樟子松的主要水分来源[73]. 在干旱条件下, 生长在沙丘顶部和底部的樟子松都调节水分利用策略，更多地利用深层水源并且提高水分利用效率，地下水位急剧下降对樟子松的生长和生存将会带来严重的负面影响[17]. 如何从更深的机理层面揭示樟子松人工林退化的生理学机制呢？水力学失败机制导致樟子松人工林退化的研究得到了更多的关注.

水分亏缺导致土壤水势降低，树木为了吸收水分会进一步降低木质部水势，然而当水势降低超过一定限度时, 空气进入木质部细胞形成空穴, 水分输导出现间断, 发生气穴栓塞(cavitation embolism), 导致树木从远端组织开始逐渐缺水, 呈现枝梢枯黄等现象. 部分学者通过比较人工林和天然林不同树龄大小等级的樟子松的水力结构，来检验随着树龄的增加水力限制是否对樟子松退化起重要作用[48]. 研究发现, 樟子松人工林整体表现出明显较低的茎水力效率，水力安全范围显著下降, 并且随着树龄的增加, 干旱胁迫症状加重, 而在天然林中没有观察到这种趋势[48]. 当环境中的水分限制持续时间和强度不断增加时，水分输导组织压力增大，无法正常供应冠层上部枝叶正常生理过程所需的水分, 樟子松树冠上部会出现明显的水力限制, 在蒸腾拉力的作用下水分输导出现间断, 发生气穴栓塞, 枝条导水率接近于零，导致樟子松从枝梢末端开始缺水，长此以往呈现枝梢枯黄、脱落等现象. 所以在水分胁迫发生期间，樟子松的栓塞抵抗是评价其生存力和恢复力的一个非常关键的指标，是水分胁迫时樟子松是否会发生退化以及退化程度的决定因素之一，并可以作为预测未来干旱导致樟子松退化程度的关键因子.

3.1.2 碳饥饿机制导致樟子松人工林退化

非结构性碳(nonstructural carbon, NSC)影响树木对干旱的适应能力和对病虫害的抵御能力，对于理解半干旱区森林退化机制具有重要意义[7,11,74]. 当树木受到水分胁迫时, 会采取一系列水力学御旱措施, 为了防止出现气穴栓塞，树木会降低气孔开放程度以降低蒸腾作用对木质部水分输送的压力，气孔的关闭同时会导致光合作用合成的非结构性碳减少，无法满足树木正常生长和抵御水分胁迫所需要的能量，呈现树势衰弱的退化现象. 针对樟子松人工林树木NSC的研究主要集中于各器官分配特征、不同树龄的含量特征以及NSC含量与干旱的关系等方面. 未退化樟子松NSC(可溶性糖和淀粉)的浓度在器官间存在显著差异，遵循“就近”和“按需”的原则，各器官中可溶性糖浓度顺序为叶>枝>根>干，淀粉浓度顺序为叶>枝>干>根，NSC浓度顺序为叶>枝>根>干[52]. 樟子松枝条淀粉含量仅在降水量减少的年份增加，在其他地区的研究也发现了类似的现象, 认为这种现象是干旱事件导致的, 而不是长期气候变化的结果[75~77]. 在轻度及中度干旱条件下，树木各器官NSC含量随着干旱持续时间的延长先逐渐减少后逐渐增加直至接近控制值(无干旱胁迫), 并且这种趋势在干旱后期仍然存在，意味着树木可能激活了生理调节机制，以增加碳储量并减少碳饥饿的风险[78,79]. 相比之下, 长期的严重干旱会导致碳水化合物的净损失, 特别是在根部, 这也意味着长期的严重干旱会导致整个植株的NSC耗竭[80,81]. 目前已有许多其他树种NSC积累和消耗的相关研究，其结论对樟子松退化的生理生态分析具有一定的借鉴意义，但仍需通过实验验证.

3.2 相关研究对樟子松人工林退化研究的启示

3.2.1 樟子松人工林退化过程中水力学失败与碳饥饿的相互作用

樟子松人工林退化过程中水力学失败与碳饥饿之间存在着相互作用，如干旱时树木抵抗细胞失水和气穴栓塞的修复都需要渗透调节物质，其中可溶性糖发挥着重要作用，并且两个假说都存在对气孔的调控[82~87]，单从一个角度不能完全解释樟子松人工林的退化机制. 植物的光合固碳过程与蒸腾耗水过程之间存在着协调与耦合的关系, 在抵御干旱胁迫时, 气孔的调控影响着水碳关系[88~95]. 目前已有研究关注水碳失衡导致树木退化的机制. Song等人[72]分析了1985~2014年暖干期樟子松、小钻杨两个非乡土树种和油松、榆树两个乡土树种的树轮δ^{13}C和内禀水分利用效率(intrinsic water use efficiency, iWUE), 发现树种间变化趋势存在差异；从iWUE的角度分析发现，非乡土树种受到了较强的水分胁迫，从而降低了气孔导度和碳的摄入, 一旦水分胁迫超过生理阈值, 在极端干旱条件下影响了树木体内水力结构和碳摄取，则发生退化的几率更高. 水碳耦合具有保守性和变异性, 水碳平衡是保守性的体现, 但保守性是相对的, 内在的和外在的许多因素都会引起水碳关系发生变异，樟子松退化过程中水力结构和非结构性碳的改变也具有相似的关系特

征[11,80,96~101]. 逆境条件下植物的水碳关系仍存在许多亟待研究的方面, 机制之间的共同作用或相互作用已得到越来越多的认可, 从水碳失衡的角度解析樟子松人工林退化机制将会是今后研究的重点.

3.2.2 病虫害与水力学失败和碳饥饿的相互作用

水力学失败和碳饥饿造成了樟子松人工林树势衰弱, 在病虫害的侵袭下最终促成了樟子松人工林退化, 目前的研究主要针对病虫害破坏树体结构进而导致树木生理功能受损, 其中具体的生理机制尚不清楚[102~106]. 健康的樟子松体内也存在潜伏侵染的病原体, 但不表露发病症状, 当樟子松生长衰弱时, 病害症状才开始显露, 从生理学的角度看, 当树木不能调动资源来修复受损组织或维持活组织时, 就会发生严重退化甚至死亡. 病虫害对樟子松水力学失败和碳饥饿产生影响, 同时水力学失败和碳饥饿的发生也会影响樟子松对病虫害的防御能力, 如NSC对樟子松自身合成抵抗病虫害的代谢物有重要作用, 影响樟子松抵御害虫和病原体的能力. 然而目前对樟子松退化过程中病虫害与水力学失败和碳饥饿相互作用的研究还很初步, 具体的生理机制仍需进一步深入研究.

4 展望

人工林占世界森林面积的7%, 过去30年来全球范围内人工林面积一直在增加, 并被作为固碳和减缓气候变化的自然气候解决方案[107]. 气候变化引发的多重干扰对森林的可持续性带来严重威胁, 作为一种严重而且影响广泛的干扰, 干旱引发或加剧了病害虫和火灾的影响, 从而进一步加剧了对森林可持续性的影响[107]. 中国具有全球面积最大的人工林, 人工林为生态建设和有效应对全球气候变化做出了巨大贡献. 但是, 也有许多人工林发生退化甚至死亡[108]. 20世纪70年代以来, 樟子松从大兴安岭北部和呼伦贝尔沙地向西向南引种, 形成大面积樟子松人工林, 成为“三北”防护林的重要组成部分. 在气候变化背景下, 樟子松人工林在多种因素作用下发生退化. 然而, 目前关于樟子松人工林退化原因的研究不够系统, 樟子松退化的生态机制还不很清楚. 以往研究大部分围绕水分因素展开, 认为樟子松引种地水分亏缺是导致樟子松人工林退化的主要因素, 重点关注樟子松人工林土壤水分变化、樟子松水量平衡和水分利用策略等. 然而水分亏缺导致樟子松退化和死亡的生理机制尚不清楚, 缺乏樟子松NSC对水分亏缺的响应及调控机制的研究, 尤其是缺乏对樟子松退化过程中病虫害与水力学失败和碳饥饿相互作用的研究. 本文梳理了导致樟子松人工林退化的主要因素及关键退化过程, 提出了樟子松人工林树木退化过程的概念模型, 并总结了导致樟子松退化的两种主要生理机制即水力学失败和碳饥饿. 水力学失败和碳饥饿降低了樟子松抵抗病虫害的能力, 而病虫害又进一步促进了水力学失败和碳饥饿的发展, 直至樟子松发生严重退化甚至死亡. 今后应加强以下几个方面的研究.

4.1 樟子松人工林退化的多因素协同作用机制

樟子松人工林退化是多种因素综合作用的结果, 然而, 目前把樟子松人工林退化主要归因于水分亏缺, 对其他因素以及各因素之间的相互作用研究较少, 生物因素与非生物因素也往往分开进行研究, 导致对樟子松退化原因的认识模糊不清. 因此, 未来需开展多因素协同作用机制研究, 如病虫害与干旱的交互作用对樟子松水力特征和NSC的影响, 病虫害与水力学失败和碳饥饿的相互作用, NSC对抵抗病虫害代谢物合成的影响等, 揭示生物因素与非生物因素协同导致樟子松人工林退化的作用机制.

4.2 林分或景观尺度樟子松人工林退化机制

当前针对樟子松树木个体的生理生态过程的研究比较多, 关于林分或景观尺度樟子松人工林生态过程的研究比较少. 然而樟子松人工林退化是林分或景观尺度上的生态过程, 仅仅依靠树木个体尺度生理生态过程的研究不足以揭示樟子松人工林退化机制. 未来需要在树木个体尺度生理生态过程研究的基础上进一步探究林分或景观尺度多种因素的协同作用, 开展林分或景观尺度樟子松人工林对环境因素的生态响应机制研究, 揭示樟子松人工林退化机制.

4.3 樟子松人工林对环境胁迫的响应及调控机制

目前对于樟子松人工林退化过程中的诸多关键生理过程的研究仍存在许多不足, 针对大树进行的长期环境胁迫研究较少, 缺乏对樟子松人工林应对环境胁迫的响应及调控机制的认识, 无法准确预测樟子松的退化及死亡风险. 未来需要进一步加强樟子松对环境胁迫响应的研究, 如根-干-枝-叶的水力特征和NSC分配特征等, 明确樟子松在适应环境胁迫过程中如何权衡水力有效性和安全性, 如何维持碳平衡; 对水和碳的耦合过程进行测定, 明确在应对干旱等突发事件时木

质部水分输导以及NSC调控的策略模式，确定诱发、激化和促成因素作用各关键因子的阈值；系统分析樟子松人工林退化过程中水力结构与NSC变化特性，确定樟子松人工林不同退化阶段水、碳等关键参数的阈值, 揭示樟子松人工林不同退化阶段的关键控制因子.

4.4 樟子松适生范围及生态适宜性评价

目前，樟子松引种范围已经从黑龙江东南部经华北北部向西一直延伸到新疆伊宁等北方广大地区，而且近年来樟子松人工林扩展速度大大加快，2013年以来樟子松人工林面积已经增加了近一倍[20]，达到近 8.0×10^5 hm^2[17]. 适地适树是指立地条件与树种特性相互适应，是选择造林树种的一项基本原则. 然而，樟子松天然分布区位于寒温带，引种地和天然分布区之间气候、土壤条件等存在较大差异，这是造成樟子松人工林退化的重要诱发因素. 未来需要对樟子松适宜生长的立地条件、生态适宜性进行系统的监测和评价，科学确定樟子松适生范围.

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Summary for “樟子松人工林退化原因及研究展望”

Causes and research prospects of the decline of *Pinus sylvestris* var. *mongolica* plantation

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Planted forests account for 70% of the world’s forest area. Over the past 30 years, the area of planted forests has been increasing worldwide and as a natural climate solution for carbon sequestration and climate change mitigation. The impact of climate change on forest sustainability is complex and the question of how to maintain the long-term stable growth of plantations is a global technical problem. Since the 1950s, a large area of *Pinus sylvestris* var. *mongolica* plantation has been built for wind prevention and sand fixation, and soil and water conservation in northern China, which has become an important part of the green ecological barrier in North China. At present, part of the Three-North Shelterbelt Forest Program has declined, especially *P. sylvestris* plantation. Although a lot of research has been carried out on the decline of *P. sylvestris* plantation on sandy land, at present, the understanding of the decline mechanism is still unclear. Most of the previous studies focused on the water factor, and considered that the water deficit in the introduction site was the main factor leading to the decline of *P. sylvestris* plantation, focusing on the soil water change, water balance and water use strategy. However, the physiological mechanism of the decline and even death of *P. sylvestris* caused by water deficit is still unclear, and there is a lack of research on the response and regulation mechanism of the non-structural carbon to water deficit, especially the interaction between diseases and pests, hydraulic failure and carbon starvation during the decline process of *P. sylvestris*. In this paper, the main factors leading to the decline of *P. sylvestris* plantation are summarized and a conceptual model of the decline process is proposed. Hydraulic failure and carbon starvation are the two main physiological mechanisms leading to the decline of *P. sylvestris* plantation. Hydraulic failure and carbon starvation reduced the ability of *P. sylvestris* to resist pests and diseases, while pests further promoted the development of hydraulic failure and carbon starvation until *P. sylvestris* seriously declined or even died. Future research should focus on the physiological process of *P. sylvestris* decline and its interaction with pests and diseases. The following aspects should be strengthened: (1) The synergistic mechanism of multiple factors on declined *P. sylvestris* plantations, such as the interaction between diseases and insect pests and hydraulic failure and carbon starvation, the impact of the interaction between diseases and insect pests and drought on the hydraulic characteristics and NSC, the impact of NSC on the synthesis of metabolites resistant to diseases and insect pests; (2) the decline mechanism of *P. sylvestris* plantation on stand or landscape scale based on the study of individual scale and the ecological response mechanism to environmental factors at stand or landscape scale; (3) the *P. sylvestris* plantation response to environmental stress and its regulation mechanism, such as how to balance the hydraulic efficiency and safety, and the strategic model of xylem water transport and NSC regulation in response to drought and other emergencies; (4) the suitable range of ecological suitability evaluation of *P. sylvestris* plantation based on long-term positioning observation data analysis.

***Pinus sylvestris* plantation, water deficit, hydraulic failure, carbon starvation, diseases and insect pests**

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