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森林木质藤本数量过度增长的机制与生态效应

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摘 要: 木质藤本是维持森林物种多样性的组成部分。近年来, 热带、亚热带森林尤其是次生林内的木质藤本数量的过度增长给森林的恢复和健康发展造成了威胁。至今, 国内尚少有研究对森林木质藤本过多的现象、增长机制与生态效应进行综合认识。该文梳理国内外相关文献, 从木质藤本数量增长的机制与生态效应进行分析和总结, 综合相关研究认为: (1) 木质藤本数量的增长与干旱化加剧、大气 CO₂ 浓度上升、自然干扰和森林破碎化有关, 在环境变化的情况下, 木质藤本在形态、行为、生理等方面比树木更具优势, 表现为更快的生长速率、更强的繁殖力和可塑性以及资源利用效率。 (2) 木质藤本主要通过遮荫胁迫、资源竞争和机械压力与损伤等方式对树木造成影响。 (3) 木质藤本过度增长在个体水平上会阻碍树木生长、生殖并引起树木死亡, 在群落水平上会改变物种组成、降低多样性, 在生态系统水平上会降低森林碳储量, 改变碳、矿质养分和水分循环过程等。因此, 建议结合野外长期监测与控制实验开展木质藤本数量动态与环境变化关系、森林干扰对木质藤本生长的影响、木质藤本对环境变化的响应及适应机理、木质藤本数量过度增长的生态效应评价研究。同时, 应积极探索合理的森林木质藤本管控方法, 为森林管理和恢复等方面的宏观决策提供科学依据。

关键词: 木质藤本, 干扰, 全球变化, 森林健康, 森林管理

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Mechanisms and ecological consequences of the over-increase of lianas in forests

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Abstract: Lianas are one of the components in maintaining forest diversity. The over-increase of lianas in tropical and subtropical forests, especially in secondary forests is threatening the restoration and healthy development of forests. Few domestic researches make a comprehensive evaluation on the mechanism of the over-increase of lianas and negative effects on forests. In this paper, we reviewed and summarized the related researches on mechanisms and ecological consequences of the over-increase of lianas both at home and abroad. Based on the relevant studies we hold the opinions: (1) The increase of lianas can be correlated with drought severity, elevated atmospheric CO₂, increased natural disturbance (gaps) and forest fragments. Lianas possess the advantages of rapid growth, strong reproductive capacity and phenotypic plasticity, and high resource use efficiency under the altered environment. Thus, the favorable environment and inherent advantages can contribute to the increase of lianas. (2) Lianas compete with trees by means of shading stress, resource competition and mechanical loading, abrasion, and strangulation, which all may increase the mortality of trees. (3) The over-increase of lianas can negatively affect the tree growth, reproduction, and survival; at community level, lianas can alter tree community composition and decrease community diversity; at ecosystem level, lianas can ramify forest ecosystem function by decreasing carbon storage and altering carbon, nutrient, and water cycling. Therefore, we recommend that future studies should be aimed at the correlations between population dynamic changes of liana species and environmental changes, the effect of forest disturbance on the growth of lianas, responses of lianas to the environmental changes and the adaption mechanisms, comprehensive evaluation on the ecological consequences of the increase of lianas by means of long-term dynamic monitoring plots and controlling experiments. It is also essential to find appropriate management and control strategies of the over-increase of lianas so as to provide reference for forest management and forest ecological restoration.

Key words: liana, disturbance, global change, forest health, forest management

木质藤本 (lianas) 是不能单独直立、通过主茎或借助攀援器官进行生长的植物类群, 与树木相比具有较大的长度和胸径比 (Schnitzer & Bongers, 2002)。木质藤本是森林群落的常见组分, 对群落结构和功能的维持具有一定的作用 (Schnitzer & Bongers, 2002)。然而, 当森林受到严重干扰时, 木质藤本数量的过度增长给森林健康造成威胁, 树木生长受抑制、群落结构单一化、物种多样性下降, 严重影响森林生态系统功能 (Schnitzer & Bongers, 2011)。这一问题已引起了国外学者的普遍关注。

国外学者较早关注到木质藤本数量的增长及其负面影响, 在木质藤本的分布格局 (Schnitzer, 2005)、数量动态 (Addo-Fordjour et al., 2021)、监测方法 (van der Heijden et al., 2022)、藤与树的关系 (Leonor et al., 2015)、木质藤本增长的机制及生态影响 (Schnitzer & Bongers, 2011; de Azevedo Amorim et al., 2018; Marshall et al., 2020; Reis et al., 2020; Meunier et al., 2021a) 等方面做了较多的研究。国内学者多关注森林木质藤本的多样性 (Hu et al., 2010; 王业社等, 2014)、经济价值 (季梦成等, 2008) 和生态功能 (张朝阳等, 2007) 等积极作用。由于野外辨识和调查的困难, 因此在很多调查与研究往往忽略这一类特殊生活型植物。实际上, 木质藤本数量过度增长的现象在我国南方很多森林, 尤其是在次生林内较为普遍。例如, 在一些自然保

护区次生林内, 木质藤本甚至形成地毯式覆盖, 严重阻碍了森林恢复, 使保护区实行的封山育林政策变成了“封山育藤” (图 1)。

目前, 国内关于木质藤本对森林影响的研究还较少。关列 (1980) 较早摘译报道了人工林受藤本植物的危害及其防治, 但当时并未得到较大响应; 陈亚军等 (2007) 综述了木质藤本在热带森林的生态学功能; 王伯荪等 (2009) 对某种木质藤本的影响进行了具体的评述。随后, 诸多学者陆续在木质藤本对森林物种多样性、群落结构及更新的影响 (郝建辉等, 2011; 王忠伟等, 2020)、木质藤本与树木的关系 (陆芳等, 2021)、藤树性状比较 (Chen et al., 2021) 等方面进行了研究。然而, 至今国内尚未见有研究对森林木质藤本过多的现象、增长机制与生态效应进行综合认识。

为引起国内学者对森林木质藤本过度增长现象及其影响的关注, 本文综合国内外研究进展, 重点分析木质藤本过度增长机制, 详细阐述木质藤本增长的潜在生态效应, 并提出新的研究方向, 期为木质藤本过度增长的防控及森林管理政策的制定提供参考。

1 木质藤本数量过度增长

木质藤本具有维持森林物种多样性 (Schnitzer &

Bongers, 2002)、经济、药用和生态功能(张朝阳等, 2009; 刘扬等, 2021)。同时, 作为层间植物, 木质藤本既是很多动物的生境和通道, 又是重要的食物来源(Adams et al., 2016, 2019; Odell et al., 2019)。然而, 当木质藤本和树木比例超出临界阈值, 木质藤本在森林中的积极作用将转变为负面作用, 尤其在次生林或破碎化森林中, 木质藤本数量的过度增长将阻碍森林演替与更新(Marshall et al., 2020)。由于外界环境的变化导致木质藤本相对或绝对数量的增长, 并给当地森林生态系统造成负面影响, 本文称为木质藤本数量过度增长, 简称为木质藤本增长。

木质藤本增长的表现形式主要为多度(密度)、断面积、生物量、丰度和攀爬覆盖树木的程度等的增加(Wright et al., 2004; Ingwell et al., 2010; Laurance et al., 2014; Wright et al., 2015)。Phillips 等(2002a)首次提出了森林木质藤本增加的现象, 通过综合分析亚马逊 4 个区域的 47 个非破碎化热带雨林木质藤本的数量变化, 发现 20 年间大型木质藤本(DBH ≥ 10 cm)相对断面积、相对多度和树木死亡风险显著增加。此后, 众多研究均得出相似的结果。例如, 在尼日利亚一个经历过火烧的低地热带雨林, 2005—2014 年间攀爬植物的种数由 49 种增至 61 种, 密度由 448~1 152 hm^2 增至 1 712~4 492 hm^2 (Uwalaka & Muoghalu, 2017); 温带森林木质藤本也有所增加, 在 1967—2007 年间欧洲温带森林林下层木质藤本出现的频率增加了近 39%(Perring et al., 2020)。虽然也有研究结果与此不同(Smith et al., 2017; Bongers et al., 2020; Umaña et al., 2020), 但多数研究认为木质藤本的数量呈递增趋势。在中国热带及亚热带区域的很多次生林内木质藤本长势旺盛、分布广泛, 如热带森林的金钟藤(*Merremia boissiana*)(王伯荪等, 2009)、亚热带森林的钩藤(*Uncaria rhynchophylla*)、葛(*Pueraria lobata*)等在林内形成大面积覆盖, 严重影响了当地森林的健康发展(图 1)。

2 木质藤本过度增长的机制

诸多研究认为木质藤本在森林群落中优势度的增加与外界环境变化有关, 主要因素为全球气候变化、自然干扰(如林窗形成)和森林砍伐等人为干扰导致的森林破碎化、次生化(图 2)。木质藤本能因环境变化做出调整和适应, 其生理、结构及行为等特征比树木更具优势。

2.1 干旱化加剧

有研究表明木质藤本数量动态与大气降水量和蒸发量密切相关。木质藤本的多度、丰度和生物量均随大气降雨量和土壤湿度的增加而减少, 随干旱程度的加剧和干旱周期的延长而增加(Schnitzer, 2005; Swaine & Grace, 2007)。例如, 在巴拿马干旱森林内, 木质藤本密度和丰度的绝对、相对值均高于湿润森林(Parolari et al., 2020)。

在干旱的条件下, 木质藤本比树木在生长和生理等方面更具优势。研究发现木质藤本在雨季的生长量比树木高出 2 倍, 而在旱季高达 7 倍(Schnitzer & van der Heijden, 2019), 木质藤本碳积累量在旱季大于湿季(van der Heijden et al., 2019)。当降雨量减少时, 木质藤本幼苗的存活量也高于树木(Umaña et al., 2019)。此外, 在干旱条件下, 木质藤本水分利用效率、导水效率和资源获取策略等均优于树木(Cai et al., 2009; Zhu & Cao, 2009; Medina-Vega et al., 2021a, b)。例如, 热带湿润雨林树木在水力安全和导水效率之间具有权衡性, 而木质藤本却没有, 较强的导水效率和抗栓塞能力表明木质藤本比树木更耐旱(van der Sande et al., 2019)。

在干旱条件下, 木质藤本各构件还表现出较强的可塑性和适应性。在旱季, 木质藤本比树木具有更强的叶片渗透调节能力, 这使其在干旱加剧的环境下更具生长优势(Maréchaux et al., 2017)。Smith-Martin 等(2019)发现在旱季进行灌溉能使树木的胸径和生物量显著增加, 而木质藤本并未发生变化, 这表明在干旱条件下木质藤本具有更强的适应力。此外, 木质藤本具有发达的根系维管系统, 可进行营养物质的高效运输与分配。

木质藤本根系长而错综复杂且具有较强的耐胁迫能力, 有些甚至能达 10 m 深(Restom & Nepstad, 2004), 可从四周或深处利用不同来源的水分, 有效减缓干旱胁迫(Chen et al., 2015)。因此, 在全球干旱加剧下, 木质藤本的形态、生理和行为特征的优势可导致其相对和绝对数量的增加。

2.2 大气 CO_2 浓度增加

持续上升的大气 CO_2 浓度是木质藤本增长的潜在因素。大气 CO_2 浓度的增加有利于木质藤本的生长(Granados & Korner, 2002)。当 CO_2 浓度增加时, 木质藤本洋常春藤(*Hedera helix*)新梢长度和生物量的增长量提高了近 60%(Zotz et al., 2006)。 CO_2 增加控制实验也发现温带森林木质藤



图 1 江西官山国家级自然保护区钩藤对树木形成地毯式覆盖(引自宋述灵, 2019)

Fig. 1 Liana *Uncaria rhynchophylla* blanketing trees in Guanshan National Nature Reserve, Jiangxi Province

本毒漆藤 (*Toxicodendron radicans*) 的生长速率、光合作用、水分利用效率显著高于正常大气 CO_2 条件下的状态 (Mohan et al., 2006)。并且, 木质藤本对 CO_2 增加的响应比树木更加迅速 (Belote et al., 2004)。木质藤本具有较高的叶茎比和较低的叶片单位面积构建成本, 这使其对 CO_2 吸收和固定比树木更具优势 (Zhu & Cao, 2010)。

2.3 自然干扰

冰雪、火灾和树木死亡等自然 (林窗) 干扰易促使林内木质藤本的增长。通常情况下, 林窗内木质藤本多度和丰度均显著高于非林窗地带 (Schnitzer & Carson, 2001)。一方面, 林窗地带土壤肥沃、光照较强和空余生态位较多, 为木质藤本生长提供了良好的环境。另一方面, 很多木质藤本在林窗内具有生长快速和繁殖力强的特征。由于减少了对自身支持结构的投资, 木质藤本可将大部分营养资源用于茎的快速生长和叶的累积 (Putz, 1984)。除通过种子萌发来进行植株定居外, 木质藤本在林窗内也可进行无性克隆繁殖, 依靠地下茎、匍匐茎不断地萌发新枝来向新地段蔓延扩散从而促使植株数量的增加 (Schnitzer et al., 2021)。此外, 即便是寄主树木倒塌死亡, 很多木

质藤本也能够通过萌发新枝重新攀爬到林冠层, 使得木质藤本绝对或相对数量有所增长 (Rocha et al., 2020)。

2.4 森林破碎化

森林砍伐、捕猎等人为干扰使森林破碎化、次生化, 会导致林缘地带或次生林内木质藤本增长。森林破碎化后, 森林环境变得干燥, 土壤肥沃, 光照增加, 植株矮小, 这些条件都有利于木质藤本的攀爬和快速生长。因此, 在林缘处和次生林木质藤本的生长速率更快、植株数量更多 (Ladwig & Meiners, 2010; Roeder et al., 2019), 并且林缘地木质藤本的丰度和碳储量也高于林内 (Londré & Schnitzer, 2006, Magnago et al., 2017; Campbell et al., 2018)。森林破碎化也为木质藤本克隆生长创造了条件, 如在拉塞尔瓦择伐的热带雨林, 木质藤本长距离克隆生殖对多度增加的贡献率达到 7.5%, 断面积增量高达 60% (Yorke et al., 2013)。

3 木质藤本与树木的竞争方式

3.1 遮荫胁迫

木质藤本借助茎、枝、叶等器官攀爬到树木的

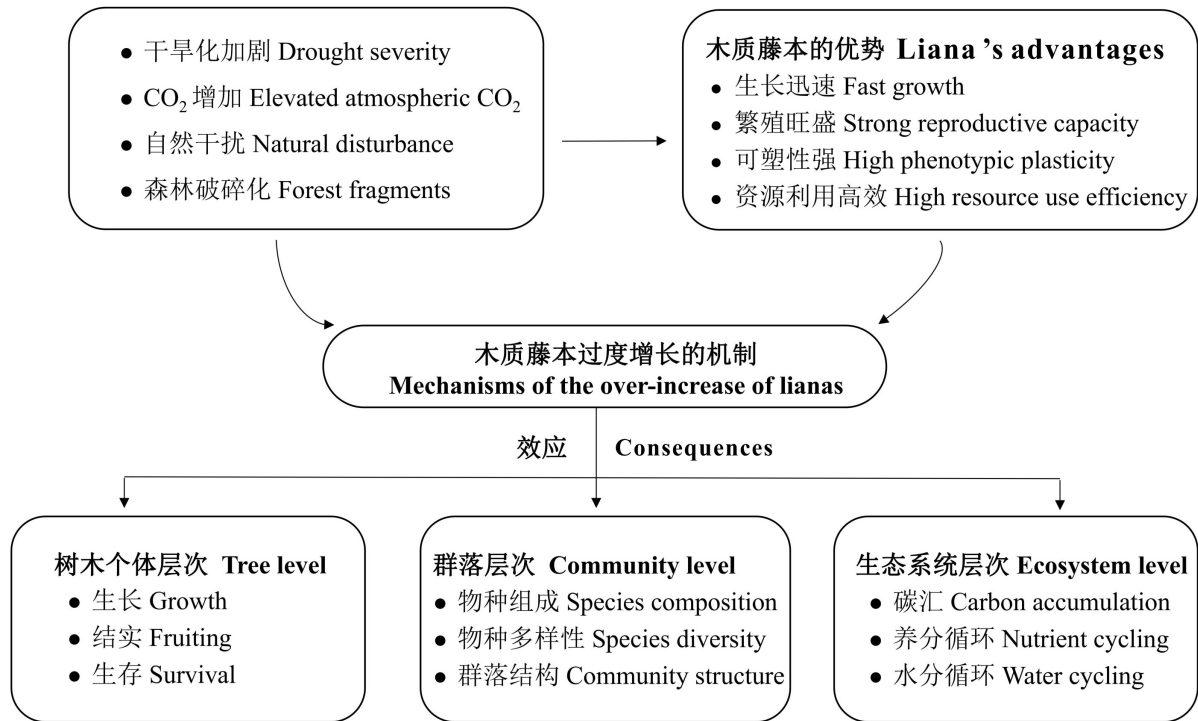


图 2 木质藤本过度增长的机制与生态效应

Fig. 2 Mechanisms and ecological consequences of the over-increase of lianas

树冠,大面积遮荫导致树木可获得光源减少,光合作用受阻,进而影响树木的生长和发育,严重时可能导致树木死亡(图 3)。木质藤本在林冠层形成的覆盖会增加林分郁闭度,从而阻碍林下幼苗更新。在巴拿马热带雨林,木质藤本对树冠的严重覆盖使树木死亡率增加了 100%(Ingwell et al., 2010);木质藤本使林窗内树木更新量下降了 46%(Schnitzer & Carson, 2010)。木质藤本叶的物候期更长,很多种甚至全年常绿(Putz & Windsor, 1987),常年的遮荫易使林下幼苗得不到充足的光照而死亡。

3.2 资源竞争

资源的争夺是木质藤本与树木的竞争方式,二者对光照、水分和养分等资源存在激烈的竞争(Meunier et al., 2021b)。在清除木质藤本后,树木的树干液流速率增加了 60%(Lemon et al., 2015)。在矿质养分与水分竞争中,藤与树的竞争甚至比树与树的竞争更加强烈。Tobin 等(2012)研究发现树木的树干液流速率在清除藤本后增加了约 8%,而对树木的清除并未做出响应。此外,木质藤本具有更高的资源吸收、运输和利用效率,对资源的争夺更具竞争力,木质藤本叶单位质量

碳同化速率、光能吸收和利用效果均高于树木(Cai et al., 2009; Asner & Martin, 2012),且木质藤本根系发达(Collins et al., 2016)。例如,当土壤养分增加时,木质藤本叶面积比和光合能力显著高于树木(Cai et al., 2008; Pasquini et al., 2015)。

3.3 机械压力与损伤

木质藤本攀爬会给树木带来机械压力与损伤(Vleut & Pérez-Salicrup, 2005)。木质藤本在树冠形成大面积覆盖,给树冠带来巨大的载重,使树梢或树枝极易折断,新梢不易萌生。一些木质藤本对树干的缠绕可导致树干扭曲、凹陷,增加树木折断和病虫害风险,影响树木水分和营养物质运输,最终导致树木死亡(图 3)。

4 木质藤本过度增长的生态效应

4.1 阻碍树木生长发育

从个体水平来看,木质藤本增长会从以下三个方面阻碍树木生长发育。(1)阻碍树木的正常生长。Finlayson 等(2022)研究表明木质藤本会使树木的生长量降低 156%;宋述灵(2019)发现



A. 钩藤在杉木树冠上的覆盖度高达 90%；B. 木质藤本对树木茎干的缠绕导致树木死亡。

A. Liana *Uncaria rhynchophylla* climbing up to the tree crowns of *Cunninghamia lanceolata* with a coverage up to 90%; B. Lianas causing tree death by twining tree stem.

图 3 木质藤本与树木的竞争方式

Fig. 3 Ways of lianas competing with trees

杉木被木质藤本攀爬后连年径向生长和胸断面面积生长分别降低 29% 和 40%。(2) 增加树木的死亡率。在亚马逊低地雨林, 大树被木质藤本攀爬后死亡率增加了 2 倍多 (Phillips et al., 2005)。(3) 降低树木的结实率和结实量。在热带雨林, 树木结实率与木质藤本的盖度成显著负相关 (Nabe-Nielsen et al., 2009), 木质藤本使坚果类树种果实产量下降了 200% (Kainer et al., 2014)。

木质藤本对幼苗和幼树的生长也会有负面影响。例如, 木质藤本会使树木幼苗的叶面积减少 5 倍 (Toledo-Aceves & Swaine, 2008); Martínez-Izquierdo 等 (2016) 将 14 种树木幼苗分别种于清除和未清除木质藤本的样地, 发现木质藤本使幼苗存活率和株高生长量分别降低了 75% 和 300%; Schnitzer 等 (2005) 将 3 个不同耐荫程度的幼树种植于木质藤本密集的低地雨林, 发现 2 a 后木质藤本使树木生物量分配格局和树形均发生变化。由此可见, 木质藤本对树木的影响贯穿了树木整个生活史。

4.2 改变群落组成与结构

从群落水平来看, 木质藤本过度增长会从以下两个方面改变群落组成与结构。(1) 改变群落物种组成。木质藤本对不同树种影响的差异性易使群落树种组成发生改变 (Visser et al., 2018; Reis et al., 2020)。例如, 在加纳热带常绿落叶混交林内木质藤本使先锋树种 *Nauclea diderichii* 和 *Khaya anthotheca* 的生物量分别下降了 32% 和 50%, 而对非先锋耐荫树种 *Garcinia kola* 并无影响 (Toledo-Aceves & Swaine, 2008)。(2) 阻碍群落更新、降低物种多样性和改变群落结构。木质藤本会降低群落树种的生殖力, 使树木开花结实的植株数、开花量和结果量显著下降 (García León et al., 2018); Schnitzer 和 Carson (2010) 发现木质藤本使林窗内树木的更新和多样性分别下降了 46% 和 65%。木质藤本对不同胸径树木影响的差异性也会导致群落结构发生变化 (Estrada-Villegas et al., 2020)。

4.3 影响生态系统功能

从生态系统层面来看, 木质藤本过度增长会

影响森林生态系统碳汇功能。在巴拿马热带雨林,由于受木质藤本的干扰,5 a 间树木生物量的增长量降低 22%,据模型预测,30 a 后树木生物量可降低 32%,60 a 后将达到 47% (Lai et al., 2017)。藤本清除实验验证了上述模型的合理性,在巴拿马 60 a 的热带雨林内,木质藤本使地上生物量的年净累积量下降了 76% (van der Heijden et al., 2015)。其他连续监测、模型预测辅助研究和木质藤本清除方式实验均得出相似结果 (di Porcia e Brugnara et al., 2019; van der Heijden et al., 2019; Estrada-Villegas et al., 2020; Meunier et al., 2021a)。虽然木质藤本生物量有所增长,但其增量远无法补偿树木生物量的损失量,对树木生物量损失量的弥补不足 30% (Schnitzer et al., 2016; Lai et al., 2017)。

木质藤本过度增长可改变森林生态系统水分动态。虽然木质藤本的胸断面积仅占热带森林的 5%,但叶蒸腾量占森林总量的 12% (Restom & Nepstad, 2001)。此外,木质藤本在水分吸收、运输和利用等过程比树木具有优势 (Andrade et al., 2005; Cai et al., 2009; Zhu & Cao, 2010; Chen et al., 2015)。木质藤本也会影响树木的水分平衡。例如,木质藤本使树木树干液流速率下降近一半 (Campanello et al., 2016)。

木质藤本过度增长亦能改变森林生态系统的矿质养分动态。较高的叶产量占比 (Schnitzer & Bongers, 2002; Kusumoto & Enoki, 2008) 和叶片性质与树木的差异 (Cai & Bongers, 2007) 能改变森林养分动态和土壤理化性质。热带森林木质藤本叶生物量占地上叶总生物量比值高达 36% (Tang et al., 2012),凋落物产量和叶面积占比均达到 40% (Schnitzer & Bongers, 2002; Tang et al., 2012)。木质藤本的养分含量 (如氮、磷) 显著高于树叶 (Asner & Martin, 2012)。因此,木质藤本的过度增长将可能加速森林叶凋落物的分解和养分释放、改变土壤的养分状态与呼吸速率、增加土壤养分异质性和养分流失的风险 (Putz, 1984; Kusumoto & Enoki, 2008; Liu et al., 2017)。

5 研究展望

虽然越来越多的学者参与到木质藤本对森林影响的研究,但是现阶段对木质藤本增长的机制和评价认识还有诸多不足,很多问题尚未解决。结合上述内容,本文认为今后研究可从以下方面开展。

5.1 重视森林动态监测样地木质藤本定位研究

长期定位监测研究是深入认识种群与森林群落特征变化的重要手段。总体上,木质藤本的定位监测研究起步较晚、研究区域有限、研究尺度较小。在森林动态监测样地网络中很多研究单位都未将木质藤本纳入监测体系 (Schnitzer & Bongers, 2011),现有主要研究地为中美洲和南美洲的巴西、巴拿马和墨西哥等地的热带雨林,非洲少量分布,其他洲较少参与,亚热带、温带森林关于木质藤本的研究十分缺乏 (Schnitzer et al., 2015)。因此,今后森林动态监测样地的相关研究应将木质藤本纳入其中,尤其是要增加亚洲、非洲的研究点,从全球尺度上认识解析木质藤本的分布格局、动态变化等问题。另外,鉴于木质藤本野外识别和数据采集难度较大,建议采用遥感信息技术开展相关研究 (Waite et al., 2019; Chandler et al., 2021)。

5.2 加强环境变化与木质藤本数量动态关系研究

现有研究从气候变化和干扰的角度对木质藤本的增长原因进行了初步探讨,但研究都较为分散、独立,环境变化导致木质藤本增长的发生机制尚不清楚。建议开展以下研究:(1) 各因子的单独和协同作用对木质藤本动态变化的影响研究,尤其是大时空尺度的大气 CO₂ 变化与木质藤本数量变化的关系研究 (Schnitzer & Bongers, 2011);(2) 森林干扰使木质藤本增长的发生机制研究,应将干扰状况、生态因子与木质藤本生物学、生理特性相结合分析木质藤本更新和多样性维持机制。同时,应加强不同森林干扰类型对木质藤本数量变化影响的比较研究;(3) 木质藤本对环境变化的响应研究,对变化环境的适应和调整是木质藤本是否具有竞争优势的关键,应从生理、行为、功能性状等方面探讨木质藤本对环境变化适应机理 (Liu et al., 2021),结合控制实验模拟多种环境因子 (如光照、CO₂、水分) 对木质藤本生长、生理及行为等特征的影响。

5.3 构建木质藤本过度增长的生态效应评价体系

评价木质藤本对森林的影响是制定管理政策的基础。木质藤本过度增长在个体、种群、群落和生态系统层面均具有一定的负面影响,而相关研究仍然存在不足,对一些领域的深入认识较为缺乏。(1) 大时空尺度研究较少。木质藤本的影响与森林类型、年龄等密切相关 (Lai et al., 2017; Estrada-Villegas et al., 2021),现有研究多位于热带森林,其他区域开展的相关研究不足且长周期的研究较为缺乏。今后应加强多区域、多种森林类型木质藤本的影响评价研究,从大时空尺度认识木质藤本如何

影响森林恢复。(2)对木质藤本增加的生态效应评价不够全面,主要集中在木质藤本对树木个体的影响,评价指标较为单一,多为树木胸径生长,而木质藤本对森林生物量、生态系统物质循环和生产力等方面的影响研究十分缺乏,建议借助模型构建木质藤本对生态系统的影响的全面认识(di Porcia e Brugnara et al., 2019; Meunier et al., 2022)。在我国南方诸多自然保护区次生林内,木质藤本过度增长严重阻碍着森林的恢复,建议开展木质藤本过度增长对自然保护区生态系统功能的潜在影响研究。(3)木质藤本与树木的关系研究通常将木质藤本和树木作为统一的整体,然而,不同树种受木质藤本的影响(Visser et al., 2018)、不同木质藤本对树木施加的压力都具有种间差异(Muller-Landau et al., 2018),因此难以准确量化出木质藤本对森林的影响。此外,树木被木质藤本干扰后的响应、环境变化如何影响木质藤本与树木的关系等方面的研究仍较为缺乏。(4)木质藤本与森林动物的相互关系缺乏关注。动物是森林生态系统的重要组成部分,虽然木质藤本是森林动物的重要食物来源(Odell et al., 2019),可增加动物的多样性(Schnitzer et al., 2020),但它对树木的负面影响会降低动物的食物来源从而影响动物群落(Adams et al., 2016; García León et al., 2018)。因此,木质藤本对动物净影响力有多大;木质藤本的增加分别对哪些种、哪些类型的动物有何影响;动物对木质藤本的取食又如何影响木质藤本数量变化,以及二者间的相互作用关系是否因森林类型、所处区域而具有差异。今后研究都需对这些问题进行系统、定量的评价(Schnitzer, 2018; Coverdale et al., 2021)。

5.4 综合木质藤本的保护和藤本过度增长的管控

木质藤本过度增长会造成诸多负面影响,而它们亦是森林物种多样性组成部分,并且部分还属于珍稀濒危物种,一些还具有一定的经济和观赏价值。由于有的木质藤本与树木具有互利共生的关系,因而在某些情况下这些木质藤本有助于森林的恢复。大型木质藤本的数量也是评价原始森林健康的指标。因此,今后应立足森林恢复和保护,开展木质藤本保护与管控权衡的研究。在生态环境良好的区域应对木质藤本加以保护,而受影响严重的森林应对木质藤本进行适当清除。然而,木质藤本管控的新技术探索将是一大挑战,当前对木质藤本管理方式呈一刀切的特点,费力耗时、成本高且成效低(Pérez-Salicrup et al., 2001)。在哪里清除、如何清除、如何评价

清除效应等问题都需深入研究,从而探索出合理的木质藤本管控方法,为森林管理和生态恢复等方面的宏观决策提供科学依据。

参考文献:

- ADAMS BJ, SCHNITZER SA, YANOVIK SP, 2016. Trees as islands: canopy ant species richness increases with the size of liana-free trees in a neotropical forest [J]. *Ecography*, 40(9): 1067–1075.
- ADAMS BJ, SCHNITZER SA, YANOVIK SP, 2019. Connectivity explains local ant community structure in a neotropical forest canopy: a large-scale experimental approach [J]. *Ecology*, 100(6): e02673.
- ADDO-FORDJOUR PL, AGYEI LA, OFOSU-BAMFO B, et al., 2021. Temporal dynamics of liana communities in moist semi-deciduous forest stands with different management histories in Ghana [J]. *For Ecol Manage*, 489: 119042.
- ANDRADE JL, MEINZER FC, GOLDSTEIN G, et al., 2005. Water uptake and transport in lianas and co-occurring trees of a seasonally dry tropical forest [J]. *Trees*, 19(3): 282–289.
- ASNER GP, MARTIN RE, 2012. Contrasting leaf chemical traits in tropical lianas and trees: implications for future forest composition [J]. *Ecol Lett*, 15(9): 1001–1007.
- BELOTE RT, WELTZIN JF, NORBY RJ, 2004. Response of an understory plant community to elevated [CO₂] depends on differential responses of dominant invasive species and is mediated by soil water availability [J]. *New Phytol*, 161(3): 827–835.
- BONGERS F, EWANGO CEN, VAN DER SANDE MT, et al., 2020. Liana species decline in Congo basin contrasts with global patterns [J]. *Ecology*, 101(5): e03004.
- CAI ZQ, BONGERS F, 2007. Contrasting nitrogen and phosphorus resorption efficiencies in trees and lianas from a tropical montane rain forest in Xishuangbanna, south-west China [J]. *J Trop Ecol*, 23(1): 115–118.
- CAI ZQ, POORTER L, HAN Q, et al., 2008. Effects of light and nutrients on seedlings of tropical *Bauhinia* lianas and trees [J]. *Tree Physiol*, 28(8): 1277–1285.
- CAI ZQ, SCHNITZER SA, BONGERS F, 2009. Seasonal differences in leaf-level physiology give lianas a competitive advantage over trees in a tropical seasonal forest [J]. *Oecologia*, 161(1): 25–33.
- CAMPBELL MJ, EDWARDS W, MAGRACH A, et al., 2018. Edge disturbance drives liana abundance increase and alteration of liana-host tree interactions in tropical forest fragments [J]. *Ecol Evol*, 8(8): 4237–4251.
- CHANDLER CJ, VAN DER HEIJDEN GMF, BOYD DS, et al., 2021. Remote sensing liana infestation in an aseasonal tropical forest: addressing mismatch in spatial units of analyses [J]. *Remote Sens Ecol Con*, 7(3): 397–410.
- CHEN YJ, CHEN JW, CAI ZQ, 2007. Lianas and their functions in tropical forests [J]. *Chin Bull Bot*, 24(2): 240–249. [陈亚军, 陈军文, 蔡志全, 2007. 木质藤本及其在热带森林中的生态学功能 [J]. 植物学通报,

- 24(2): 240–249.]
- CHEN YJ, CAO KF, SCHNITZER SA, et al., 2015. Water-use advantage for lianas over trees in tropical seasonal forests [J]. *New Phytol*, 205(1): 128–136.
- CHEN YJ, CHOAT B, STERCK F, et al., 2021. Hydraulic prediction of drought-induced plant dieback and top-kill depends on leaf habit and growth form [J]. *Ecol Lett*, 24(11): 2350–2363.
- COLLINS CG, WRIGHT SJ, WURZBURGER N, 2016. Root and leaf traits reflect distinct resource acquisition strategies in tropical lianas and trees [J]. *Oecologia*, 180(4): 1037–1047.
- COVERDALE TC, O'CONNELL RD, HUTCHINSON MC, et al., 2021. Large herbivores suppress liana infestation in an African savanna [J]. *Proc Natl Acad Sci USA*, 118(41): e2101676118.
- DE AZEVEDO AMORIM T, NUNES-FREITAS AF, ROSADO BHP, 2018. Revisiting the hypothesis for increasing liana abundance in seasonal forests: a theoretical review [J]. *Plant Soil*, 430(1): 1–6.
- DI PORCIA E, BRUGNERA M, MEUNIER F, LONGO M, et al., 2019. Modeling the impact of liana infestation on the demography and carbon cycle of tropical forests [J]. *Glob Change Biol*, 25(11): 3767–3780.
- ESTRADA-VILLEGAS S, HALL JS, VAN BREUGEL M, et al., 2020. Lianas reduce biomass accumulation in early successional tropical forests [J]. *Ecology*, 101(5): e02989.
- ESTRADA-VILLEGAS S, HALL JS, VAN BREUGEL M, et al., 2021. Lianas do not reduce tree biomass accumulation in young successional tropical dry forests [J]. *Oecologia*, 195(4): 1019–1029.
- FINLAYSON C, ROOPSIND A, GRISCOM BW, et al., 2022. Removing climbers more than doubles tree growth and biomass in degraded tropical forests [J]. *Ecol Evol*, 12(3): e8758.
- GARCÍA LEÓN MM, MARTÍNEZ IZQUIERDO L, MELLO FNA, et al., 2018. Lianas reduce community-level canopy tree reproduction in a Panamanian forest [J]. *J Ecol*, 106(2): 737–745.
- GRANADOS J, KORNER C, 2002. In deep shade, elevated CO₂ increases the vigor of tropical climbing plants [J]. *Glob Change Biol*, 8(11): 1109–1117.
- GUAN L, 1980. Damage of vines in forest plantations and of their control and management [J]. *J Jilin For Sci Technol*, (4): 120–121. [关列, 1980. 人工林受藤本植物的危害及其防治 [J]. *吉林林业科技*, (4): 120–121.]
- GOLDSTEIN G, SANTIAGO LS, 2016. Tropical tree physiology [M]// CAMPANELLO PI, MANZANÉ E, VILLAGRA M, et al. Carbon allocation and water relations of lianas versus trees. Switzerland: Springer; 103–124.
- HAO JH, TAO JP, ZHAO K, et al., 2011. The effects of lianas on community structure and regeneration of *Vatica astrotricha* plantations in Bawangling Nature Reserve, Hainan Province, China [J]. *J SW Univ (Nat Sci Ed)*, 33(2): 34–39. [郝建辉, 陶建平, 赵科, 等, 2011. 木质藤本对人工林群落结构及更新的影响 [J]. *西南大学学报(自然科学版)*, 33(2): 34–39.]
- HU L, LI MG, LI Z, 2010. Geographical and environmental gradients of lianas and vines in China [J]. *Global Ecol Biogeogr*, 19(4): 554–561.
- INGWELL LL, WRIGHT SJ, BECKLUND KK, et al., 2010. The impact of lianas on 10 years of tree growth and mortality on Barro Colorado Island, Panama [J]. *J Ecol*, 98(4): 879–887.
- JI MC, ZHENG G, YU SG, 2008. Resources and landscape application of wild vine in Longwangshan National Nature Reserve, Zhejiang Province [J]. *Sci Silv Sin*, 44(9): 165–169. [季梦成, 郑钢, 俞曙光, 2008. 浙江龙王山自然保护区藤本植物资源及园林应用 [J]. *林业科学*, 44(9): 165–169.]
- KAINER KA, WADT LHO, STAUDHAMMER CL, 2014. Testing a silvicultural recommendation: Brazil nut responses 10 years after liana cutting [J]. *J Appl Ecol*, 51(3): 655–663.
- KUSUMOTO B, ENOKI T, 2008. Contribution of a liana species, *Mucuna macrocarpa* Wall., to litterfall production and nitrogen input in a subtropical evergreen broad-leaved forest [J]. *J For Res*, 13(1): 35–42.
- LADWIG LM, MEINERS SJ, 2010. Spatiotemporal dynamics of lianas during 50 years of succession to temperate forest [J]. *Ecology*, 91(3): 671–680.
- LAI HR, HALL JS, TURNER BL, et al., 2017. Liana effects on biomass dynamics strengthen during secondary forest succession [J]. *Ecology*, 98(4): 1062–1070.
- LAURANCE WF, ANDRADE AS, AINHOA M, et al., 2014. Long-term changes in liana abundance and forest dynamics in undisturbed Amazonian forests [J]. *Ecology*, 95(6): 1604–1611.
- LEONOR AC, SCHNITZER SA, REID JP, et al., 2015. Liana competition with tropical trees varies seasonally but not with tree species identity [J]. *Ecology*, 96(1): 39–45.
- LIU Q, STERCK FJ, ZHANG JL, et al., 2021. Traits, strategies, and niches of liana species in a tropical seasonal rainforest [J]. *Oecologia*, 196(2): 499–514.
- LIU Y, ZHANG N, LUO J, et al., 2021. Chemical constituents of stems and leaves from *Uncaria rhynchophylla* in Guizhou and their antitumor activities [J]. *Guizhou*, 41(7): 1061–1069. [刘扬, 张妮, 罗俊, 等, 2021. 黔产钩藤茎、叶化学成分及抗肿瘤活性研究 [J]. *广西植物*, 41(7): 1061–1069.]
- LIU YC, SHANG Q, ZHANG B, et al., 2017. Effects of understory liana *Trachelospermum jasminoides* on distributions of litterfall and soil organic carbon in an oak forest in central China [J]. *Sustainability*, 9(6): 1019.
- LONDRÉ RA, SCHNITZER SA, 2006. The distribution of lianas and their change in abundance in temperate forests over the past 45 years [J]. *Ecology*, 87(12): 2973–2978.
- LU F, LI XK, WANG B, et al., 2021. Spatial pattern of lianas of *Litsea dilleniifolia* community and its relationship with main tree species in Nonggang, Guangxi [J]. *Acta Ecol Sin*, 41(15): 6191–6202. [陆芳, 李先琨, 王斌, 等, 2021. 广西弄岗五桠果叶木姜子群落木质藤本空间格局及其与树种间的关系 [J]. *生态学报*, 41(15): 6191–6202.]
- MAGNAGO LFS, MAGRACH A, BARLOW J, et al., 2017. Do fragment size and edge effects predict carbon stocks in trees and lianas in tropical forests? [J]. *Funct Ecol*, 31(2): 542–552.
- MARÉCHAUX I, BARTLETT MK, IRIBAR A, et al.,

2017. Stronger seasonal adjustment in leaf turgor loss point in lianas than trees in an Amazonian forest [J]. *Biol Lett*, 13(1): 20160819.
- MARSHALL AR, PLATTS PJ, CHAZDON RL, et al., 2020. Conceptualising the global forest response to liana proliferation [J]. *Front For Glob Change*, 3: 35.
- MARTÍNEZ-IZQUIERDO L, GARCÍA MM, POWERS JS, et al., 2016. Lianas suppress seedling growth and survival of 14 tree species in a Panamanian tropical forest [J]. *Ecology*, 97(1): 215–224.
- MEDINA-VEGA JA, BONGERS F, POORTER L, et al., 2021a. Lianas have more acquisitive traits than trees in a dry but not in a wet forest [J]. *J Ecol*, 109(6): 2367–2384.
- MEDINA-VEGA JA, BONGERS F, SCHNITZER SA, et al., 2021b. Lianas explore the forest canopy more effectively than trees under drier conditions [J]. *Funct Ecol*, 35(2): 318–329.
- MEUNIER F, VAN DER HEIJDEN GMF, SCHNITZER SA, et al., 2021a. Lianas significantly reduce aboveground and belowground carbon storage: a virtual removal experiment [J]. *Front For Glob Change*, 4: 663291.
- MEUNIER F, VERBEECK H, COWDERY B, et al., 2021b. Unraveling the relative role of light and water competition between lianas and trees in tropical forests: a vegetation model analysis [J]. *J Ecol*, 109(1): 519–540.
- MEUNIER F, VISSER MD, SHIKLOMANOV A, et al., 2022. Liana optical traits increase tropical forest albedo and reduce ecosystem productivity [J]. *Glob Change Biol*, 28(1): 227–244.
- MOHAN JE, ZISKA LH, SCHLESINGER WH, et al., 2006. Biomass and toxicity responses of poison ivy (*Toxicodendron radicans*) to elevated atmospheric CO₂ [J]. *Proc Natl Acad Sci USA*, 103(24): 9086–9089.
- MULLER-LANDAU HC, VISSER MD, GODOY O, 2018. How do lianas and vines influence competitive differences and niche differences among tree species? Concepts and a case study in a tropical forest [J]. *J Ecol*, 107(3): 1469–1481.
- NABE-NIELSEN J, KOLLMANN J, PEÑA-CLAROS M, 2009. Effects of liana load, tree diameter and distances between conspecifics on seed production in tropical timber trees [J]. *For Ecol Manage*, 257(3): 987–993.
- ODELL EH, STORK NE, KITCHING RL, 2019. Lianas as a food resource for herbivorous insects: a comparison with trees [J]. *Biol Rev*, 94(4): 1416–1429.
- PAROLARI AJ, PAUL K, GRIFFING A, et al., 2020. Liana abundance and diversity increase with rainfall seasonality along a precipitation gradient in Panama [J]. *Ecography*, 43(1): 25–33.
- PASQUINI SC, WRIGHT SJ, SANTIAGO LS, 2015. Lianas always outperform tree seedlings regardless of soil nutrients: results from a long-term fertilization experiment [J]. *Ecology*, 96(7): 1866–1876.
- PÉREZ-SALICRUP DR, CLAROS A, GUZMÁN R, et al., 2001. Cost and efficiency of cutting lianas in a lowland liana forest of Bolivia [J]. *Biotropica*, 33(2): 324–329.
- PERRING MP, DE FRENNE P, HERTZOG LR, et al., 2020. Increasing liana frequency in temperate European forest understories is driven by ivy [J]. *Front Ecol Evol*, 18(10): 550–557.
- PHILLIPS OL, VÁSQUEZ MARTÍNEZ R, ARROYO L, et al., 2002. Increasing dominance of large lianas in Amazonian forests [J]. *Nature*, 418(15): 770–774.
- PHILLIPS OL, VÁSQUEZ MARTÍNEZ R, MONTEAGUDO MENDOZA A, et al., 2005. Large lianas as hyperdynamic elements of the tropical forest canopy [J]. *Ecology*, 86(5): 1250–1258.
- PUTZ FE, 1984. The natural history of lianas on Barro Colorado Island, Panama [J]. *Ecology*, 65(6): 1713–1724.
- PUTZ FE, WINDSOR DM, 1987. Liana phenology on Barro Colorado Island, Panama [J]. *Biotropica*, 19(4): 334–341.
- REIS SM, MARIMON BS, MORANDI PS, et al., 2020. Causes and consequences of liana infestation in southern Amazonia [J]. *J Ecol*, 108(6): 2184–2197.
- RESTOM TG, NEPSTAD DC, 2001. Contribution of vines to the evapotranspiration of a secondary forest in eastern Amazonia [J]. *Plant Soil*, 236(2): 155–163.
- RESTOM TG, NEPSTAD DC, 2004. Seedling growth dynamics of a deeply rooting liana in a secondary forest in eastern Amazonia [J]. *For Ecol Manage*, 190(1): 109–118.
- ROCHA EX, SCHIETTI J, GEROLAMO CS, et al., 2020. Higher rates of liana regeneration after canopy fall drives species abundance patterns in central Amazonia [J]. *J Ecol*, 108(4): 1311–1321.
- ROEDER M, LIU JJ, PASION B, et al., 2019. Wood density, growth and mortality relationships of lianas on environmental gradients in fragmented forests of montane landscapes [J]. *J Veg Sci*, 30(6): 1143–1152.
- SCHNITZER SA, 2005. A mechanistic explanation for global patterns of liana abundance and distribution [J]. *Am Nat*, 166(2): 262–276.
- SCHNITZER SA, 2018. Testing ecological theory with lianas [J]. *New Phytol*, 220(2): 366–380.
- SCHNITZER SA, BONGERS F, 2002. The ecology of lianas and their role in forests [J]. *Trends Ecol Evol*, 17(5): 223–230.
- SCHNITZER SA, BONGERS F, 2011. Increasing liana abundance and biomass in tropical forests: emerging patterns and putative mechanisms [J]. *Ecol Lett*, 14(4): 397–406.
- SCHNITZER SA, BONGERS F, BURNHAM RJ, et al., 2015. Ecology of lianas [M]//DEWALT SJ, SCHNITZER SA, ALVES LF, et al. Biogeographical pattern of liana abundance and diversity. Oxford: Wiley-Blackwell: 132–143.
- SCHNITZER SA, CARSON WP, 2001. Treefall gaps and the maintenance of species diversity in a tropical forest [J]. *Ecology*, 82(4): 913–919.
- SCHNITZER SA, CARSON WP, 2010. Lianas suppress tree regeneration and diversity in treefall gaps [J]. *Ecol Lett*, 13(7): 849–857.
- SCHNITZER SA, DEFILIPPIS DM, VISSER M, et al., 2021. Local canopy disturbance as an explanation for long-term increases in liana abundance [J]. *Ecol Lett*, 24(12): 2635–2647.
- SCHNITZER SA, GEERTJE VDH, MASCARO J, et al., 2016. Lianas in gaps reduce carbon accumulation in a tropical forest [J]. *Ecology*, 95(11): 3008–3017.
- SCHNITZER SA, MICHEL NL, POWERS JS, et al., 2020.

- Lianas maintain insectivorous bird abundance and diversity in a neotropical forest [J]. *Ecology*, 101(12): e03176.
- SCHNITZER SA, KUZEE ME, BON GERS F, 2005. Disentangling above- and below-ground competition between lianas and trees in a tropical forest [J]. *J Ecol*, 93(6): 1115–1125.
- SCHNITZER SA, VAN DER HEIJDEN GMF, 2019. Lianas have a seasonal growth advantage over co-occurring trees [J]. *Ecology*, 100(5): e02655.
- SMITH-MARTIN CM, BASTOS CL, LOPEZ OR, et al., 2019. Effects of dry-season irrigation on leaf physiology and biomass allocation in tropical lianas and trees [J]. *Ecology*, 100(11): e02827.
- SMITH JR, QUEENBOROUGH SA, ALVIA P, et al., 2017. No strong evidence for increasing liana abundance in the Myristicaceae of anetropical aseasonal rain forest [J]. *Ecology*, 98(2): 456–466.
- SONG SL, 2019. Liana diversity and its effects on tree growth and community structure in Guanshan evergreen broad-leaved forest [D]. Nanchang: Jiangxi Agricultural University. [宋述灵, 2019. 官山大样地木质藤本对树木生长与群落结构的影响 [D]. 南昌: 江西农业大学.]
- SWAINE MD, GRACE J, 2007. Lianas may be favoured by low rainfall: evidence from Ghana [J]. *Plant Ecol*, 192(2): 271–276.
- TANG Y, KITCHING RL, CAO M, 2012. Lianas as structural parasites: a re-evaluation[J]. *Chin Sci Bull*, 57(4): 307–312.
- TOBIN MF, WRIGHT AJ, MANGAN SA, et al., 2012. Lianas have a greater competitive effect than trees of similar biomass on tropical canopy trees [J]. *Ecosphere*, 3(2): 1–11.
- TOLEDO-ACEVES T, SWAINE MD, 2008. Effect of lianas on tree regeneration in gaps and forest understorey in a tropical forest in Ghana [J]. *J Veg Sci*, 19(5): 717–728.
- UMAÑA MN, FORERO-MONTAÑA J, NYTCH CJ, et al., 2019. Dry conditions and disturbance promote liana seedling survival and abundance [J]. *Ecology*, 100(1): e02556.
- UMAÑA MN, MANZANÉ-PINZÓN E, COMITA LS, 2020. Long-term dynamics of liana seedlings suggest decelerating increases in liana relative abundance over time [J]. *J Ecol*, 108(2): 460–469.
- UWALAKA NO, MUOGHALU JI, 2017. Nine years of climber community dynamics in a Nigerian lowland rain forest 31 years after a ground fire [J]. *Biodivers Conserv*, 26(4): 997–1008.
- VAN DER HEIJDEN GMF, POWERS JS, SCHNITZER SA, 2015. Lianas reduce carbon accumulation and storage in tropical forests [J]. *Proc Natl Acad Sci USA*, 112(43): 13267–13271.
- VAN DER HEIJDEN GMF, POWERS JS, SCHNITZER SA, 2019. Effect of lianas on forest-level tree carbon accumulation does not differ between seasons: results from a liana removal experiment in Panama [J]. *J Ecol*, 107(4): 1890–1900.
- VAN DER HEIJDEN GMF, PROCTOR ADC, CALDERS K, et al., 2022. Making (remote) sense of lianas [J]. *J Ecol*, 110(3): 498–513.
- VAN DER SANDE MT, POORTER L, SCHNITZER SA, et al., 2019. The hydraulic efficiency-safety trade-off differs between lianas and trees [J]. *Ecology*, 100(5): e02666.
- VISSER MD, MULLER-LANDAU HC, SCHNITZER SA, et al., 2018. A host-parasite model explains variation in liana infestation among co-occurring tree species [J]. *J Ecol*, 106(6): 2435–2445.
- VLEUT I, PÉREZ-SALICRUP DR, 2005. Lianas and their supporting plants in the understorey at Los Tuxtlas, Mexico [J]. *J Trop Ecol*, 21(5): 577–580.
- WAITE CE, VAN DER HEIJDEN GMF, FIELD R, et al., 2019. A view from above: unmanned aerial vehicles (UAVs) provide a new tool for assessing liana infestation in tropical forest canopies [J]. *J Appl Ecol*, 56(4): 902–912.
- WANG YS, YANG XJ, CHEN LJ, et al., 2014. Biodiversity of wild woody vine resources in Yunshan, Hunan [J]. *Acta Bot Boreal-Occident Sin*, 34(3): 604–613. [王业社, 杨贤均, 陈立军, 等, 2014. 湖南云山野生木质藤本植物资源及多样性研究 [J]. 西北植物学报, 34(3): 604–613.]
- WANG ZW, ZHANG KM, WU N, et al., 2020. Effect of liana on the understory species richness in deciduous broadleaf forest of Jigong Mountain in Henan [J]. *J Yunnan Agric Univ (Nat Sci Ed)*, 35(3): 476–482. [王忠伟, 张科萌, 邹娜, 等, 2020. 河南鸡公山落叶阔叶林藤本植物对林下物种多样性的影响 [J]. 云南农业大学学报(自然科学版), 35(3): 476–482.]
- WANG BS, PENG SL, LI DJ, et al., 2009. Research progress on *Merremia boissiana* [J]. *Chin J Ecol*, 28(11): 2360–2365. [王伯荪, 彭少麟, 李代江, 等, 2009. 金钟藤研究述评 [J]. 生态学杂志, 28(11): 2360–2365.]
- WRIGHT SJ, CALDERÓN O, HERNANDÉZ A, et al., 2004. Are lianas increasing in importance in tropical forest? A 17-year record from Panama [J]. *Ecology*, 85(2): 484–489.
- WRIGHT SJ, SUN IF, PICKERING M, et al., 2016. Long-term changes in liana loads and tree dynamics in a Malaysian forest [J]. *Ecology*, 96(10): 2748–2757.
- YORKE SR, SCHNITZER SA, MASCARO J, et al., 2013. Increasing liana abundance and basal area in a tropical forest: the contribution of long-distance clonal colonization [J]. *Biotropica*, 45(3): 317–324.
- ZHANG ZY, ZHOU FX, XU GF, 2009. Application of liana in ecological restoration of side slope [J]. *Res Soil Water Conserv*, 16(3): 291–293. [张朝阳, 周凤霞, 许桂芳, 2009. 藤本植物在边坡生态恢复中的应用 [J]. 水土保持研究, 16(3): 291–293.]
- ZHU SD, CAO KF, 2009. Hydraulic properties and photosynthetic rates in co-occurring lianas and trees in a seasonal tropical rainforest in southwestern China [J]. *Plant Ecol*, 204(2): 295–304.
- ZHU SD, CAO KF, 2010. Contrasting cost-benefit strategy between lianas and trees in a tropical seasonal rain forest in southwestern China [J]. *Oecologia*, 163(3): 591–599.
- ZOTZ G, CUENI N, KOERNER C, 2006. *In situ* growth stimulation of a temperate zone liana (*Hedera helix*) in elevated CO₂ [J]. *Funct Ecol*, 20(5): 763–769.