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岩溶区植被与岩石地球化学背景间相互作用机制研究进展

朱帅[1,2], 曹建华[1*], 杨慧[1], 梁建宏[1], 劳昌玲[3]
(1. 中国地质科学院岩溶地质研究所, 广西 桂林 541004;
2. 国家地质实验测试中心, 北京 100037;
3. 桂林理工大学地球科学学院, 广西 桂林 541004)

摘要: 岩溶地貌主要是由碳酸盐溶解形成的特殊景观,岩溶区植被的生长发育受到基岩的制约,并演化出各种机制来适应岩溶区的独特环境。本文综述了岩溶地区植物对岩溶环境适应机制及植物生长对碳酸盐岩风化的驱动作用。通过总结发现:①植物主要通过分泌碳酸酐酶等有机物促进矿物分解、生物钻孔作用改善岩石表面的持水性能、根劈作用加速破碎岩石的崩解等化学生物和物理作用,促进了碳酸盐岩的风化溶解,形成独特的岩溶地球化学背景。②岩溶区植物通过调整自身结构和生理功能来适应干旱、高钙和营养元素缺乏等逆境。植物的抗旱性主要通过生理生化过程、形态结构和水分的利用方式来适应干旱或缺水环境,不同的植物进化出不同水分利用方式,提高水分利用效率,减少蒸腾;植物的高钙适应性是通过生理结构和生理过程来实现的,在高钙环境下的优势植物可通过形成钙化根、草酸钙含晶细胞和叶片调节等方式保持植株钙含量处于相对稳定的状态,并且植物还可以通过调节体内钙库和控制钙的吸收转运来控制细胞内钙离子浓度;根系分泌的有机酸和菌根能帮助植被在土壤中获取营养元素,以应对土壤的营养元素缺乏。③岩溶植被在正向演替过程中,土壤保水保肥能力增强、稳定性增加,物种的生存几率增加,物种多样性也随着增加。植被演化出的适应机制影响了植物的分布和生长,推进植物群落的演替过程和促进植物多样性的形成。但是多样性与群落生态系统的稳定性间的内在关系,以及与非岩溶区的对比特征仍需要开展深入的研究和探索。
关键词: 碳酸盐岩; 植被; 植物适应策略; 生物多样性; 演替

要点:

(1) 植物的岩溶作用、适应机制、演替特征和生物多样性是一个相互作用的整体。

(2) 植被的立地生长促进了碳酸盐岩的风化成土,植被的演替改变了土壤的理化性质,土壤的特性影响植物的生长和多样性。

(3) 植被演化出的适应机制影响植物的分布和生长,这种影响促进了植物群落的演替和多样性的形成。

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岩溶景观占世界陆地面积的 10%~15%[1],中国是世界上岩溶分布面积最为广泛的国家之一[2],大约有 344 万平方公里的岩溶地区,主要分布在西南地区[3],裸露的碳酸盐岩地区有 130 万平方公里[4]。在碳酸盐岩溶地区,离子含量明显高于硅酸盐地区,碳酸氢盐和钙占主导地位[5]。碳酸盐岩以化学溶蚀作用为主,在长期的风化、生物等作用下形成以石灰土为主的土壤[6]。岩石风化形成的土

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第一作者: 朱帅,硕士,助理研究员,主要从事岩溶区元素迁移研究。E-mail: zhu15131215153@126.com。
通信作者: 曹建华,博士,研究员,主要从事生物岩溶、岩溶生态系统、岩溶碳循环及碳汇效应研究。
E-mail: cjianhua@mail.cgs.gov.cn。

壤是支撑植被群落生长发育主要的物质基础,土壤的主量元素是硅、铝、铁,而碳酸盐岩的主量元素是碳、钙、镁,SiO_2 含量则仅为酸性土的 1/5~1/3。因此,岩溶环境中土壤资源先天不足,土层浅薄、土被不连续;同时,由于碳酸盐岩的可溶性,水文系统形成地表和地下双层空间结构,降雨通过竖井、落水洞、漏斗迅速汇入地下[7],地下水资源难以被利用,使得当地植物可利用的水资源有限,极易遭受干旱胁迫[8],尤其是在枯水期时,由于地表水系不发育,地下水深埋,导致地表植物遭受干旱胁迫[9]。由于碳酸盐岩的磷含量低,形成的岩溶土壤的磷含量往往较低,Ca^{2+} 进一步降低了磷的生物有效性[10],并且土壤总磷含量随着次生演替而下降[11],可见富钙的岩溶地球化学背景,不仅制约着养分元素的迁移,更制约着岩溶区植被群落的生长发育,可以认为岩溶环境中物质能量迁移“携带”着碳酸盐岩岩石地球化学的“烙印”[9]。

植被退化可能导致一系列环境问题,如水土流失、洪水、石漠化等[9,12-13]。中国南方岩溶区是国家石漠化综合治理工程的主战场,植被群落的保护修复是重要的目标和任务,深入认识岩溶区植被新陈代谢与碳酸盐岩岩石地球化学过程间的相互协同作用,对脆弱岩溶区植被仿自然修复和抚育具有十分重要的意义。本文从植被群落对碳酸盐岩风化的促进作用、碳酸盐岩风化形成岩石地球化学背景对植被的制约两方面,阐述岩溶区植被与岩石地球化学背景间相互作用机制与规律。

1 植被群落对碳酸盐岩风化的促进作用

陆地碳酸盐化学风化作用即岩溶作用[14],植物的岩溶作用很早就被研究学者所关注,早在 1973 年 Folk 等提出了“植物岩溶(Phytokarst)”的概念[15]。植物对碳酸盐岩风化的促进机制可表现为三个方面:①分泌碳酸酐酶(CA)促进 CO_2 溶解于水形成碳酸,提高 CO_2 对碳酸盐岩的化学溶解效应[16];②生物钻孔使得碳酸盐岩浅表层(1~10mm)形成疏松多孔层,增加了岩石表面的持水性能,延长水-岩相互作用时间;③通过植物根系机械作用,崩解碳酸盐岩,提高岩石表面积,促进岩石风化溶解。

碳酸酐酶等有机物可促进碳酸盐岩风化溶解[17]。碳酸酐酶是普遍存在于自然界中的一种酶,可以催化 CO_2+H_2O 的反应,也可以催化碳酸氢根(HCO_3^-)和二氧化碳间相互转化[18]。CA 对碳酸盐岩的溶解具有驱动作用,通过催化形成矿化所需的反应性前体(即 HCO_3^- 和 CO_3^{2-} 离子),加速亚稳态无定形碳酸钙的沉淀[19]。Xie 等[20]的研究发现未加入碳酸酐酶抑制剂的石灰石中 Mg^{2+} 的释放单位生物量,是加入 CA 抑制剂的石灰石中 Mg^{2+} 的释放单位生物量的 2 倍。也有学者认为 CA 可能是影响自然岩溶系统 Ca^{2+} 释放和淋溶的主要因素[21]。不同岩溶生态系统土壤中的 CA 活性具有明显差异:植被覆盖率低的土壤,CA 的活性最低,而植被种类丰富且生长较好的土壤,CA 的活性较高[22]。然而,关于植物生物有机物和 CA 的研究,主要集中在有机酸和 CA 含量对岩石溶蚀过程的促进作用方面,对植物中 CA 分泌量、分泌速率和 CA 活性对溶蚀速率的影响不甚清楚。

植物立地生长提高了表面持水性,覆盖在碳酸盐岩表面的苔藓、藻类和地衣等低等植物在碳酸盐岩表面的殖居,以及对浅表层的改造,被认为对高等植物的萌发和生长起到先锋作用。已有研究报道了低等生物在岩面的殖居形成的生物钻孔,使得浅表层呈现 1~10mm 的疏松多孔层,改善了岩石表面的持水性能[23]。地衣覆盖的碳酸盐岩样品的侵蚀速率提高了 26%~64%[24]。藻类分泌的胶壳、地衣分泌的地衣酸和苔藓等植物能够分泌有机酸,及当植物死亡时,有机物被降解,产生具侵蚀性的酸性物质和螯合物质,不仅对周围碳酸盐岩产生侵蚀作用,同时也在碳酸盐岩表面形成了一层有机物质,对高等植物种子萌发提供养分和水分条件,并最终形成土壤[25]。

与非岩溶区植被相比,岩溶区的木质藤本、灌木和乔木等能够直接扎根在碳酸盐岩裂隙中,通过根劈作用提高碳酸盐岩风化速率,同时根系分泌酸性物质会破坏岩石结构、增加表面积,从岩石中获得必需的矿质营养元素,有根植物相比无根植物更能提高单位面积的风化率[26]。植物枯枝落叶不仅是土壤有机质形成、团聚体的改善、质量提升的主要途径,同时枯枝落叶微生物降解的土壤呼吸和根系的呼吸,提高了土壤 CO_2 的浓度,促进土壤下面碳酸盐岩的风化溶解。如广西弄岗森林岩溶区内溶蚀速度变化幅度为 9.19~15.15mg/100d,在树木覆盖较稀疏的山顶,则为 8.22~29.97mg/100d,两者相差 3.65 倍[27]。

植物生长发育对碳酸盐岩风化溶解的促进,已经取得较多的认识,但仍存在进一步深化的方面:碳酸盐岩风化同时需要 CO_2 和 H_2O 的作用,植物的生长发育也需要 CO_2 和 H_2O,不同植被群落的蒸腾强

度存在较大的差异。换言之，就是植被一方面供给大量的 CO_2 源，另一方面，提供蒸腾散失，减少水分下渗，最终碳酸盐岩风化强度的效果还需要深入的研究和定量数据支撑。

2　碳酸盐岩地球化学背景对植被发育制约及适应特征

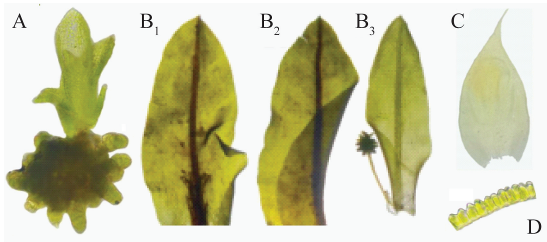
土壤是植物生长的主要基质，相对于非碳酸盐岩分布区而言，碳酸盐岩岩石风化形成的石灰土，具有成土速率慢、土层薄且零散、空间异质性、富钙、偏碱、营养元素有效态低等特征[28]。因此，特殊的碳酸盐岩岩石地球化学背景制约着植物的发育，植物也演化出系列适应特征[29-30]。

2.1　植物对干旱胁迫的响应和适应特征

岩溶生境浅薄的土壤和快速的地下排水等形成岩溶干旱环境，引起水分胁迫在岩溶区森林要比非岩溶区森林严重[31]。在干燥的气候条件下，水分不足限制了植被覆盖率，降低植物的光合作用[32]。在全球范围内，降水是影响岩溶植被分布的最主要因素[33]。研究表明，岩溶区物种呈现出应对季节性干旱的两类机制。

第一类，植物根据自身可获取的水资源调整自身结构和生理功能。植株在干旱条件下往往表现出明显的气孔调控，气孔的关闭能最大限度地减少植物的蒸腾失水，以维持木质部较高的水势[34]。不同植物之间，存在着形式和程度上的差别，即使同一种植物也因生态环境的变化而有所差异，山顶青冈栎下表皮毛比山腰青冈栎的浓密且长，山顶青冈栎的叶片比较弯曲，山腰的叶片则比较平整，位于山顶的青冈栎受到水分的胁迫，在形态解剖上呈现出中生偏旱的结构[35]。岩溶区与非岩溶区檵木叶片在宽度和厚度、气孔分布频率、上表皮细胞大小和栅栏组织厚度等方面存在显著差异，岩溶区檵木叶片呈现出旱生结构特征[36]。如图 1 所示，岩溶石漠化地区的苔藓叶片有明显的凹陷，叶片呈卵圆形，有利于储水；叶色多为灰绿色、黄绿色或黄棕色，茎顶端为淡绿色，能反射较多的光，降低叶温，减少水分流失；叶皮表面的疣状物有助于反射阳光和减少蒸腾作用[25]。

一些岩溶植物还可以通过植物化学物质增加抗氧化酶的活性和积累渗透调节物质来减少干旱胁迫造成的损害[37]。在岩溶地貌条件下的药材散光通与对照组相比，干旱胁迫下叶片的过氧化物酶活性和 SOD 活性几乎翻倍，脯氨酸和可溶性糖含量提高 2 倍，表明散光通可以通过调节物质积累和酶活性



A—苔藓幼苗；$B_1 \sim B_3$—苔藓叶片；C—叶片的凹陷；D—叶横切面，细胞表面显示疣状结构。

图 1　岩溶地区苔藓叶片形态[25]

Fig. 1　Leaf morphology of bryophytes in karst area.
A—Showing a young plant; B1-B3—Leaves; C—Obviously concaved leaf to reserve more water; D—Portion of leaf transeverse section showing mamilla on cell surface.

以及分析转录组变化来提高其适应岩溶干旱环境的能力[38]。岩溶区苔藓通过积累游离脯氨酸来增加细胞内溶质浓度，减少水分以适应干旱胁迫。细胞内各种抗氧化酶的活性提高，消除活性氧对苔藓细胞膜的破坏，保护细胞膜结构的完整性，抵御干旱胁迫[25]。可通过 Ca^{2+}-脱落酸(ABA)途径和 H^+-ATP 酶活性调控对水分的吸收和利用，可溶性糖可作为渗透溶质适应水分亏缺[39]。

第二类，改变植物利用水的策略。中国云南南部的热带岩溶区森林中的木本植物在旱季充分利用日温差带来的雾水，藤本植物(41.3%)比树木(21.4%)所使用的雾水更多[40]；岩溶区植物在旱季，在降低植物蒸腾的同时，在碳酸酐酶酶促下，充分利用岩溶水体中 HCO_3^- 转化为 CO_2，以适应干旱胁迫[41]。根据植物木质部水分同位素组成在生长季存在季节性波动，反映了植物水源的季节性变化[42]，一些植被在雨季使用表层水，在旱季植物木质部水 $\delta^{18}O$ 值始终表现出较低且稳定，意味着植物吸收利用了较深的基岩水或地下水[34,43]。生长于岩溶裂隙生境中的凤仙花在雨季以土壤水、表层岩溶水和浅层岩溶裂隙水为主，旱季主要用水是深部土壤水和浅层岩溶裂隙水[44]。

2.2　植物对岩溶区高钙环境的响应和适应特征

高钙(Ca)是岩溶地区显著的生态地质特征。在高钙胁迫下，大量 Ca^{2+} 的吸收降低了质膜 H^+-ATP 酶的活性，从而抑制了 H^+的外流，最终导致植物气孔关闭，光合作用和蒸腾作用下降[45]。植物 Ca^{2+} 摄入过多，还会造成细胞壁硬化、细胞生长抑制、能量代谢紊乱等，富钙土壤已成为影响岩溶区植物生理特征和分

布环境因素。植物可以将过量的钙转移到其他部位、优先储存机制来适应富钙环境(图 2)[46]。

在植物生理结构方面,在高钙环境下的优势植物可形成钙化根,钙化根还可将过量的钙固定在根际周围,限制其地上部运输,形成特有的解毒机制。植物细胞中的草酸钙晶体也在调节植物钙含量中发挥作用,一些植物会形成草酸钙晶体细胞,以固定过剩的 Ca^{2+}。此外,植物可通过叶片调节土壤中高钙离子得以生长。例如,植物中过量的 Ca^{2+} 通过叶片背面的气孔排出,维持叶片较低浓度的 Ca[47]。旋蒴苣苔是通过将根部过量的钙转运到海绵细胞和栅栏细胞中而在钙浓度较高的环境中存活的[48]。不同植物在钙的吸收、运输和储存等生理过程上存在差异,这些差异导致了植物对高钙环境的适应程度不同。忍冬属植物为缓解钙离子在体内过多积累而造成伤害,则通过 ATP 酶将钙离子运出细胞外,并以腺体的形式贮存起来[49]。不同科、属苔藓植物的钙含量存在显著差异,藓类植物适应高钙环境的策略可分为 3 种:①随机,即植物钙含量随土壤钙含量变化而变化,对植物生长影响不显著;②高钙,即在不同土壤钙水平下,植物钙含量均保持较高水平;③低钙,即在不同土壤钙水平下,植株钙含量均较低[50]。

在生理过程中,植物通过调节体内钙库和控制钙的吸收转运来控制细胞内钙离子浓度。植物细胞中存在良好的调节机制,该机制不仅可以迅速地增加细胞质的游离 Ca^{2+} 浓度以适应环境变化,而且还可以保持低钙浓度以防止高钙伤害[51]。有机酸(OA)在维持 Ca 浓度上占据主导地位,岩溶生境和非岩溶生境中 OA 的作用都是将叶片 Ca 维持在中等水平。生长在岩溶栖息地的植物叶片中钙含量较高时会在叶子中积累 OA,以维持平衡并减少过量 Ca 对植物生长的伤害;生长在非岩溶栖息地的植物需要通过增加叶子中的 OA 来增强 Ca 的含量以维持正常的生理功能[52]。在高钙环境下,岩溶地区的先锋植物卷柏根系分泌 OA 质量分数相对降低,但能保持在一个稳定范围内,是根系分泌 OA 对高钙环境的适应机制[53]。此外,不同的植物利用不同的内生真菌适应岩溶区高钙环境[54]。

2.3　植物对岩溶区易利用营养元素缺乏的响应和适应特征

植物获得生长发育的能量主要通过光合作用,而生长快慢、质量高低,受制于水分和养分。植物最主要的养分是 N、P、K,岩溶区植被演化初期主要受 N 制约,而后期主要受 P 制约。在岩溶区退化草地的生产力主要受 N、P 限制,K 次之[55];岩溶区森林和非岩溶区森林都受到磷的限制,但非岩溶区森林磷缺乏比岩溶区森林更为明显[56]。

植物根系分泌有机酸和丛枝菌根协同作用

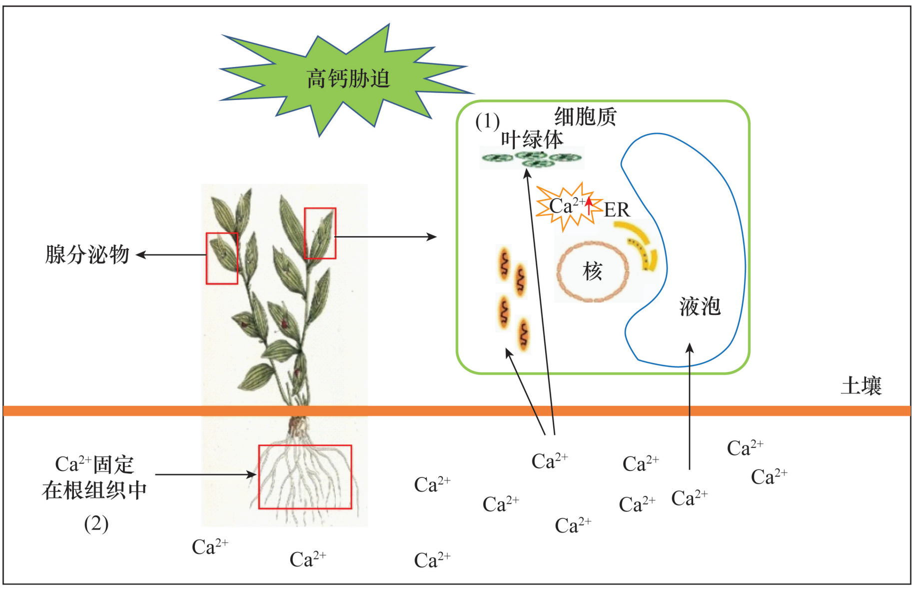


图 2　岩溶植物在高钙环境中的适应机制[46]

Fig. 2　Adaptation mechanism of karst plants under high calcium stress. Under high calcium stress, karst plants can regulate excessive calcium in two ways: (1) Absorbing excessive calcium through organelles in plants (mitochondria, chloroplasts, vacuoles, etc.); (2) Transferring excess calcium to other parts of plant, such as the cell wall, stoma, gland, epidermal hair, root, etc. Therefore, plants can adapt well to the high calcium environment.

是植物应对营养元素缺乏一种适应性机制。有机酸对植物的生长及对生存环境的适应有很大的影响,土壤微生物和植物根系可以通过分泌胞外酶来催化土壤有机质(SOM)的矿化,并通过产生 H^+和低分子量有机酸来释放束缚 P,促进植物从土壤中获取营养元素,以应对土壤的营养元素缺乏[57]。岩溶植物根系分泌有机酸含量通常高于非岩溶植物,有机酸含量升高有助于植物对微量元素 Fe、Mn、Cu 和 Zn 等元素的吸收[58]。丛枝菌根真菌(AM)和外生菌根(ECM)能够帮助植物从土壤中吸收矿质养分,来适应营养元素缺乏环境[59]。AM 真菌通过增加鬼针草干重、长度、表面积等的根系发育促进 N、P 和 K 的获取和养分吸收[60]。岩溶乔木、灌木共生的 AM,对根际土壤 N、P 的来源效率要高于 ECM[61]。亚热带岩溶区原生森林植物菌根根际土壤与相邻的土壤相比,根际土壤的养分活性均有所增强(图 3)[62],AM、ECM 分泌的生物酶使得植物能更多地获取氮酶,而 AM 分泌磷酸酶将磷从磷酸钙化合物中的活化效率更大。因此,植物通过调节根-菌根相互作用来适应岩溶生态系统养分贫乏的困境[63]。

3 岩石地球化学背景下岩溶植被演替特征

岩溶区植物演化出各种机制适应岩溶环境的同时,还会通过植被演替过程适应岩溶环境。演替通过生物和非生物环境调节物种的丰富度[64]。随着植物演替,非生物条件逐渐改善环境因素可以作为"筛",选择适合在群落中生存和维持的物种或性状,因此植物群落组配的过程随演替而变化[65]。岩溶植被的生长受到地质背景的限制,对岩溶地区生态系统的形成和演化具有重要的制约作用。在区域尺度上,气候、母质、植物区系决定了植被类型,它们之间的协同作用形成了不同的植被演替和分布格局[66]。有研究证实岩溶地区的森林受到土壤肥力的显著影响[67]。李亚锦等[65]的研究证实土壤含水量、全氮含量、容重和有机质是影响岩溶植物演替过程中功能性状变化的关键环境因子。

虽然岩溶区植被的演替,与常态地貌上植被演替

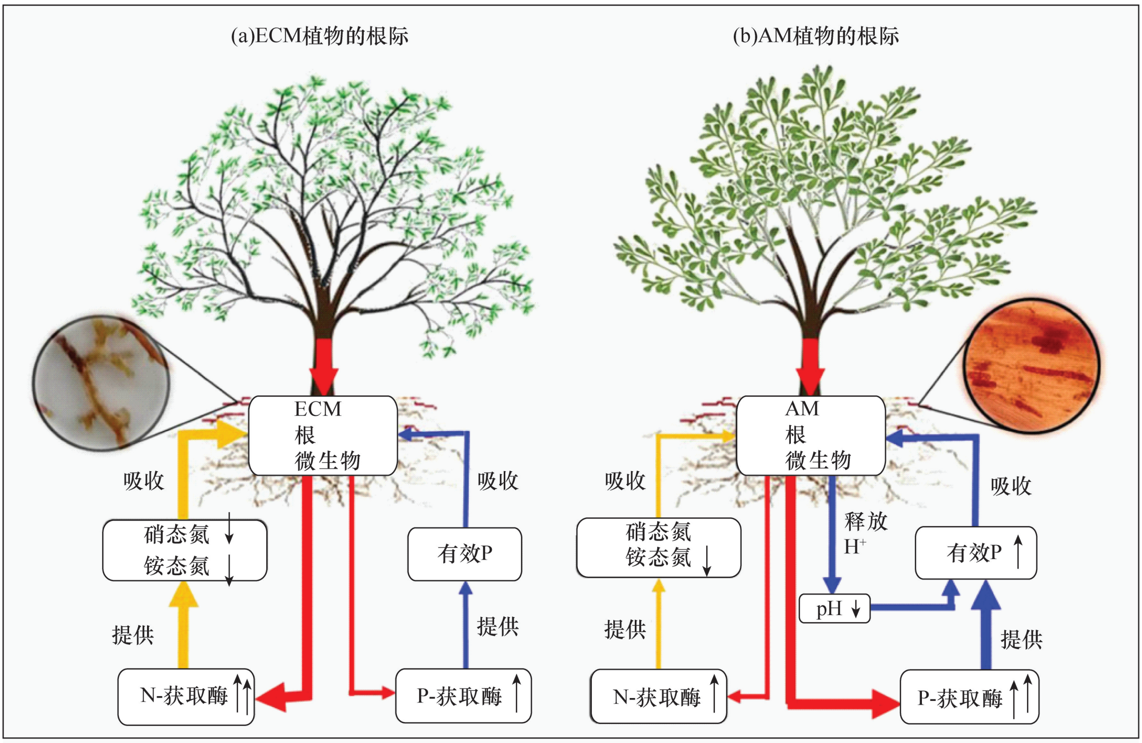


图 3 AM 和 ECM 型植被根系影响根际土壤养分转运吸收的示意图[62]

Fig. 3 Schematic diagram of AM and ECM plant roots affecting nutrient transport and absorption in rhizosphere soil. Ectomycorrhizal associations may invest more C in the production of N-acquisition enzymes to adapt to lower N availability and greater N acquisition capacity (relative to AM plants) in the rhizospheres. Arbuscular mycorrhizalassociations may increase rhizosphere soil P availability (relative to bulk soils) by allocating more C to produce P-acquisition enzymes that mineralizing organic P, and by secreting acidic compounds that liberate P from calcium compounds.

的一般阶段相似,但是岩溶植被演替具有自生的特殊性。一般而言,在山地中下部,土层相对较厚(30~50cm),水肥条件相对较好,植被演替的过程所需时间较短。在山地中上部,各阶段所需的时间相应延长,大约需 10 年时间才有乔木植物的幼苗入侵定居;尤其在山顶,由于土层薄、湿度小、岩石裸露面积大,植被的形成需要相当长的时期,并且在原生性植被破坏之后,恢复到原生状态几乎不可能,所以现存的岩溶山顶部森林较少,多为藤刺灌丛[68]。

植被演替过程会影响土壤性质和土壤质量。首先,植被演替过程中土壤的物理性状明显改善,如在贵州省普定县岩溶植被自然恢复演替过程中,随着时间的推移,土壤容重逐渐降低,孔隙度逐渐上升[69]。其次,土壤养分随着植被正向演替的进行而积累[70]。植被类型对土壤有机碳(SOC)有显著影响[71]。植被演替过程中土壤微生物群落的变化既促进了菌根的形成和矿质养分的吸收,还帮助改善土壤性质[72]。桂西北岩溶土壤微生物生物量碳(SMBC)、微生物生物量氮(SMBN)也随着草地、灌丛、次生林、原生林演替而呈逐渐增加趋势,土壤有机碳、全氮、全钾、速效氮、速效磷和速效钾含量随着演替也呈逐渐增加趋势[73]。Song 等[74]的研究也证实了相似的结果:在植被演替过程中,土壤有机碳和全氮含量同步增加,同时还发现土壤 C/P 和 N/P 比率增加,而 C/N 比率几乎保持不变,SMBC 和 SMBN 浓度升高。再次,随着演替的进行,土壤质量得到了改善。贵州省普定县典型岩溶区植被演替的研究证实植被演替与土壤质量密切相关,研究发现从农田到次生林的植被演替阶段土壤质量呈上升趋势,并且发现植被类型对土壤质量指数(SQI)的影响最大[67]。次生林演替可以导致土壤养分和碳循环功能的相对快速恢复[75]。Yan 等[76]通过土壤质量指标评估次生演替过程中地表和浅层岩溶裂隙(SKF)土壤的土壤质量,结果表明经过二次演替,表层土壤和 SKF 土壤的土壤特性和土壤质量得到了显著改善。最后,植被改善可促进岩溶作用,促进成土。植被的正向演替对土层较深处的岩石溶蚀更有利,在演替初期,上层(-20cm 处)的溶蚀率高于下层(-50cm 处),而在演替后期则相反[77]。

4 岩石地球化学作用下岩溶区植物多样性特征

物种多样性不仅可以反映群落中物种的丰富度与均匀度,也能直接或间接地体现植物群落的生境状况和演替规律。岩溶区特殊的岩石地球化学背景,导致其土壤资源的空间分布变化明显。高度土壤异质性为植物多样化和物种形成提供了大量的生态位,促使植物群落的物种多样性的形成[78]。

云南西双版纳热带岩溶区面积 3600km^2,占土地面积的 19%,海拔 600~1600m,岩溶区森林调查结果显示,拥有维管束植物 153 科、640 属、1394 种,分别占区系总科数的 77.7%、属数的 56.1%和种数的 37.9%[79]。广西岩溶区面积 8.21 万 km^2,占土地面积的 34.8%,早期的调查揭示广西岩溶植被区由 175 科、662 属、1500 种组成[80];其后对广西弄岗北热带岩溶森林区面积 100km^2 的深入调查显示拥有维管束植被 184 科、810 属、1752 种[81]。贵州岩溶区面积 11.61 万 km^2,占土地面积的 61.2%,已有调查结果显示贵州共有维管束植物 250 科、1551 属、5691 种[82]。宽阔水国家级自然保护区是黔北喀斯特地貌物种多样性最丰富的地区之一,总面积 26231hm^2,共有草本植物 58 科、183 属、277 种[83],分别占贵州省植物区系的 23.2%、12.0%、4.87%。

物种多样性的变化格局与演替阶段密切相关。许多研究证实,物种多样性并非随着演替的不断深入而增大,而是从草丛阶段开始,物种多样性不断增加,至亚顶极阶段达到最大值,到达顶极阶段时物种多样性却有一定下降。例如,在桂西南岩溶植被演替的不同阶段,物种多样性表现为:灌木层>草本层和灌木层>乔木层,其灌木层的物种多样性是最大的[84]。王万海等[85]的研究发现岩溶森林样地内各个垂直层次的被子植物乔木层的种和属数量,包括独有种和属数量,均高于灌木层和草本层,与植被正向演替相关。

5 结语与展望

岩溶植物群落是栖息在岩溶地貌上特殊自然环境中,植物与环境经过漫长的相互作用,不断地适应环境并生长繁殖的结果。植物的岩溶作用、植物在干旱、高钙胁迫和营养元素缺乏等典型岩溶土壤环境下的适应机制以及在适应过程中表现出来的岩溶植被演替特征和植被的生物多样性是一个相互作用的整体,植被的立地生长促进碳酸盐岩风化,促使其成土,为自身的生长创造条件,同时土壤面积和土壤厚度与植物多样性呈正相关[86]。植被的演替改变了土壤的理化性质,提高了土壤质量,碳酸盐岩的岩溶作用又促进了植被的生长。

同时,植被演化出的适应机制影响了植物的分

布和生长,这种影响可能对植物群落的聚集产生影响,推进植物群落的演替过程和促进植物多样性的形成[87],这对维持岩溶生态系统结构和功能的稳定性极为重要。岩溶环境的空间异质性、植物生境的多样性,导致岩溶区植物多样性表现为少属科、寡种属和特有种,但其多样性与群落生态系统的稳定性之间的内在关系,以及与非岩溶区的对比特征仍需要开展深入的研究和探索。

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A Review of the Interaction Mechanism and Law between Vegetation and Rock Geochemical Background in Karst Areas

ZHU Shuai[1,2], *CAO Jianhua*[1*], *YANG Hui*[1], *LIANG Jianhong*[1], *LAO Changling*[3]

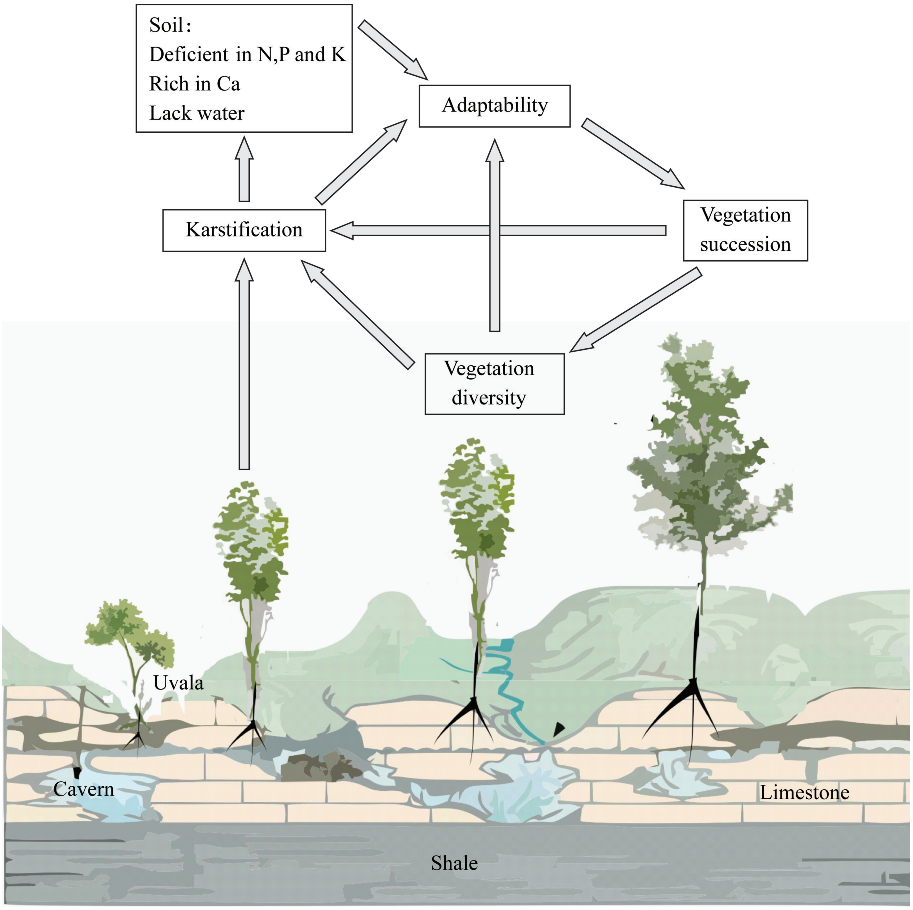
(1. Institute of Karst Geology, Chinese Academy of Geological Sciences, Guilin 541004, China;
2. Key Laboratory of Eco-Geochemistry, Ministry of Natural Resources, National Research Center for Geoanalysis, Beijing 100037, China;
3. College of Earth Science, Guilin University of Technology, Guilin 541004, China)

HIGHLIGHTS

(1) The four aspects of karstification, plant adaptation mechanisms, karst vegetation succession characteristics shown in the adaptation process, and vegetation biodiversity formed in the adaptation and succession process are an interactive whole.

(2) The vegetation promotes the dissolution and weathering of carbonate rocks, the succession of vegetation changes the physical and chemical properties of soil and improves the soil quality, and the karst of carbonate rocks promotes the growth of vegetation and the formation of species diversity.

(3) The adaptive mechanism evolved by vegetation affects the distribution and growth of plants, which promotes the succession and diversity of plant communities.



ABSTRACT: Karst landforms are mainly special landscapes formed by carbonate dissolution. They are characterized by calcium abundance, lack of soil resources, and insufficient water resources. The growth and development of vegetation in the karst area is restricted by the bedrock. It is very important to understand the synergistic interaction between vegetation metabolism and geochemistry of carbonate rocks in karst areas to maintain the stability of structure and function of the karst ecosystem.

The mechanism and law of interaction between vegetation and rock geochemical background in karst areas from two aspects is expounded in this paper: vegetation community promotes weathering of carbonate rocks and geochemical background restricts vegetation.

Through summarizing: (1) Plants promote the weathering and dissolution of carbonate rocks through physicochemical and biological actions, such as secreting carbonic anhydrase organic matter, improving the water retention performance of rock surface through boring by organisms and accelerating the disintegration of broken rocks through root splitting, thus forming a unique karst geochemical background of drought, high calcium, shallow soil layer and lack of nutrients in the soil layer.

(2) With the long-term interaction between plants and the karst environment, plants adapt to environmental stress by adjusting their own structures and physiological functions, and even their unique plant succession rules. The plants that survived eventually evolved into unique karst plants that were drought-resistant, adaptable to high-calcium environments, and able to cope with nutrient deficiencies.

Due to the solubility of carbonate rocks, the hydrologic system forms a two-layer spatial structure of surface and underground, which makes it difficult to utilize groundwater resources. As a result, the available water resources of local plants are limited, and are prone to drought stress. The drought resistance of plants adapts to the drought or water shortage environment mainly through physiological and biochemical processes, morphological structure and water use. In the morphological structure of the plant, through the stomatal regulation and the xeric

structural characteristics of the leaves, the transpiration water loss of the plant is minimized. Some karst plants can cope with drought stress through physiological and biochemical processes, which can reduce the damage caused by drought stress by increasing the activities of antioxidant enzymes and accumulating osmoregulatory substances through phytochemicals. Karst plants improve water use efficiency and reduce transpiration through different water use methods in the dry season. For example, some plants absorb deep soil, deep bedrock water or groundwater water through developed deep roots, and some plants even use fog water.

The adaptability of plants to high calcium is realized through physiological structure and process. In a high calcium environment, karst plants can limit the excess calcium transfer upward by forming calcified roots and keeping the calcium content in plants in a relatively stable state through the regulation of calcium oxalate crystal cells and leaves. Plants can also control the intracellular calcium ion concentration by regulating the calcium pool *in vivo* and controlling the absorption and transport of calcium.

Organic acids and mycorrhiza secreted by roots can help vegetation obtain nutrients in the soil to cope with nutrient deficiency in the soil. The organic acid content secreted by the roots of karst plants is usually higher than that of non-karst plants, and the increase of organic acid content can help plants to absorb trace elements. Arbuscular mycorrhizal fungi (AM) and ectomycorrhizal fungi (ECM) help plants adapt to nutrient deficiency by absorbing mineral nutrients from the soil.

(3) The vegetation succession in the karst area is similar to the general stage of vegetation succession in normal landforms, but the vegetation succession in the karst area has the particularity of self-generation. The vegetation succession from the middle to the top of the mountain takes a longer time. Vegetation succession changed physical and chemical properties and soil quality. In the process of succession, soil bulk density gradually decreases, and porosity gradually increases over time. At the same time, soil nutrients accumulate with the positive succession of vegetation. During the positive succession process of karst vegetation, the soil water and fertilizer retention capacity is enhanced, the stability is increased, and the survival probability of species and the species diversity are also increased. The special rock geochemical background in the karst area leads to the obvious changes in the spatial distribution of soil resources. High soil heterogeneity promotes the formation of plant community species diversity. For example, the tropical karst area in Xishuangbanna, Yunnan Province covers an area of 3600km^2, accounting for 19% of the land area. The forest survey results in the karst area show that there are 153 families, 640 genera and 1394 species of vascular plants, accounting for 77.7% of the total floristic families, 56.1% of the genera and 37.9% of the species, respectively.

The karst plant community is the result of the long interaction between the plant and the environment, the continuous adaptation to the environment and the growth and reproduction. The karstification of plants, the adaptation mechanism of plants under the typical karst soil environment such as drought, high calcium stress and lack of nutrient elements, as well as the succession characteristics of karst vegetation shown in the adaptation process and the biodiversity of vegetation are a whole interaction. The site growth of vegetation promotes the weathering of carbonate rocks and the formation of soil, creating conditions for their own growth. Meanwhile, soil area and soil thickness are positively correlated with plant diversity. The succession of vegetation changes the physical and chemical properties of soil and improves the quality of soil, and the karstification of carbonate rocks promotes the growth of vegetation. The adaptive mechanism of vegetation affects the distribution and growth of plants and promotes the succession process of plant communities and the formation of plant diversity. Due to the spatial heterogeneity of the karst environment and the diversity of plant habitats, plant diversity in karst areas is manifested as few genera, few species and endemic species. However, the internal relationship between plant diversity and the stability of the community ecosystem, as well as the comparative characteristics with non-karst areas still need to be further studied and explored.

KEY WORDS: carbonate rock; vegetation; plant adaptation strategy; biodiversity; succession