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荒漠生态系统磷循环及其驱动机制研究进展

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摘要:磷(P)循环在维持荒漠生态系统的生物多样性水平、结构和功能的稳定性、元素的动态平衡,以及荒漠自然资源的可持续利用方面有重要作用。通过查阅国内外有关 P 循环的文献资料,发现当前国内尚缺乏针对荒漠生态系统 P 循环的系统研究,特别是 P 循环的生物和非生物驱动机制。综述了荒漠生态系统 P 的输入-输出过程,植物对 P 的吸收转运机制以及对 P 循环的作用,生物土壤结皮(BSC)有机分泌物对 P 循环的贡献,以及荒漠生态系统 P 循环过程对气候变化的响应机制等。文末展望了荒漠生态系统 P 循环的一些重要研究方向和亟需解决的科学问题,包括(1)P 在荒漠生态系统中的存在形态、分配及动态平衡;(2)土壤微生物对荒漠植物获取土壤有效 P 的驱动作用;(3)入侵植物对 P 循环的影响与潜在生态风险评估;(4)利用分子生物学和基因组学手段揭示真菌-荒漠植物根系系统 P 循环的基因调控机制;(5)微生物分泌物、土壤磷酸酶类(包括磷酸单酯酶、磷酸二酯酶和三磷酸单酯水解酶)和作用于含磷酸酐和 N—P 键的酶对土壤 P 循环的调控;(6)气候变化(干旱、高温和降水节律变化等)如何影响 P 的生物和非生物转化过程;(7)基于同位素示踪和生态化学计量学理论解释荒漠生态系统 P 循环路径及其稳定性维持机制。

关键词:P 限制; 荒漠植物; 菌根真菌; 土壤磷酸酶; 生物土壤结皮; 气候变化

Advances on phosphorus cycle and their driving mechanisms in desert ecosystems: A review

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Abstract: Phosphorus (P) cycle is critical for maintaining biodiversity, structural and functional stability, elemental balance and natural resources for sustainable development in desert ecosystems. To date, by the published works referring to P cycle in desert ecosystems worldwide, we found that studies of P cycle covering desert ecosystems of China is much less comprehensive in particular in elucidating biotic and abiotic driving mechanisms of P cycle. Thereby, we reviewed those shreds of publishes to produce an advance that focused on the P input and output, the mechanisms of adsorbed and transported P by plants and their actions on P cycle, the contribution of organic secretions from biological soil crusts (BSC) on P cycle, and the process of P cycle how to respond to climatic changes. Here, seven impending scientific questions need to be addressed in future studies, including (1) to reveal the chemical fractions, allocation and dynamic balance of P in desert ecosystems; (2) to elucidate the driving functions of soil microorganisms acting on plants uptake available P; (3) to

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evaluate the potential effects and ecological risks of alien plants acting on P cycle; (4) to explore the mechanisms of gene-regulating P cycle in the fungi-root system by using the approaches of molecular biology and genomics; (5) to explore microbial secretions, soil phosphatase (including phosphomonoesterases, phosphodiesterases, triphosphoric monoester hydrolases), enzymes acting on phosphoryl-containing anhydrides and P-N bonds how to regulate the biological processes of P cycle; (6) to explain the transformation process between organic P and inorganic P under climatic changes; and (7) to quantify P cycle path and uncover the mechanism of P cycle in regulating desert system stability by using isotope tracing and ecology stoichiometry.

Key Words: P limitation; desert plants; mycorrhizal fungi; soil phosphatase; biological soil crusts; climatic change

荒漠生态系统约占陆地面积的 1/3,覆盖热带、亚热带、温带和极地地区,承载了全球近 25 亿人口[1—3]。荒漠环境高温少雨、干旱频发、降水年际波动大且季节分配不均、风/水蚀作用显著,外加土壤发育时间短,肥力较低[2—4],导致荒漠中植被稀疏,生物多样性低,环境脆弱。二十世纪以来,随着全球气候变化和人类活动的过度干扰和破坏,使荒漠生态系统的稳定性、恢复力、服务功能和可持续发展等正面临严峻挑战[4—5]。

在荒漠中,碳(C),氮(N)和磷(P)参与了生态系统的能流和物流过程,通过与水作用调控着荒漠生态系统的持续稳定性。作为构成细胞膜、DNA、RNA 和 ATP 的关键元素,P 是荒漠生态系统中生命存在的物质基础。相较 C 和 N,P 因其自身的来源和有效性使其成为了荒漠生态系统中重要的限制因子之一。在自然界中,植物能获取的有效 P 量非常有限,一方面是因为 P 循环属于相对封闭的沉积型循环,自然环境中其周转时间极为漫长(10^7—10^8 a)[6];另一方面则受限于 P 循环的驱动机制。且后者是控制磷循环的关键。

荒漠中 P 循环的驱动机制十分复杂。首先,荒漠中母岩风化、大气尘埃的干湿沉降、土壤微生物和动植物生物量的输入/输出均影响 P 的循环[7]。其次,P 元素通过参与荒漠植物光合和呼吸等过程维持植物正常的生理活动,改变荒漠植物生理功能、生活策略和种群密度,进而影响整个植被系统[8—9]。如北美荒漠中土壤低有效 P 浓度限制了三齿蒿(*Artemisia tridentata* Nutt.)[10]和旱雀麦(*Bromus tectorum* L.)的生长[11—12],而总磷和有效磷量变化改变了中国阿拉善荒漠区沙蒿种群密度[9]。所以,对于荒漠生态系统有限的有效磷,荒漠植物进化出了适应低 P 环境的特征或通过其他媒介获取足够的有效 P 以完成自己的生活史,如荒漠植物会通过根系分泌有机物获取 P 和/或对其植物叶内 P 进行重吸收利用[13—14];也会通过根系-菌根网络系统扩大与土壤接触面积来增加有效 P 的获取量以满足自身生长需求;又如荒漠中生物土壤结皮(BSC)通过截留降尘和改变降水分布增加土壤有效 P 量,同时,结皮生物分泌有机酸等能从土壤胶体中解吸出 P 以供荒漠植物生长[15—17]。最后,气候变化通过多种方式影响荒漠中 P 的循环,如干旱阻碍荒漠土壤中 P 的矿化过程[18—19],脉冲式降水和 N 沉降影响土壤有效 P 的解吸[20—22],水 P 耦合和氮磷耦合限制植物生长[8,23—24]等。

综上,P 在荒漠生态系统中凸显出至关重要的地位。且对于我国而言,荒漠生态系统面积有 1.65×10^6 km^2,约占国土面积的 17%,其服务总价值约为 42279 亿元人民币(2014 年价格),主要体现在防风固沙(40.1%)、水文调控(24.2%)、土壤保育(18.1%)和固碳(17.0%)方面[25]。而 P 作为构建荒漠生态系统的关键元素,目前国内仍缺乏其在荒漠生态系统中的综合研究。随着新技术的涌现,如分子生物学、基因组学和同位素示踪技术等的发展,P 循环的研究更应该得到加强。因此,基于国内外已有研究,本文从(1)荒漠中 P 的来源、输入和输出过程;(2)荒漠中植物-土壤系统间 P 循环过程及机理;(3)气候变化对荒漠生态系统 P 循环影响机制,并得出结论和提出展望,旨在为 P 循环、生态系统能/物流的科学管理、生态系统服务价值评估、生态安全和荒漠化土地的生态恢复提供参考。

1 荒漠中磷的来源、输入和输出

母岩风化是荒漠生态系统中 P 的重要来源,但该过程非常缓慢,且输入量少[6](一般为每年 0.05—

1.0 kg/hm^2,部分地区可以达到每年 5.0 kg/hm^2)。风化作用包括物理和化学风化。物理风化:荒漠昼夜温差、光照、风力和水蚀等外营力综合作用下对岩石表面碎屑化,形成含 P 的细小颗粒物,如在寒漠地区,冻融作用加速地表岩石风化产生含 P 的细小颗粒物[7];化学风化:土壤微生物和隐花植物(如地衣和藓类等)通过生物化学作用促进土壤母质释放 P[26—27]。除了母质风化外,大气干湿沉降是荒漠中 P 的主要输入方式。在干湿沉降作用下,颗粒物沉降和植物凋落物沉积在荒漠土壤表面,导致 P 分布的浅层化和表聚性[28—30]。全球尺度而言,非洲和欧亚大陆荒漠区的降尘输入量远高于北美(北美的年均降尘输入量为 20—40 g/m^2)[31—32]。另外,荒漠中动物(爬行类、啮齿类、鸟类及蝗虫等)排泄物及动植物死亡后均成为重要的 P 源。

P 的输出在荒漠中主要包括动植物生物量及相关产品(如薪材、牧草和动物产品)和风蚀和/或搬运过程损失。生物量及相关产品的输出主要以荒漠草原中牧草、畜牧业产品和中草药的输出为主[6,33]。当然,人类放牧和耕作及其他动物行为(如荒漠中动物的掘洞行为)会移动土壤,在外营力作用下使 P 在该过程中损失[34—36]。荒漠中尽管降水量少(<250mm),但降水作用仍导致了土壤表土 P 的部分损失[37—38](图 1)。

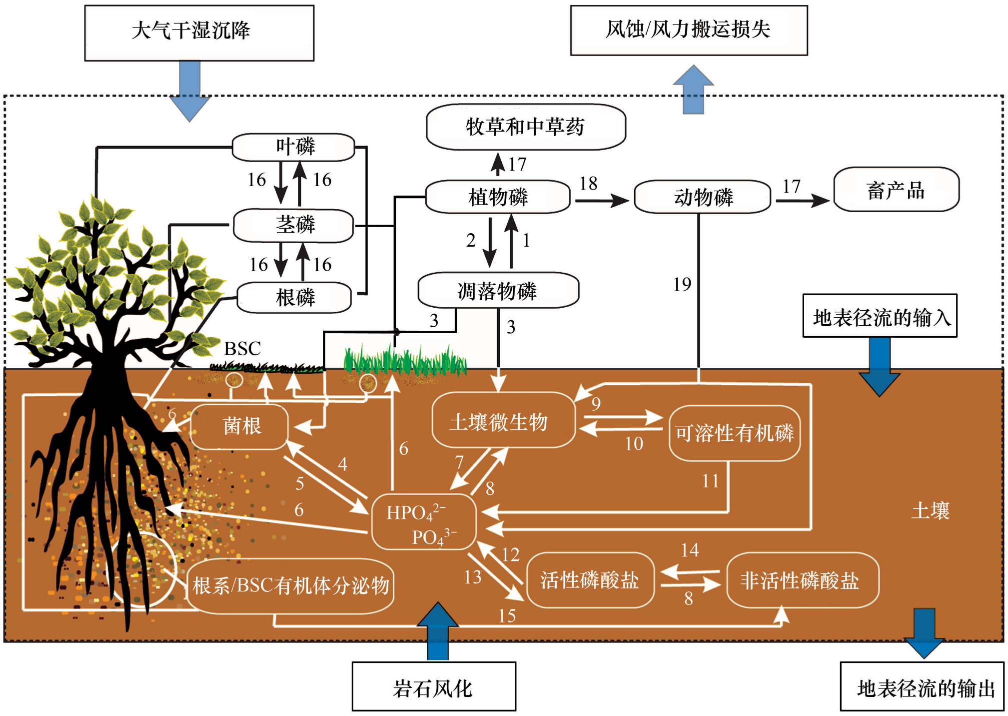

图 1　荒漠生态系统 P 循环示意图

Fig.1　A schematic diagram of P cycling in desert ecosystem

1:磷重吸收 P re-uptake;2:植物归还 Plant return;3:微生物矿化 Microbial minaralization;4:菌根吸收 Micorrhiza uptake;5:菌根释放 Micorrhiza release;6:植物根系吸收 Plant root uptake;7:释放 Release;8:固定 Immobilization;9:死亡 Microbial died;10:同化 Assimilation;11:酶水解 Enzyme Hydrolysis;12:解吸和溶解 Desorption and dissolution;13:吸附和沉淀 Adsorption and sediment;14:活化 Mobilization;15:溶解 Dissolution;16:迁移和再分配 Migration and relocation;17:生物量/产品输出 Biomass/products output;18:动物取食 Animal feeding;19:动物尸体和粪便归还 Carcass and excrement return;BSC:生物土壤结皮 Biological soil crust

2　植物-土壤系统间 P 循环过程及机理

2.1　植物对磷的吸收

2.1.1　根系对磷的吸收

在荒漠生态系统中,P 的形态包括有机 P 和无机 P。有机 P 包括植素类,核酸类和磷脂类;无机 P 包括磷酸铝类化合物(Al-P),磷酸铁类化合物(Fe-P),磷酸钙类化合物(Ca-P)和闭蓄态磷(O-P),其中,Ca-P 是荒漠

土壤中主要的磷组分。如在库布齐沙漠,TP 含量为 137.21—362.09 μg/g,其中 Ca-P 占了 58.95%—80.05%,其他各形态 P 含量的顺序为:有机 P(Or-P) > 吸附态 P(Ads-P) > 铁结合态 P(Fe-P) > 闭蓄态 P(O-P) > 铝结合态 P(Al-P)[39];在阿拉善荒漠区,土壤中 Ca-P>Al-P>Fe-P[40];在巴丹吉林沙漠,土壤中 Ca-P>Or-P>Al-P>交换态 P(Ex-P) > Fe-P>O-P[41]。

在荒漠中,植物有多种策略去获取磷[13]。首先,植物改变根系特征增加对有效 P 的吸收[7],如增加植物根系与土壤接触的表面积[42—43]。其次,植物通过分泌多种复杂的有机酸混合物(如草酸、苹果酸、琥珀酸等)、植物铁磷酸酯、糖、维生素、氨基酸、嘌呤、核苷酸、无机离子、气态分子、螯合剂和根表面的磷脂活性剂等活化结合态 P,达到吸收 P 和促进 P 循环的目的[7,44]。此外,在低水分、高盐分的胁迫作用下荒漠灌木根系分泌磷酸酶和植酸酶矿化土壤中有机 P[14,45—46]。同时,一些植物如牧豆树(*Prosopis juliflora* (Swartz) DC.)通过根系分泌物、豚草(*Ambrosia artemisiifolia* L.)利用根系识别反应等方式维持一定范围的根系空间[47],以获得足够的 P 供给植物地上部分生长。这种植物根系在土壤中的排他性增加了获得有效 P 的机会,提升了植物的竞争力[48—49]。此外,植物根部较高的阳离子交换能力[50—51],根系释放的 H^+或 HCO_3^- 均有助于植物获取和利用土壤中的有效 P 和结合态 P[40]。但土壤中多价阴离子结合金属离子(锌、铁、锰)会抑制植物磷酸酶和植酸酶活性,限制 P 的矿化。

2.1.2 根系-菌根系统对磷的吸收

菌根在荒漠植物获取 P 及驱动 P 循环中扮演着重要角色。一方面,菌根真菌通过与植物根系形成网络系统,扩大与土壤的接触面积,增加植物获取土壤 P 的机会[26,52]。如隔内生真菌与鼠茅属植物 *Vulpia ciliate* 和四翅滨藜(*Atriplex canescens* (Pursh) Nutt.)形成的网络系统有助于植物获取土壤有效 P[7],因为隔内生真菌在植物和蓝藻结皮之间每天转移营养物质的距离达 1 m,大大增加了植物获取有效 P 的范围[53]。另一方面,真菌通过自身分泌物溶解磷酸岩增加植物可获取的 P 量[54]。然而,荒漠区干旱程度的增加会导致菌根真菌被隔内生子囊菌所取代,降低了菌根丰富度[53,55]。此外,荒漠植物的菌根侵染率受到生物土壤结皮(BSC)表面积的显著影响,如美国犹他州东南部的沙漠地区,BSC 分布区植物的菌根侵染率是裸土环境中植物的 3 倍[56]。

2.1.3 植物叶磷含量变化与磷循环

荒漠植物叶片通过自身凋落、分泌物和重吸收的方式影响 P 的循环。植物凋落的叶片被分解进入土壤时增加了土壤 P 含量[57];不同植物凋落物通过刺激土壤磷酸酶,对土壤有效 P 的循环产生了显著的影响[58]。同时,植物叶片分泌的化合物多是水溶性的,当叶片分泌物浸入土壤时可以使邻近的植物和微生物受益,促进土壤 P 的解吸/溶解及微生物量 P 的矿化[7]。此外,荒漠区干旱程度增加会增加植物对其叶片中 P 的重吸收,减少其凋落物中 P 含量[14]。当前,对植物叶中 P 含量变化原因有三种观点:一种观点认为荒漠植物叶片中 P 含量变化主要与土壤中 P 含量有关,如克氏针茅(*Stipa krylovii* Roshev.)叶片的 C∶P 和 N∶P 与其所处的土壤中 C∶P 和 N∶P 具有一定的协同变化能力[36],土壤 P 是植物叶片 P 潜在的元素库[59]。第二种观点认为荒漠植物叶片 P 含量变化主要因为植物自身遗传特性,如在塔里木河上游荒漠区的 4 种灌木植物,其自身遗传特性影响了叶片 C∶P 和 N∶P,而不是由土壤中养分含量直接决定[60]。第三种观点认为荒漠植物叶片 P 含量变化与降水有显著的正相关关系[61]。综上,P 在土壤-植物间的循环受到植物叶片分泌物、土壤 P 库、植物自身遗传特性和环境的影响。

2.2 入侵植物对磷的吸收

荒漠入侵植物对 P 的获取较本地植物具有显著的优势,其可将非可用态 P 转化为有效 P,能促进土壤非可用态 P 的生物循环。对于荒漠而言,入侵植物的成功是由于它们[7]:(1)比起本地植物能更有效的吸收和利用土壤中非生物有效 P;(2)同样条件下对土壤有效 P 有更强的竞争能力。入侵植物利用土壤 P 的策略一方面是其根系分泌物和地上叶片渗滤液进入土壤将非可用态 P 转化为可用态 P 以供其吸收和利用;另一方面是入侵植物侵入荒漠时有少数本地植物或真菌协助其吸收土壤有效 P[7]。

旱雀麦是荒漠中一种一年生草本入侵植物,其在美国犹他州东南部荒漠秋冬季的相对增长率可以依据土壤 P 含量来预测[62—63]。如当土壤有效 P 降低时,旱雀麦的萌发被抑制[11—12]。此外,旱雀麦可将土壤中非可用态 P 转换为有效 P。如在一个从未放牧过的荒漠草原,旱雀麦侵入该环境后,当其盖度从 0%增加 10%再增加到 40%时,土壤中有效 P 从 14.6 μg/g 增加到 19.5 μg/g 再到 28.2 μg/g[64]。旱雀麦对那些本地植物不能利用的非可用态 P 的利用潜力使其在可控范围内有成为荒漠生态环境恢复材料的趋势。

2.3　荒漠中生物土壤结皮(BSC)对磷循环的作用

2.3.1　BSC 对含磷降尘的固定

BSC 由蓝藻、绿藻、地衣、藓类和异养型微生物及相关的其他生物体通过菌丝体、假根和分泌物等与土壤表层颗粒胶结形成的十分复杂的复合体,其对荒漠区土壤形成、改善土壤理化性质、调节土壤水分的再分配格局等方面有重要作用[7,63]。BSC 覆盖荒漠表面,增加了地表粗糙度,对大气含 P 降尘有很好的截留和保存能力[56,63,65],防止了含 P 降尘流失或重新分布[66]。被 BSC 捕获的营养丰富的粘土颗粒增加了荒漠土壤的肥力和持水能力,使结皮生物在较长的时间内保持代谢活性[7]。此外,BSC 也为植物生长提供丰富的 P 源[56,67]。

2.3.2　BSC 中生物对结合态磷的释放和溶解

BSC 中生物对荒漠土壤中磷的释放有重要作用。如 BSC 中地衣呼吸代谢产生 H^+ 释放碳酸盐结合的 P,增加 P 的有效性;或分泌有机酸,如柠檬酸、苹果酸、乙酸、丙酮酸、乳酸和甲酸等[11,68]溶解土壤中结合态 P[27,69]。BSC 中真菌黑曲霉和细菌青霉菌产生柠檬酸溶解土壤结合态 P[70]。BSC 中真菌在岩石中也能分泌酸去溶解营养物质,并将这些营养物质直接转移到植物根系[71—72]。此外,BSC 中蓝藻可以分泌金属螯合剂稳定土壤溶液中的金属而增加有效 P 含量[11,73];也可以分泌肽 N 和核黄素,在螯合剂作用下与磷酸三钙、铜、锌、镍和铁形成络合物,保持植物所需的有效营养[74];还可以分泌乙二醇酯,刺激植物摄取 P[75]。

BSC 中的大多数蓝藻、绿藻、地衣和藓类会分泌磷酸酶到周围的土壤,导致有机磷酸盐水解释放 P,这些 P 会立刻被微生物固定并转移到宿主植物根上,或者被腐殖质稳定下来[76—79]。此外,BSC 中蓝藻能固定 N,当土壤 N 升高时,磷酸酶含量和活性增加[21,80],进而能增加土壤有效 P[81]。BSC 发育较好的环境中磷酸酶的活性相对较高[82]。然而,由于磷酸酶与土壤有机质高度相关,而荒漠土壤中有机质含量相对较低,导致磷酸酶活性也相对较低[83]。

3　气候变化对荒漠中磷循环的影响机制

气候变化对荒漠中 P 循环的影响,当前可通过温度、降水和 N 沉降等实现。三者可以直接或间接影响土壤中有效 P 含量,限制植物获取有效 P,改变荒漠生态系统植被的功能和稳定性[84—86]。下面主要讨论干旱、降水节律和 N 沉降对荒漠生态系统 P 循环的影响机制。

3.1　干旱对磷循环的影响

干旱对荒漠中 P 循环的影响主要通过影响植物和微生物实现。对植物而言,在气温上升而降水下降的荒漠区,干旱增加降低了植物叶片 P 含量[23],使荒漠中 P 的生物地球化学循环受到限制[7];同时,干旱降低了 P 的有效性而使植物吸收 P 受限,阻碍土壤中营养物质扩散和能量流动[18—19,87]。对微生物而言,干旱阻碍土壤中 P 的矿化过程。如干-湿交替、高温干旱和辐射损伤导致多达 58%的土壤微生物死亡[88],使得这些有机 P 会和降尘一起聚集在土壤表层[89],成为荒漠中重要的 P 源。微生物对荒漠生态系统至关重要,其细胞中的 P 大部分以核酸和磷脂的形式存在,并在死亡后能补充土壤中 P 的匮乏[90]。如在澳大利亚干旱土壤中微生物死亡释放的 P 占土壤水溶性 P 的 95%,可使水溶性土壤 P 增加到 1900%[91]。此外,土壤微生物活动的独立性和干-湿交替循环过程通过破坏有机质涂层,分离和移动土壤胶体来增加土壤有机 P 的溶解度,从而增加土壤溶液中 P 含量[92]。然而,这些驱动力并不经常出现[93]。

3.2　降水节律对磷循环的影响

水是荒漠中 P 循环的第一驱动力[94],更有效地吸收或使用水分的植物比其他植物在获取营养上具有竞

争优势。土壤水分的减少将减缓所有释放生物有效 P 的非生物过程。荒漠中脉冲降水事件导致的土壤快速湿润、干旱的频率和持续时长等通过影响植物和微生物来影响 P 的循环。对荒漠植物而言,水分与养分吸收之间的正反馈非常重要[48,94],如降水减少会增加不易降解的凋落物的产生,进一步减缓凋落物的分解速率[7]。此外,植物分泌的磷酸酶活性主要依赖于土壤水分有效性,降水减少将使它们的有效性降低[95];磷酸酶添加试验表明在土壤湿润时,干旱土壤中高达 87%的有机 P 是可水解的[96—97];磷酸酶活性与降水和温度的关系也影响荒漠区结合态 P 的释放。此外,适宜的降水有利于一年生植物的生长,因为一年生植物通常比多年生植物更易受低 P 条件的限制[51]。对于微生物而言,虽然温度升高会增加土壤微生物活性,但土壤水分减少会限制其活性时间,进而导致微生物丰度和活性的降低[14]。当温度变暖,降雨出现,土壤微生物种群和活性会迅速增加,进而增加土壤有效 P 含量[57],促进了 P 的循环过程。然而,降水的持续时长也影响 P 的矿化和固定过程。

大多数情况下,植物和微生物对不同荒漠环境变化有不同的响应,这有利于它们在资源的获取上进行协同作用。如当降水量减少时,土壤表层微生物率先对降水事件作出反应并开始进行生命活动,提供植物所需的养分[94];当降水量持续增加时,维管植物的生命活动则占据主导地位[98—100]。然而,较大的降水会减少土壤微生物和植物在养分获取和利用方面的合作,如植物在降水充足时可以直接摄取可水解的有机 P[101—103]。此外,湿润土壤条件能降低土壤 pH,溶解碳酸盐,使结合态 P 转变为生物有效 P,如在科罗拉多高原地区和奇瓦瓦沙漠,冬季潮湿寒冷的环境增加了土壤有效 P 含量[62—63,104]。另外由于荒漠降水量少,如减少微生物生物量、植物生物量、土壤水分、土壤 P 向根际圈的扩散量和植物根系对 P 的吸收量均会降低土壤对 P 的吸附。

3.3 氮沉降对磷循环的影响

N 沉降通过影响土壤中磷酸酶活性、植物和微生物的生态化学计量关系来影响 P 的循环。土壤中 N 的增加一方面能提高磷酸酶活性,激发束缚 P 的释放,提高土壤有效 P[21,80];另一方面也增加土壤 P 的吸附和沉淀,导致荒漠环境出现 P 限制现象[20—21]。目前在荒漠生态系统中 N 和 P 之间的阈值还不清楚。而在荒漠草原,过高的植物叶片 N∶P 增加了 P 对荒漠植物的生长限制[105],较低的 N∶P 也限制了植物叶片的生长[24]。前者认为植物叶片生长与 P 呈正相关,与 N 呈负相关,符合“生长速率假说”;后者认为植物叶片的增长与 P 呈负相关,与 N 呈正相关,违背“生长速率假说”。这两种结果都忽视了植物种间差异和长期以来植物与环境之间的协同进化关系。对荒漠草原而言,N 沉降增加,最大 N 矿化率和硝化率消耗 P,使环境中 P 减少,P 便成了植物生长的限制因子[106]。此外,在荒漠草原中,N 添加不仅增大了 BSC 的 N∶P,改变 C∶N∶P,影响 P 的生物循环过程[107],也增加了土壤微生物量 N 和 N∶P,最终影响植物群落组成。当然,N 沉降与 P 的关系在评估荒漠绿洲过渡带土地的利用程度、维护绿洲生态安全和绿洲稳定上具有重要作用。

4 结论与展望

目前荒漠生态系统 P 循环取得的主要结论:(1)大气降尘和母质风化输入 P,干湿沉降作用增加植物基部土壤 P 含量;(2)植物通过根系和叶片分泌有机物或与其他生物(如真菌和细菌)形成共生或合作系统获取有效 P;(3)入侵植物能高效利用荒漠土壤中非生物有效 P;(4)BSC 有机体通过分泌胞外聚合物、有机酸、磷酸酶和呼吸代谢 H^+来释放土壤有效 P,促进 P 的生物循环;(5)气候变化下,干旱和降雨改变磷酸酶活性、阻碍 P 循环的非生物过程和生物过程,进而影响荒漠中营养物质扩散和能量流动;N 沉降改变土壤微生物活性、磷酸酶活性和 N∶P 等来改变 P 循环。因此,基于以上结论,结合当前国内外研究热点和重点及研究物质循环的新技术的涌现(分子生物学、基因芯片和同位素示踪等),遂对国内荒漠生态系统 P 循环的研究方向和科学问题提出如下展望:(1)P 在荒漠生态系统中的分配、存在形态及动态平衡;(2)土壤微生物对荒漠植物获取土壤有效 P 的驱动作用[98];(3)入侵植物对 P 循环的影响与潜在生态风险评估;(4)利用分子生物学和基因组学方法揭示真菌-植物根系间 P 循环的基因调控机制[6,17,99];(5)微生物分泌物、土壤磷酸酶类(包括磷酸单酯酶、磷酸二酯酶和三磷酸单酯水解酶)和作用于含磷酸酐和 N-P 键的酶对土壤 P 循环的调控[6—7];(6)气候

变化(干旱、高温和降水节律变化)如何影响 P 的生物和非生物转化过程[84,86,100];(7)基于同位素示踪和生态化学计量学理论量化荒漠生态系统 P 循环路径及其稳定性维持机制[108—110]。

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