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亚热带常绿阔叶林土壤胞外酶活性对碳输入变化及增温的响应

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摘 要 土壤胞外酶来源于土壤微生物、植物和动物, 是土壤生物地球化学过程的积极参与者, 在森林生态系统的物质循环和能量流动过程中扮演着重要角色。为探明土壤胞外酶活性对碳输入变化及增温的响应, 该研究基于长期增温、去除地表凋落物(以下简称去凋)和切根处理的云南哀牢山亚热带常绿阔叶林控制实验平台, 研究了不同处理(对照、去凋、切根、切根并增温)下表层矿质土壤(0–5和5–10 cm)与碳氮磷获取相关的胞外酶活性, 包括多酚氧化酶(POX)、过氧化物酶(PER)、β-葡萄糖苷酶(BG)、β-1,4-N-乙酰氨基葡萄糖苷酶(NAG)和酸性磷酸酶(AP)。结合铵态氮(NH_4^+-N)含量、硝态氮(NO_3^--N)含量、溶解有机碳(DOC)含量、溶解总氮(DN)含量、土壤含水量(*SWC*)等相关指标, 探讨凋落物碳输入、根系碳输入和温度变化对土壤胞外酶活性及其生态化学计量特征的影响。研究结果表明: 在对照样方, 除POX外其余酶活性均为0–5 cm层显著高于5–10 cm层。与对照相比, 长期的凋落物去除显著降低了0–5 cm层土壤AP和BG活性, 对NAG、PER和POX活性则无显著影响; 长期切根处理显著降低了0–5 cm层土壤BG活性, 但提高了两个土层PER活性; 长期切根并增温处理显著降低了0–5 cm层AP和BG活性, 对其余酶活性无显著影响。冗余分析结果显示*SWC*和NH_4^+-N含量是驱动土壤酶活性变化的重要因子。本研究为该生态系统土壤碳氮磷生物地球化学关键过程对全球变化的响应提供了土壤酶学的依据。

关键词 土壤胞外酶活性; 生态化学计量学; 去除地表凋落物; 切根; 增温

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Responses of soil extracellular enzyme activities to carbon input alteration and warming in a subtropical evergreen broad-leaved forest

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Abstract

Aims The objective was to investigate the responses of soil extracellular enzyme activities to carbon input alteration and warming in a subtropical evergreen broad-leaved forest of Ailao Mountain, Yunnan, southwest China.

Methods This study was based on two soil depths (0–5 and 5–10 cm) for four treatments under a long-term soil warming experiment in a subtropical evergreen broad-leaved forest of Ailao Mountain, Yunnan, southwest China. Potential activities of β-glucosidase (BG), polyphenol oxidase (POX), peroxidase (PER), β-1,4-N-acetylglucosaminidase (NAG) and acid phosphatase (AP) and their stoichiometric ratios were measured. Soil physical and chemical properties were also analyzed.

Important findings The results showed that in the control treatment, activities of all enzymes except POX decreased significantly with soil depth. Compared with the control treatment, long-term litter removal significantly reduced AP and BG activities at 0–5 cm soil depth, but had no significant effect on NAG, PER and POX activities

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at both 0–5 and 5–10 cm soil depths. Long-term root removal significantly reduced BG activity at 0–5 cm soil depth, while increased PER activity at both soil depths. Long-term root removal and warming treatment significantly reduced AP and BG activities at 0–5 cm soil depth, but had no significant effect on activities of other enzymes at both soil depths. The results of redundancy analysis showed that soil water content and NH_4^+-N content were likely important factors driving the changes soil enzyme activities among treatments. This research provides critical information on the activities of soil enzymes related to carbon, nitrogen and phosphorus cycling in response to global change in this subtropical forest ecosystem.

Key words soil extracellular enzyme activity; ecological stoichiometry; litter removal; root removal; warming

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土壤酶是来自土壤微生物、植物和动物的生物活性物质, 是专一生物化学反应的生物催化剂, 作为土壤生物地球化学过程的积极参与者, 在森林生态系统的物质循环和能量流动过程中扮演着重要的角色(Sardans *et al*., 2008)。土壤中以游离态存在或与土壤有机质及矿质组分结合的酶称为土壤胞外酶。当温度、降水量和底物输入产生变化时, 土壤胞外酶活性将会发生相应改变(Seo *et al*., 2015; Chen *et al*., 2020; Hu *et al*., 2020), 表现为促进或抑制土壤养分、有机物分解, 进而影响陆地生态系统的物质循环过程(Karhu *et al*., 2014)。因此, 气候变化可能对陆地生态系统土壤胞外酶活性产生复杂的影响, 而探讨各环境因子的变化对土壤胞外酶活性的影响是预测未来气候变化对森林生态系统过程影响的关键(Xiao *et al*., 2018)。

工业革命以来, 全球平均气温呈上升趋势, 预计21世纪全球气温将增加0.3–4.8 ℃ (IPCC, 2013)。温度是土壤酶活性的重要调控因子(Rustad *et al*., 2001; Kang & Lee, 2005; Luo *et al*., 2009), 直接影响了土壤酶活性, 进而影响土壤呼吸、土壤有机物分解等生化过程(Lu *et al*., 2013)。McDaniel等(2013)对砍伐后的森林土壤进行模拟增温实验, 发现增温显著降低了土壤中β-葡萄糖苷酶、β-1,4-N-乙酰氨基葡萄糖苷酶和多酚氧化酶活性。但亦有研究表明, 短期增温和长期增温均未显著改变土壤胞外酶的活性(Wang *et al*., 2012)。此外, 除土壤温度变化外, 土壤水分能直接影响土壤中的生化反应强度和土壤胞外酶活性。相关研究表明, 土壤水分与土壤胞外酶活性之间有显著的正相关关系(Ren *et al*., 2017; Li *et al*., 2018)。Zhou等(2013)对温带草原的研究发现增加降雨会提高土壤碱性磷酸酶和脲酶的活性, 说明适量的增加土壤水分能够提升土壤胞外酶活性。

由于土壤酶主要来自土壤微生物及植物根系分泌的具有催化作用的蛋白质, 因此根系分泌物是土壤酶的重要来源(杨万勤和王开运, 2004)。同时在森林生态系统中, 凋落物是土壤有机质的重要来源, 凋落物输入量的改变会造成土壤微生物及其代谢方式的改变, 进而影响土壤胞外酶活性, 故碳源输入方式的改变可对土壤胞外酶活性产生影响。森林土壤中与碳、氮、磷循环相关的胞外酶活性对土壤有机质的输入较为敏感。Weintraub等(2013)发现, 减少凋落物输入后, 热带森林土壤磷限制性增强, 与磷循环相关的酶活性增强; 魏翠翠等(2018)研究发现凋落物加倍和凋落物去除均降低了亚热带森林酸性磷酸酶、β-葡萄糖苷酶和多酚氧化酶的活性; Ge等(2017)对亚热带马尾松林研究发现, 凋落物输入量与纤维素酶、脲酶和多酚氧化酶活性呈显著线性相关关系, 并证明土壤温度、凋落物含水量和凋落物氮含量是影响酶活性的主要因素。由此可见, 凋落物输入变化会引起微生物碳源和养分源变化, 进而影响土壤胞外酶活性(Allison & Vitousek, 2004)。根系分泌物作为土壤酶的重要来源, 也发挥着重要作用, 研究表明根际土壤中有机碳含量较高, 根际碳的输入可以刺激根际微生物活动和胞外酶的活性, 因此根际土壤的酶活性普遍高于整体(Brzostek *et al*., 2013; Gianfreda, 2015)。切根通常会导致土壤有机碳含量的下降(Crow *et al*., 2009; Fekete *et al*., 2014), 随之影响土壤酶活性。Spohn和Kuzyakov (2014)研究表明切根后纤维素酶和几丁质酶活性均升高, 但根系与胞外酶活性的相互影响机制还缺乏进一步研究。

土壤酶生态化学计量比可以衡量土壤微生物的养分需求及限制状况(Moorhead *et al*., 2016; Peng & Wang, 2016)。近年来, 土壤酶生态化学计量比日益

受到重视, 主要研究与碳氮磷循环相关的土壤胞外酶活性的比值, 目前多以参加碳循环的β-葡萄糖苷酶(BG)、参加氮循环的亮氨酸氨基肽酶(LAP)和β-1,4-N-乙酰氨基葡萄糖苷酶(NAG)以及参加磷循环的酸性(或碱性)磷酸酶(AP)的比值为研究对象, 即(BG:(NAG+LAP):AP)或BG:NAG:AP (Sinsabaugh *et al*., 2009)。Sinsabaugh等(2008)研究发现, 在全球尺度上, 与碳氮磷循环相关的土壤酶生态化学计量比, 即ln BG:ln (NAG+LAP):ln AP (土壤酶C:N:P)近似为1:1:1, 说明全球尺度上酶的生态化学计量比是相对稳定的, 但是局部区域受不同环境因素影响, 其比值呈现不同的趋势, 以此可深入探讨土壤养分限制状况(Sinsabaugh & Follstad Shah, 2012)。因此, 研究土壤酶生态化学计量比有助于深入了解胞外酶活性对土壤养分限制的响应。

亚热带森林水热条件较好, 群落物种组成丰富, 自我调节能力强, 生产力较高, 具有较强的物质循环及能量转化能力。由于土壤胞外酶活性与生态系统碳氮循环紧密相关, 可以通过土壤胞外酶活性的动态, 反映森林土壤碳氮关键过程对气候变化的响应。中国科学院生态系统研究网络(CERN)哀牢山亚热带森林生态系统研究站位于云南省景东县太忠镇的徐家坝, 植被为典型的亚热带常绿阔叶林。前期研究表明, 该生态系统具有一定的碳汇能力(Tan *et al*., 2012), 土壤碳排放对增温、去除地表凋落物(以下简称去凋)、切根处理响应显著(Wu *et al*., 2014, 2016), 但是仍不能明确凋落物碳输入、根系碳输入和温度变化对土壤胞外酶活性的影响。为探明亚热带森林与碳氮磷相关的土壤胞外酶活性对长期土壤增温、去凋和切根的响应, 本研究基于哀牢山亚热带常绿阔叶林土壤长期增温研究平台, 在已有土壤碳氮和土壤理化性质、土壤呼吸及土壤氮矿化相关研究(Wu *et al*., 2014, 2016; 鲁志云, 2016)的基础上, 结合土壤不同形态碳氮含量开展与碳氮磷生物地球化学过程相关的土壤酶活性的研究(土壤酶的名称、缩写及功能详见表1), 探讨长期去凋、切根、切根并增温处理对哀牢山亚热带常绿阔叶林土壤胞外酶活性的影响, 得出土壤酶动态对碳源输入变化和温度变化的响应, 探明土壤胞外酶与土壤不同形态碳氮之间的关系, 为该生态系统土壤碳氮生物地球化学关键过程对全球变化的响应提供土壤酶学的依据。

1 材料和方法

1.1 研究区概况

研究样地位于景东县太忠镇徐家坝的中国科学院哀牢山亚热带森林生态系统研究站(24.53° N, 101.02° E, 海拔2 480 m)。研究区域属亚热带山地常绿阔叶林潮湿气候带, 干湿季分明, 年平均气温11.3 ℃, 年降水量1 881.5 mm, 降水主要集中在5–10月。区域内土壤为山地黄棕壤, 质地为砂壤土, 植物种类丰富、群落类型多样、垂直带谱完整、过渡性特征明显(朱华, 2016), 表层土壤理化性质见表2 (鲁志云, 2016)。

1.2 实验设计

利用哀牢山亚热带常绿阔叶林模拟增温实验平台, 林下随机设置20个90 cm × 90 cm × 50 cm (长×宽×高)的呼吸箱(每个呼吸箱覆盖面积为0.81 m^2), 分别进行4种处理: 对照(CK)、切根(TR)、切根并增温(TR+W)、去凋(LR), 每种处理分别设置5个重复(Wu *et al*., 2014), 土壤酶相关实验均在呼吸箱内采样。各处理样方面积均为0.81 m^2, 对照不做实验处理。

表1 土壤酶的名称、缩写及功能
Table 1 Name, abbreviation and function of soil enzymes

酶 Enzyme	缩写 Abbreviation	功能 Function
β-葡萄糖苷酶 β-glucosidase	BG	分解易降解碳 Decomposition of labile carbon
多酚氧化酶 Polyphenol oxidase	POX	分解难降解碳 Decomposition of recalcitrant carbon
过氧化物酶 Peroxidase	PER	分解难降解碳 Decomposition of recalcitrant carbon
β-1,4-N-乙酰氨基葡萄糖苷酶 β-1,4-N-acetylglucosaminidase	NAG	分解氮 Hydrolyze nitrogen
酸性磷酸酶 Acid phosphatase	AP	分解磷 Hydrolyze phosphorus

表2 实验前土壤基本理化性质(平均值±标准偏差)
Table 2 Basic physical and chemical properties of soil before the experiment started in 2010 (mean ± *SD*)

观测项目 Observation item	测定值 Value
酸碱度 pH	4.25 ± 0.05
容重 Bulk density ($g·cm^{-3}$)	0.54 ± 0.02
总孔隙度 Total porosity (%)	71.7 ± 2.0
土壤最大持水量 Maximum water capacity of soil (%)	119.1 ± 6.0
有机质含量 Organic matter content ($g·kg^{-1}$)	175.1 ± 11.7
总氮含量 Total nitrogen content ($g·kg^{-1}$)	7.18 ± 0.34
碳氮比 C:N	14.1 ± 1.6

切根是通过在样方四周人工挖开一条0.5 m深的沟槽, 插入0.5 m高的塑料挡板以阻断活根进入。去凋则是定期人工移除呼吸箱内地表凋落物, 模拟增温采用红外辐射法, 即在切根并增温的呼吸箱上方约1.7 m高度安装一个800 W碳素红外辐射器, 采用连续增温的方式, 对下方的土壤进行持续的增温处理, 通过安装的高度与角度来调节增温的幅度, 使得增温处理下表层10 cm深度土壤温度与对照区相比, 升温幅度在(2.0 ± 0.5) ℃的范围内(Wu *et al*., 2016), 该模拟增温实验平台于2010年开始正式运作, 对照、去凋、切根、切根并增温处理均始于2010年。

1.3 样品采集与处理

2019年5月在20个呼吸箱内, 用环刀取0–5和5–10 cm的矿质土壤, 采用五点交叉取样法取样, 取样后将采集的新鲜土壤放进无菌袋中, 置于保温箱中迅速带回实验室进行分析。去除石砾、可见根系和动植物残体后, 过2 mm筛, 样品置于4 ℃无菌冰箱中保存, 用于测定铵态氮、硝态氮、溶解有机碳含量等基本理化指标, 并在两周内完成土壤酶活性测定。

1.4 测定指标及方法

土壤含水量(*SWC*)采用烘干称质量法测定(张学礼等, 2005)。土壤溶解有机碳(DOC)、溶解有机氮(DON)和溶解总氮(DN)含量用TOC/TN分析仪(Liqui TOC II, Elementar Analyzer system GmbH, Frankfurt, Germany)测定, 方法为Pt-催化高温煅烧法(680 ℃)(Zhou *et al*., 2019)。土壤硝态氮(NO_3^--N)和铵态氮(NH_4^+-N)含量使用连续流动分析仪(Skalar San++, Breda, the Netherlands)测定(Jones & Willett, 2006)。土壤矿质氮(Mineral-N)是以离子态存在于土壤中的氮, 以土壤NH_4^+-N及NO_3^--N含量相加进行计算。

土壤酶的分析方法: BG及NAG均采用硝基酚比色法进行测定, 分别以对硝基苯-β-D-吡喃葡糖苷、β-1,4-乙酰氨基葡萄糖苷为基质, 水解产生对硝基苯酚, 最后进行比色测定; 多酚氧化酶(POX)采用邻苯三酚比色法测定, 以邻苯三酚为基质, 反应生成醌类物质后进行比色测定; 过氧化物酶(PER)采用愈创木酚比色法测定, 以邻甲氧基苯酚为基质, 反应生成红棕色的4-邻甲氧基苯酚后进行比色测定; AP活性采用磷酸苯二钠比色法测定, 以磷酸酯作为基质, 通过比色测定水解后生成的酚量确定其活性(Martens *et al*., 1992)。

1.5 数据分析

所有数据均使用Excel 2018、R software和Canoco 5进行处理和统计分析。通过单因素方差分析对不同处理、不同深度间的土壤酶活性及其生态化学计量比、土壤碳氮养分含量及土壤理化性质的差异显著性进行分析(显著性水平设为$p = 0.05$)。酶C:N、C:P和N:P分别通过BG:NAG、BG:AP和NAG:AP计算, 并使用标准主轴分析(SMA)对lg (BG)、lg (NAG)、lg (AP)两两间进行回归, 通过回归斜率判断土壤养分的受限制情况(Hill *et al*., 2014), 为使该数据符合方差齐性和正态分布, 所有数据经过lg转化。方差分析和多重比较及标准主轴回归分别使用agricolae和smatr等R程序包完成(Warton *et al*., 2012)。使用Canoco 5软件, 以5种酶活性为响应变量, 并以土壤理化性质为解释变量做冗余分析(RDA), 所选的解释因子通过前向选择后使模型解释率达到最佳。用SigmaPlot 12.5及Canoco 5完成作图。

2 结果和分析

2.1 不同处理土壤理化性质比较

不同处理间0–5及5–10 cm层土壤基本理化性质见表3。以对照组为基准, 发现*SWC*、NO_3^--N和DOC含量在不同土层间无显著差异, 而NH_4^+-N、DN、DON、Mineral-N含量随土层深度增加分别显著下降了52.3%、59.5%、72.0%与51.2% ($p < 0.05$)。去除凋落物后, *SWC*、DN、DON和Mineral-N含量随土层深度增加均显著下降($p < 0.05$), 且去凋分别使0–5和5–10 cm的土壤含水量显著减少了23.0%和7.5% ($p < 0.05$); 去凋并未显著改变0–5 cm土层的其他理化性质, 但使5–10 cm土层的DOC和DN含量显著增加了29.5%和27.7% ($p < 0.05$)。

切根处理使NH_4^+-N、DOC、DN、DON和Mineral-N含量随土层深度增加均显著下降($p < 0.05$), 而NO_3^--N含量则随土层深度增加显著上升($p < 0.05$); 与对照处理相比, 切根并未显著改变0–5 cm土层的理化性质, 且仅使5–10 cm土层NO_3^--N含量显著增加了63.2% ($p < 0.05$); 切根并增温使NH_4^+-N、DN、DON和Mineral-N含量随土层深度增加均显著下降($p < 0.05$)。与切根处理相比, 切根并增温显著减少

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了0–5 cm土层NH_4^+-N和Mineral-N含量的41.0%和38.4%, 以及5–10 cm土层NO_3^--N含量的44.6% (p < 0.05)。

2.2 各处理不同深度土壤酶活性的比较

各实验处理下不同深度土壤酶活性见图1。对照组结果表明, 除土壤POX外, 0–5 cm土层的酶活性显著高于5–10 cm土层(p < 0.05)。与对照相比, 去凋使0–5 cm土层的AP活性显著下降(p < 0.05), 去凋和切根分别消除和弱化了AP随土层深度增加显著降低的效应(图1A)。与对照相比, 去凋、切根和切根并增

表3 不同处理下亚热带常绿阔叶林土壤基本理化性质(平均值±标准偏差, n = 5)
Table 3 Basic physical and chemical properties of soil in the subtropical evergreen broad-leaved forest under different treatments (mean ± *SD*, n = 5)

处理 Treatment	土壤含水量 Soil water content (%)	铵态氮含量 NH_4^+-N content ($mg \cdot kg^{-1}$)	硝态氮含量 NO_3^--N content ($mg \cdot kg^{-1}$)	溶解有机碳含量 Dissolved organic carbon content ($mg \cdot kg^{-1}$)	溶解总氮含量 Total dissolved nitrogen content ($mg \cdot kg^{-1}$)	溶解有机氮含量 Dissolved organic nitrogen content ($mg \cdot kg^{-1}$)	矿质氮含量 Mineral-N content ($mg \cdot kg^{-1}$)
0–5 cm							
CK	34.35 ± 2.30^{aA}	61.11 ± 11.30^{abA}	10.26 ± 3.75^{aA}	235.88 ± 21.76^{aA}	118.79 ± 16.82^{abA}	47.43 ± 7.77^{aA}	71.36 ± 9.19^{abA}
LR	26.35 ± 0.81^{bA}	43.74 ± 4.55^{bA}	10.03 ± 3.31^{aA}	267.48 ± 21.10^{aA}	93.92 ± 4.01^{bA}	40.16 ± 3.41^{aA}	53.76 ± 1.49^{bA}
TR	33.65 ± 1.35^{aA}	89.08 ± 6.10^{aA}	2.49 ± 0.27^{aA}	259.62 ± 17.47^{aA}	143.56 ± 7.52^{aA}	51.99 ± 8.12^{aA}	91.57 ± 5.93^{aA}
TR+W	29.41 ± 1.16^{abA}	52.56 ± 1.19^{bA}	3.90 ± 0.16^{aA}	232.33 ± 20.29^{aA}	103.89 ± 7.87^{abA}	47.44 ± 8.38^{aA}	56.45 ± 1.31^{bA}
5–10 cm							
CK	32.44 ± 1.07^{aA}	29.12 ± 3.22^{aB}	5.73 ± 0.23^{bA}	207.73 ± 13.46^{bA}	48.11 ± 2.88^{bB}	13.27 ± 4.96^{aB}	34.84 ± 3.09^{aB}
LR	30.00 ± 0.58^{bB}	28.72 ± 1.68^{aA}	7.55 ± 0.74^{abA}	269.07 ± 13.14^{aA}	61.43 ± 2.79^{aB}	25.16 ± 1.52^{aB}	36.27 ± 2.34^{aB}
TR	32.56 ± 0.72^{aA}	28.88 ± 1.77^{aB}	9.35 ± 0.90^{aB}	189.94 ± 10.05^{bB}	52.78 ± 4.49^{abB}	14.55 ± 3.98^{aB}	38.23 ± 1.73^{aB}
TR+W	30.95 ± 0.37^{abA}	33.42 ± 1.94^{aB}	5.18 ± 0.75^{bA}	214.82 ± 9.62^{bA}	53.44 ± 3.15^{abB}	14.83 ± 2.20^{aB}	38.60 ± 2.01^{aB}

CK, 对照处理; LR, 去除地表凋落物处理; TR, 切根处理; TR+W, 切根+增温处理。不同小写字母表示相同深度不同处理间差异显著(p < 0.05), 不同大写字母表示相同处理不同深度土壤之间差异显著(p < 0.05)。
CK, control; LR, litter removal; TR, root removal; TR+W, root removal + warming. Different lowercase letters indicate significant differences among different treatments at the same soil depth (p < 0.05). Different uppercase letters indicate significant differences among different soil depths in the same treatment (p < 0.05).

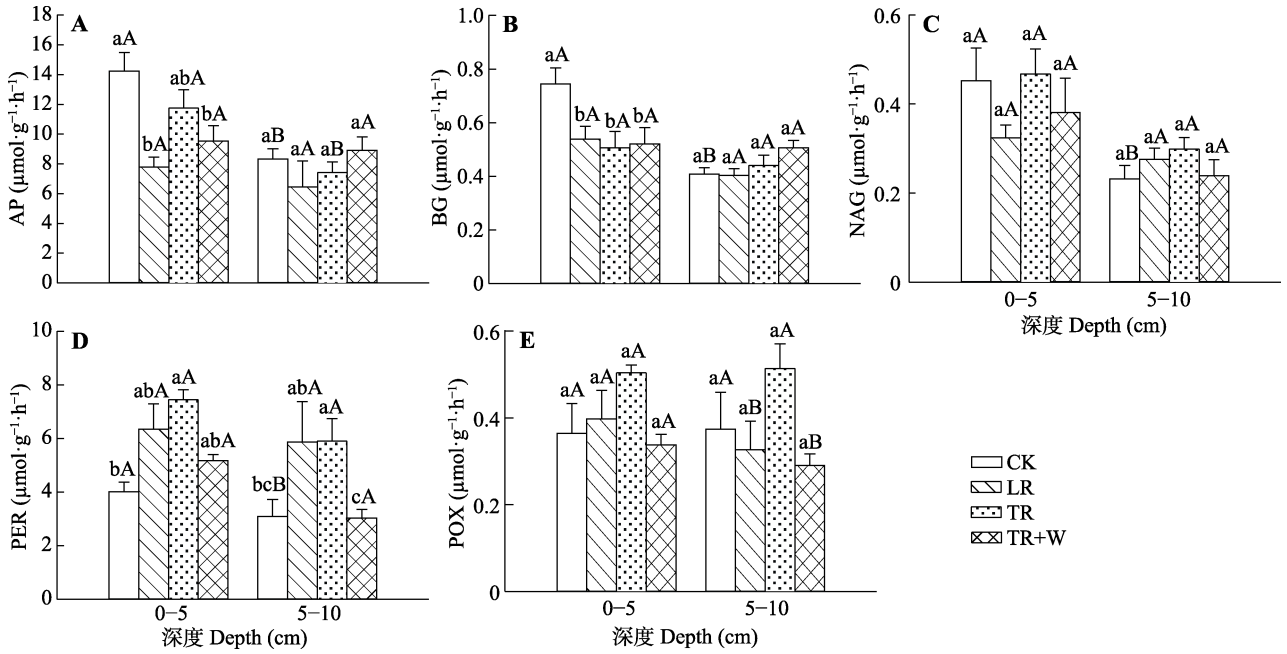

图1 亚热带常绿阔叶林不同处理和深度土壤酶活性的变化(平均值+标准偏差, n = 5)。CK, 对照处理; LR, 去除地表凋落物处理; TR, 切根处理; TR+W, 切根+增温处理。不同小写字母表示相同深度不同处理间差异显著(p < 0.05), 不同大写字母表示相同处理不同深度土壤之间差异显著(p < 0.05)。AP, 酸性磷酸酶; BG, β-葡萄糖苷酶; NAG, β-1,4-N-乙酰氨基葡萄糖苷酶; PER, 过氧化物酶; POX, 多酚氧化酶。

Fig. 1 Changes of enzyme activities under different treatments and depths in the subtropical evergreen broad-leaved forest (mean + *SD*, n = 5). CK, control; LR, litter removal; TR, root removal; TR+W, root removal + warming. Different lowercase letters indicate significant differences among different treatments at the same soil depth (p < 0.05). Different uppercase letters indicate significant differences among different soil depths in the same treatment (p < 0.05). AP, acid phosphatase; BG, β-glucosidase; NAG, β-1,4-N-acetylglucosaminidase; PER, peroxidase; POX, polyphenol oxidase.

温均显著降低了0–5 cm土层的BG活性($p < 0.05$), 但是对5–10 cm土层的BG活性影响不显著, 各处理的BG活性在0–5和5–10 cm土层中无显著差异(图1B)。NAG活性并未随着土层深度的变化而变化, 对去凋、切根和切根并增温的响应在不同土层均不显著(图1C)。与对照相比, 切根显著增加了两个土层土壤PER活性($p < 0.05$), 但切根并增温后5–10 cm土层PER活性则表现为显著下降(图1D)($p < 0.05$)。与对照相比, 不同土层中POX活性对实验处理的响应不显著, 与0–5 cm土层相比, 去凋和切根并增温使5–10 cm土层的POX活性显著下降($p < 0.05$)。

2.3 不同深度土壤酶的生态化学计量比

对照组结果表明, 哀牢山亚热带常绿阔叶林0–5和5–10 cm土层BG:NAG分别为1.80和1.89; BG:AP均为0.05; NAG:AP均为0.03。BG、NAG和AP的生态化学计量比在相同土层的不同处理下无显著差异, 在相同处理下的不同土层之间也无显著差异(图2)。主轴回归分析结果表明lg (BG)、lg (NAG)和lg (AP)之间只有0–5 cm土层存在显著的线性关系, 回归斜率见图3, 0–5和5–10 cm层土壤lg (BG):lg (NAG):lg (AP)均为1:0.9:1.5。

2.4 不同深度土壤酶活性的冗余分析

不同深度土壤酶活性的冗余分析结果见图4, 通过前向选择筛选出NH_4^+-N、NO_3^--N、DOC含量及*SWC* 4个解释率较高的因子作为解释变量, 探讨其与0–5和5–10 cm土壤酶活性的关系。在0–5 cm层(图4A)中, RDA1和RDA2分别解释了51.18%和4.50%的变量, 其中*SWC*对0–5 cm层的土壤酶活性的影响最大($p = 0.002$), 解释了0–5 cm层土壤酶活性变化的37.4%。5–10 cm土层(图4B)中, RDA1和RDA2的总解释率仅30.1%, 低于0–5 cm层。5–10 cm层的土壤酶活性则主要受NH_4^+-N含量影响($p = 0.03$), 其解释了5–10 cm层土壤酶活性变化的20.4%。

3 讨论

3.1 土壤酶活性对增温和碳源输入变化的响应

过氧化物酶(PER)、多酚氧化酶(POX)和β-葡萄糖苷酶(BG)与碳循环密切相关, 可催化木质素、腐殖质以及纤维素的降解(Baldrian, 2009)。该研究中PER活性不同于POX和BG活性, 切根显著增加了两个土层PER活性, 去凋、切根并增温处理下活性未显著改变, 这与前人研究结果(Michalak, 2006)一致。说明凋落物的存在对PER活性影响较小, 而根系分泌物可能会抑制PER活性, 增温则消除了该抑制现象, 说明PER活性对温度可能更敏感。对POX而言, 两个土层中POX活性对实验处理的响应均不显著, 与魏翠翠等(2018)的结果相同, 但本实验设置已有9年, 仍未出现随培养时间延长显著降低(Veres *et al*., 2015)的现象。对BG而言, 其酶解产物是土壤微生物生长的重要碳来源。本研究中, 实验处理降低了0–5 cm土层BG活性, 却不影响在5–10 cm土层BG活性。其中去凋后土壤含水量显著下降, 土壤含水量影响着BG催化土壤碳转化过程, 多项研究表明, 当土壤含水量降低时, BG活性会显著降

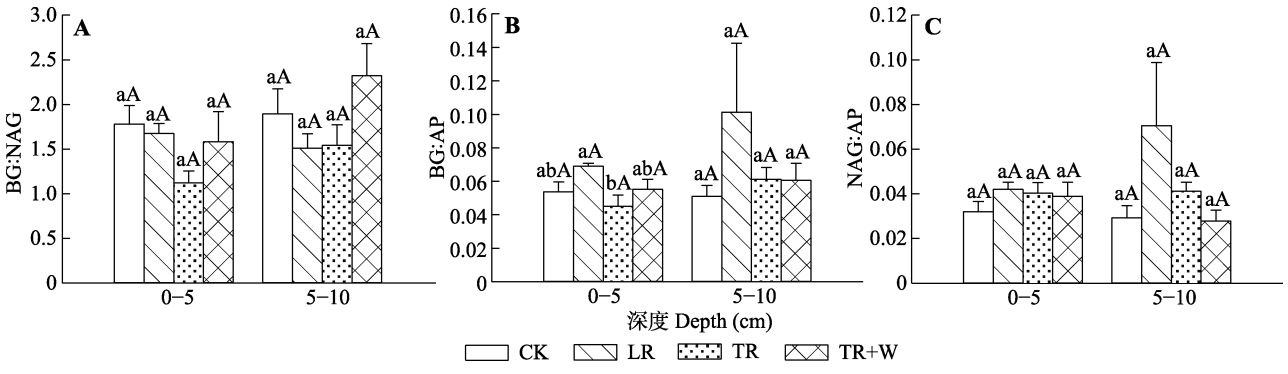

图2 亚热带常绿阔叶林不同处理和深度土壤酶的化学计量比(平均值+标准偏差, $n = 5$)。CK, 对照处理; LR, 去除地表凋落物处理; TR, 切根处理; TR+W, 切根+增温处理。不同小写字母表示相同深度不同处理间差异显著($p < 0.05$), 不同大写字母表示相同处理不同深度土壤之间差异显著($p < 0.05$)。AP, 酸性磷酸酶; BG, β-葡萄糖苷酶; NAG, β-1,4-N-乙酰氨基葡萄糖苷酶。

Fig. 2 Stoichiometric ratios of soil enzymes at different treatments and depths in the subtropical evergreen broad-leaved forest (mean + *SD*, $n = 5$). CK, control; LR, litter removal; TR, root removal; TR+W, root removal + warming. Different lowercase letters indicate significant differences among different treatments at the same soil depth ($p < 0.05$). Different uppercase letters indicate significant differences among different soil depths in the same treatment ($p < 0.05$). AP, acid phosphatase; BG, β-glucosidase; NAG, β-1,4-N-acetylglucosaminidase.

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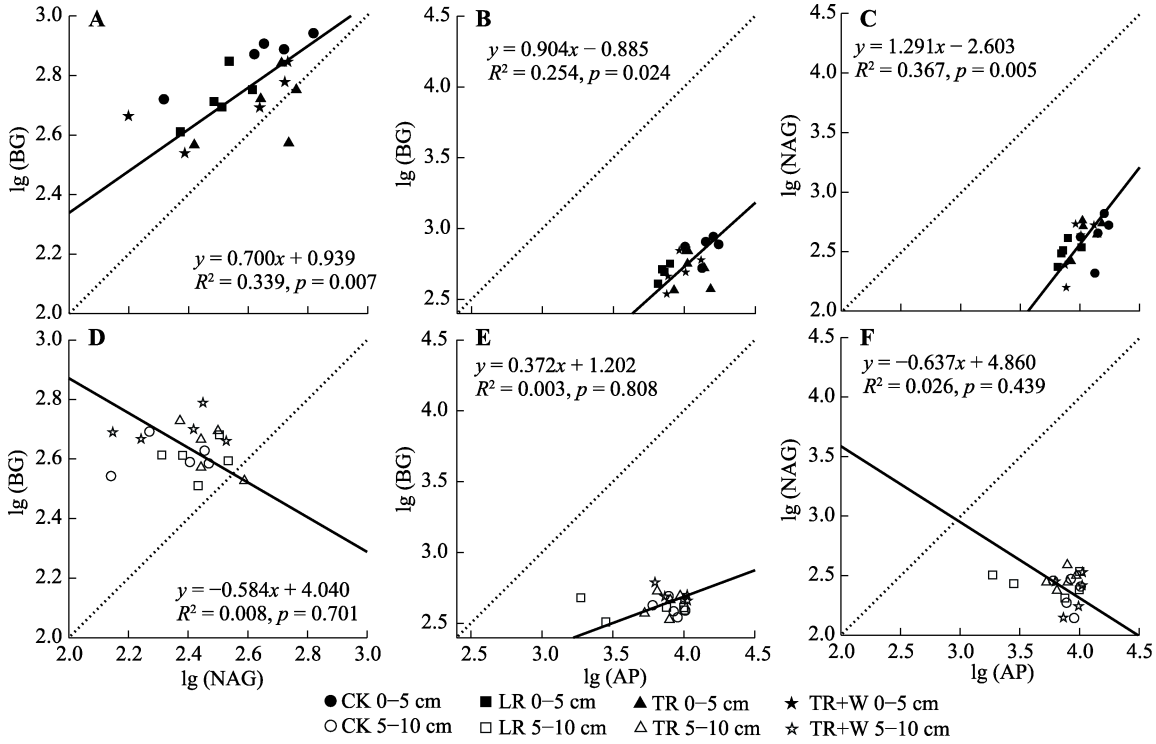

图3 亚热带常绿阔叶林0–5 (**A**、**B**、**C**)和5–10 cm (**D**、**E**、**F**)土层BG、NAG和AP活性关系的标准主轴回归分析(n = 20)。CK, 对照处理; LR, 去除地表凋落物处理; TR, 切根处理; TR+W, 切根+增温处理。AP, 酸性磷酸酶; BG, β-葡萄糖苷酶; NAG, β-1,4-N-乙酰氨基葡萄糖苷酶。

Fig. 3 Standardized major axis regressions of the log-transformed soil BG, NAG and AP activities in 0–5 (**A, B, C**) and 5–10 cm (**D, E, F**) soil layers in the subtropical evergreen broad-leaved forest (n = 20). CK, control; LR, litter removal; TR, root removal; TR+W, root removal + warming. AP, acid phosphatase; BG, β-glucosidase; NAG, β-1,4-N-acetylglucosaminidase.

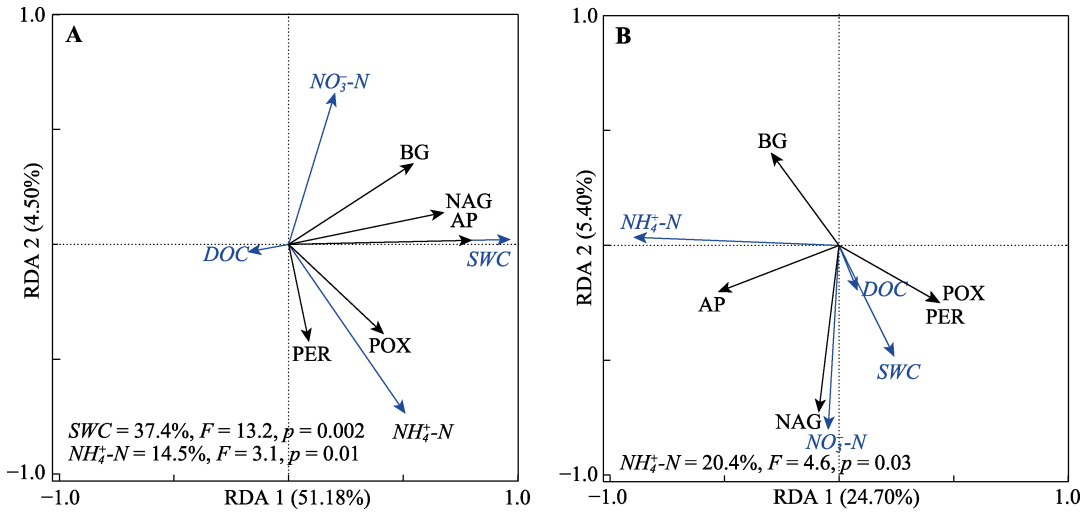

图4 亚热带常绿阔叶林土壤酶活性与土壤理化性质关系的冗余分析(RDA)。NH_4^+-*N*, 铵态氮含量; NO_3^--*N*, 硝态氮含量; *DOC*, 溶解有机碳含量; *SWC*, 土壤含水量。AP, 酸性磷酸酶; BG, β-葡萄糖苷酶; NAG, β-1,4-N-乙酰氨基葡萄糖苷酶; PER, 过氧化物酶; POX, 多酚氧化酶。

Fig. 4 Redundancy analysis (RDA) of soil enzyme activities and physical and chemical properties in the subtropical evergreen broad-leaved forest. NH_4^+-*N*, ammonium nitrogen content; NO_3^--*N*, nitrate nitrogen content; *DOC*, dissolved organic carbon content; *SWC*, soil water content. AP, acid phosphatase; BG, β-glucosidase; NAG, β-1,4-N-acetylglucosaminidase; PER, Peroxidase; POX, Polyphenol oxidase.

低(Wang & Lu, 2006; Steinweg *et al*., 2012), 这是由于BG的活性很大程度上依赖于基质的供应, 而主要产生这种酶的微生物在表层土壤中最为活跃(Wang & Lu, 2006), 因此, 去凋会显著降低0–5 cm土

层BG活性, 与前人研究结果(Chaer *et al*., 2009)一致。

β-1,4-N-乙酰氨基葡萄糖苷酶(NAG)与氮循环密切相关, 它主要被认为是一种甲壳素降解酶, 其活性可以表征土壤氮状况(Stone *et al*., 2014)。本研究中, 两个土层中NAG活性对实验处理的响应均不显著, 只有去凋显著降低了土壤含水量, 但处理后的土壤含水量似乎未达到NAG的临界阈值, 因此NAG活性也并未受到抑制, 与前人研究结果(江淼华等, 2018)一致。

AP可将有机磷转化为无机磷, 与磷循环关系密切, 其活性的高低可以作为植物和微生物无机磷有效性的指标(Piotrowska-Długosz & Charzyński, 2015)。本研究中去除凋落物显著降低了0–5 cm土层AP活性, 但没有引起5–10 cm土层AP活性的显著变化(图1A), 这与前人研究结果(郑卫国等, 2011)相似, 说明凋落物的存在有利于增加AP活性, 但该效应很难到达5–10 cm土层。切根本身不显著影响AP活性, 但切根并增温处理对两个土层AP活性的影响和去凋处理相同。一般而言增温可促进AP活性(Sardans *et al*., 2008; Stone *et al*., 2012), 但考虑到AP活性易受自身酶解产物影响而可能出现先升后降的情况, 同时增温和切根也可能出现交互效应, 使总体表现为显著降低。可见未来全球变暖的情况下, 云南哀牢山亚热带常绿阔叶林0–5 cm土层AP活性可能会受到限制, 而凋落物输入对AP活性存在促进作用, 切根则无显著影响。

3.2 土壤酶生态化学计量特征

由于微生物生物量C:N:P具有一定的稳定性(Cleveland & Liptzin, 2007), 因此土壤酶生态化学计量比也表现为相对稳定(Sinsabaugh *et al*., 2008)。该研究中酶C:P和N:P远低于全球主要陆地生态系统土壤酶C:P和N:P的平均值0.62和0.44, 而酶C:N则略高于平均值1.14 (Sinsabaugh *et al*., 2009), 说明AP活性远远高于BG和NAG活性, 基于全球尺度上BG、NAG和AP对数转化后比值约为1:1:1 (Sinsabaugh *et al*., 2008)。本研究中两个土层比值大体相同, 都表现为lg (AP)比值偏大, 说明该地区受磷限制。Allison等(2010)研究表明当微生物的生长受到某元素限制时, 会增加与该元素相关胞外酶的活性, 因此该地土壤AP活性较高, 与Waring等(2014)的研究结果一致。另有研究表明丰富的降水也会增加表层土壤中磷的淋溶, 这会进一步降低磷的有效性(Waring *et al*., 2014), 本研究样地年降水量可达1 800 mm以上, 且集中在5–10月, 属于典型的湿性常绿阔叶林(朱华, 2016), 土壤磷淋溶强烈, 本地土壤AP活性偏高和降水量大联系紧密。

3.3 酶活性变化的关键驱动因子

驱动土壤胞外酶活性变化的生态环境因子十分复杂, 由于时间和空间的异质性, 不同生态系统的关键生态因子是动态变化的。冗余分析结果表明土壤含水量和NH_4^+-N含量是驱动0–5 cm深度土壤胞外酶活性变化的主要影响因子, 并且NH_4^+-N含量也对5–10 cm深度土壤胞外酶活性影响显著。水分的减少可能造成多种酶活力的降低(Steinweg *et al*., 2013), 结合不同处理结果发现去凋显著降低了土壤含水量, 且造成0–5 cm深度AP和BG活性的显著降低, 冗余分析结果也表明AP与BG与土壤含水量呈显著正相关关系, 也说明在云南哀牢山亚热带常绿阔叶林地区, 土壤胞外酶活性易受水分条件的制约。土壤有效氮含量对于森林生态系统的物质转化和能量循环具有重要意义, Sinsabaugh等(2002)研究表明, 有效氮含量与碳循环相关的酶活性呈正相关趋势。此外, 土壤中有效氮含量与磷循环相关酶活性之间的联系在磷限制地区尤其重要(Harrington *et al*., 2001), 本研究中的βG、POX和PER活性均与碳循环密切相关, AP活性与磷循环密切相关, 且该地区是磷限制区, 冗余分析的结果也显示出NH_4^+-N含量与PER、POX和AP活性呈显著正相关关系, 故可以解释有效氮中的NH_4^+-N含量在驱动不同深度土壤胞外酶活性变化的过程中起到了关键作用。

4 结论

本研究中去凋后0–5 cm层土壤含水量、AP和BG活性均显著下降, 说明0–5 cm土层AP和BG活性更可能受土壤含水量调控。切根后只有PER活性上升, 土壤理化性质并无显著改变, 说明植物根系本身对PER活性可能存在一定的抑制作用。此外, 去凋、切根及切根并增温处理对土壤POX和NAG活性的影响不显著, 说明本地土壤POX和NAG活性较为稳定。综上, 凋落物、根系是森林生态系统养分循环的重要参与者, 它们通过影响土壤理化性质而影响土壤酶活性, 而根系本身对部分土壤酶也可能存在一定的抑制作用, 但也有一些土壤酶的活性则保持稳定, 并不受凋落物、根系等的影响, 故探明土壤

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胞外酶活性与凋落物碳输入、根系碳输入和温度变化关系, 可为该生态系统土壤碳氮生物地球化学关键过程对全球变化的响应提供土壤酶学的依据。

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