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科尔沁沙质草地不同水热梯度 土壤胞外酶活性

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摘要: 土壤胞外酶被认为是有机质分解的直接因素, 而草地生态系统脆弱且对气候变化敏感。全球变化背景下胞外酶活性在沙质草地土壤碳和养分循环过程中扮演重要角色。本研究以水热梯度明显的科尔沁沙质草地为研究对象, 探究区域水热梯度变化对沙质草地土壤胞外酶活性 (EEA) 的影响规律及环境因子与 EEA 的相关关系。酶活性测定包括参与土壤碳循环的纤维素酶及参与氮循环的脲酶与碱性蛋白酶。结果表明: 1) 随着温度升高 (2.1~6.4 °C), 土壤脲酶活性先升高后降低, 但随着降水减少 (451.1~370.0 mm), 脲酶活性先降低后升高。温度升高显著增加了土壤碱性蛋白酶活性 ($P < 0.05$), 降水减少显著降低了碱性蛋白酶活性 ($P < 0.05$)。此外温度和降水条件变化对土壤纤维素酶活性无显著影响 ($P > 0.05$)。2) 土壤脲酶活性与电导率、含水率、极细砂及黏粉粒含量呈显著正相关关系 ($P < 0.05$), 与土壤温度、中粗砂、细砂含量呈负相关; 土壤纤维素酶活性与含水率呈正相关关系, 与土壤温度呈负相关关系; 土壤碱性蛋白酶活性与含水率呈显著正相关关系 ($P < 0.05$), 与土壤温度呈负相关关系。3) 土壤含水率、温度、黏粉粒含量是沙质草地土壤 EEA 的重要影响因素, 其中土壤含水率是 EEA 最主要的驱动因子。本研究结果为水热条件变化对沙质草地生态系统土壤碳氮生物地球化学循环过程的影响提供了土壤生态酶学理论依据。

关键词: 水热梯度; 增温; 降水减少; 沙质草地; 土壤温度; 土壤含水率; 土壤胞外酶活性

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Soil extracellular enzyme activities in different Horqin sandy grassland soil hydrothermal gradients

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Abstract: Soil extracellular enzymes affect organic matter decomposition, whereas grassland ecosystems are unstable and sensitive to climate change. Extracellular enzyme activity is important in carbon and nutrient cycling in sandy grassland soils considering global climate change. The present study investigates the effect of regional hydrothermal gradient changes on the extracellular enzyme activity (EEA) in the Horqin sandy grassland soils and the correlation between environmental factors and EEA. The enzyme activity indicators included cellulase involved in the soil carbon cycle and urease and alkaline protease involved in the nitrogen cycle. The results showed that soil urease activity increased and then decreased with increasing regional temperature (2.1~6.4 °C). Contrastingly, with decreasing regional precipitation (451.1~370.0 mm), the

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urease activity decreased and then increased. An increase in regional temperature significantly increased soil alkaline protease activity ($P < 0.05$), whereas a decrease significantly decreased alkaline protease activity ($P < 0.05$). However, there was no significant difference in the effect of changes in regional temperature and precipitation on soil cellulase activity ($P > 0.05$). Soil urease activity was significantly and positively correlated with electrical conductivity, water content, very fine sand, and clay and silt ($P < 0.05$). Contrastingly, soil urease activity was negatively correlated with soil temperature and coarse and fine sand contents. Soil cellulase activity was positively correlated with water content and negatively correlated with soil temperature. Soil alkaline protease activity was positively correlated with soil water content ($P < 0.05$) and negatively correlated with soil temperature. Furthermore, soil water content, temperature and clay and silt influenced EEA in the Horqin sandy grassland soils, among which the direct and indirect effects of soil water content on EEA were higher than those of other environmental factors. The results of the present study provide a theoretical basis for soil ecoenzymology on the effects of changing hydrothermal conditions on the soil carbon and nitrogen biogeochemical cycling processes in sandy grassland ecosystems.

Keywords: hydrothermal gradient; warming; precipitation reduction; sandy grassland; soil temperature; soil moisture content; soil extracellular enzyme activity

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土壤微生物及胞外酶在生态系统生物地球化学循环过程中发挥着重要作用。在全球气候变化背景下,生物与环境因子的改变深刻影响了土壤微生物新陈代谢活动及胞外酶活性(extracellular enzyme activity, EEA)^[1]。生物圈的净初级生产主要由微生物消耗,微生物代谢驱动了全球碳循环和养分循环^[2]。土壤中生物生长所需的碳源和养分等生长基质主要通过发生在细胞外的酶催化反应分解^[3],如胞外酶可以分解植物和微生物细胞壁,解聚有机大分子物质并产生可溶性的底物供微生物同化利用^[4],土壤胞外酶可催化有机化合物的矿化、氧化和水解,从而在环境中发挥关键作用^[5]。因此,EEA被认为是微生物介导的有机质分解的直接因素和限速步骤^[6]。当前土壤EEA的测定已成为气候变化实验中检查土壤微生物反应的普遍工具^[7],可以对其其他土壤碳及养分过程分析方法起到有益补充^[8],对于探索气候变化对土壤有机质分解的影响机制至关重要^[9]。

工业革命以来,全球气温显著升高。与气候变暖同步,全球降水格局也发生了明显改变。气候变暖和降水格局的改变已经对陆地生态系统的结构和功能产生了重大影响^[10]。气候变化可以直接或间接地影响土壤EEA,其中关键的影响因素包括EEA的温度依赖性、水分对酶的扩散性和底物可利用性^[9]。已有研究证明土壤温度^[11]、水分^[12]、pH、有机

质含量等土壤理化因子^[13]是土壤EEA变化的重要驱动因素。植被类型和土地利用方式也会影响土壤酶的分布^[14]。但EEA具有高度的动态性和环境依赖性,在不同的生态系统对环境因子的响应表现特殊。草地是中国最大的陆地生态系统^[15],干旱半干旱草地水资源有限、植被覆盖稀少、土壤相对贫瘠^[16]、生态系统脆弱且对气候变化敏感^[17],温度和水分已成为干旱半干旱草地生态系统可持续发展的主要限制性因素^[18-19]。

科尔沁沙地位于中国北方干旱半干旱农牧交错带,多种生态系统并存,水热梯度变化明显,其沙质土壤极易受到风力侵蚀^[20],气候变化背景下草地沙化、盐渍化及退化现象严重^[21],是中国北方沙漠化最严重的地区之一。近60年来科尔沁沙地年平均气温显著上升,以冬、春两季表现明显。降水年际变化大,其中夏季降水显著下降^[22]。气温和降水格局的变化一定程度上加剧了科尔沁沙地干旱化、荒漠化进程。目前关于水热条件变化对于干旱半干旱沙质草地土壤胞外酶活性的研究较少,尤其是自然水热梯度上胞外水解酶活性的变化规律还有待深入探究^[1],厘清温度和降水格局变化对沙质草地生态系统的影响特征和机制尤为重要。因此本研究以科尔沁沙质草地为研究对象,分析不同水热梯度下土壤理化性质和EEA,揭示土壤EEA对温度与降水变化的响应规律,为北方农牧交错带生态修复、沙质

土壤治理及区域可持续发展提供科学依据和理论支撑。

1 材料与方法

1.1 研究区概况

研究区位于我国北方农牧交错带东南部的科尔沁沙地 (118°30′~123°30′ E, 42°30′~45°10′ N), 海拔 180~650 m。该区域属于温带大陆性半干旱气

候, 年均气温 5.8~6.4 ℃, 年均差与日均差均较大; 年均降水量 350~500 mm, 降水年际变化较大, 主要集中在 6 月—8 月, 年均蒸发量 1 500~2 500 mm, 干燥系数为 1.0~1.8。沙质平原广泛分布, 其中风沙土是主要土壤类型。该区域地上一地下生态系统水热条件梯度变化明显, 草地、沙地、农田多种生态系统并存, 是我国农牧交错带过渡型特征最为典型的区域。研究区植被基本特征如表 1 所列。

表 1 研究区域植被基本特征
Table 1 Basic characteristics of the vegetation in the study region

水热梯度 Hydrothermal gradient		主要物种 Main species
T	LT	盐蒿(<i>Artemisia halodendron</i>)、虎尾草(<i>Chloris virgata</i>)、狗尾草(<i>Setaria viridis</i>)、芦草(<i>Phragmites australis</i>)、尖头叶藜(<i>Chenopodium acuminatum</i>)、蒺藜(<i>Tribulus terrester</i>)、大果虫实(<i>Corispermum macrocarpum</i>)、猪毛菜(<i>Salsola collina</i>)、画眉草(<i>Eragrostis pilosa</i>)
	MT	盐蒿(<i>Artemisia halodendron</i>)、胡枝子(<i>Lespedeza bicolor</i>)、狗尾草(<i>Setaria viridis</i>)、虎尾草(<i>Chloris virgata</i>)、尖头叶藜(<i>Chenopodium acuminatum</i>)、草麻黄(<i>Ephedra sinica</i>)、蒺藜(<i>Tribulus terrester</i>)、马齿苋(<i>Portulaca oleracea</i>)
	HT	盐蒿(<i>Artemisia halodendron</i>)、狗尾草(<i>Setaria viridis</i>)、胡枝子(<i>Lespedeza bicolor</i>)、大果虫实(<i>Corispermum macrocarpum</i>)、虎尾草(<i>Chloris virgata</i>)、蒺藜(<i>Tribulus terrester</i>)、砂蓝刺头(<i>Echinops gmelini</i>)、尖头叶藜(<i>Chenopodium acuminatum</i>)、地锦(<i>Euphorbia humifusa</i>)、雾冰藜(<i>Bassia dasyphylla</i>)
P	HP	胡枝子(<i>Lespedeza bicolor</i>)、糙隐子草(<i>Cleistogenes squarrosa</i>)、狗尾草(<i>Setaria viridis</i>)、大果虫实(<i>Corispermum macrocarpum</i>)、毛马唐(<i>Digitaria chrysoblephara</i>)、大麻(<i>Cannabis sativa</i>)、地梢瓜(<i>Cynanchum thesioides</i>)、长萼鸡眼草(<i>Kummerowia stipulacea</i>)
	MP	盐蒿(<i>Artemisia halodendron</i>)、狗尾草(<i>Setaria viridis</i>)、胡枝子(<i>Lespedeza bicolor</i>)、大果虫实(<i>Corispermum macrocarpum</i>)、虎尾草(<i>Chloris virgata</i>)、蒺藜(<i>Tribulus terrester</i>)、砂蓝刺头(<i>Echinops gmelini</i>)、尖头叶藜(<i>Chenopodium acuminatum</i>)、地锦(<i>Euphorbia humifusa</i>)、雾冰藜(<i>Bassia dasyphylla</i>)
	LP	糙隐子草(<i>Cleistogenes squarrosa</i>)、盐蒿(<i>Artemisia halodendron</i>)、胡枝子(<i>Lespedeza bicolor</i>)、狗尾草(<i>Setaria viridis</i>)、蒺藜(<i>Tribulus terrester</i>)、砂蓝刺头(<i>Echinops gmelini</i>)、猪毛菜(<i>Salsola collina</i>)

T表示温度梯度, LT、MT、HT分别表示低温、中温、高温度区域; P表示降水梯度, HP、MP、LP分别表示高降水、中降水、低降水区域; 下同。
T: temperature gradient, LT: low temperature, MT: medium temperature, HT: high temperature; P: precipitation gradient, HP: high precipitation, MP: medium precipitation, LP: low precipitation regions. This is applicable for the following figures and tables as well.

1.2 试验设计

如图 1 所示, 在科尔沁沙地主体区域的纬度方向上由北向南依次选择扎鲁特旗 (年均温 2.1~5.8 ℃^[23], 相对低温区, LT)、阿鲁科尔沁旗 (年均温 5.5 ℃^[24], 相对中温区, MT)、奈曼旗 (年均温 6.1~6.4 ℃^[25], 相对高温区, HT) 作为温度梯度区域; 经度方向上由东向西依次选择科尔沁左翼后旗 (年均降水量 451.1 mm^[26], 相对高降水区域, HP)、奈曼旗 (年均降水量 343.3~451.4 mm^[25], 相对中降水区域, MP)、翁牛特旗 (年均降水量 370 mm^[27], 相对低降水区域,

LP) 作为降水梯度区域。
植被生长盛期分别在每个温度与降水区域随机选取植被与土壤异质性较小的各 3 个调查点作为代表性取样点 (温度梯度: LT₁、LT₂、LT₃、MT₁、MT₂、MT₃、HT₁、HT₂、HT₃; 降水梯度: HP₁、HP₂、HP₃、MP₁、MP₂、MP₃、LP₁、LP₂、LP₃), 采样点均为自然围封沙质草地, 无放牧践踏与明显刈割, 草地植被高度、盖度均匀。在每个取样点的 100 m×100 m 区域内随机选取 6 个 1 m×1 m 的样方作为样点取样重复。试验设置两类自然区域梯度, 15 个取样点, 共 90 个样方重复。

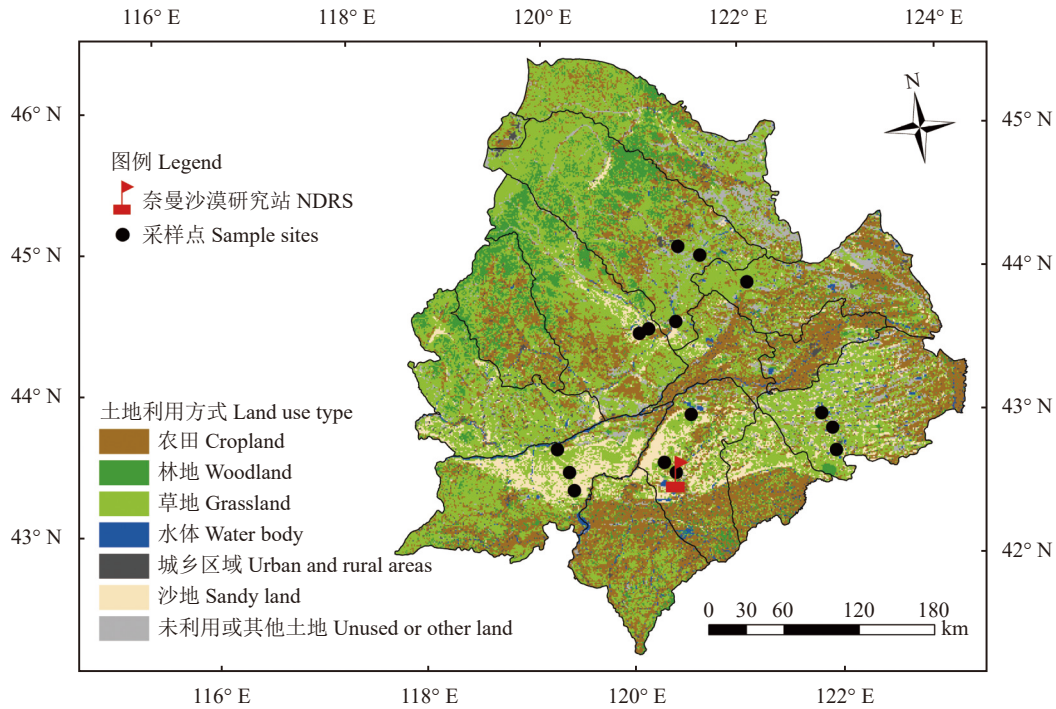


图 1 科尔沁沙地研究区位置与研究采样点

Figure 1 Horqin sandy grassland map indicating sampling sites in the present study

1.3 样品采集与测定

2021 年 7 月下旬对科尔沁沙地随机选定的温度和降水梯度样点进行植被调查和土壤随机混合取样。用直径 2.8 cm 土钻于 1 m × 1 m 样方的 0—10 cm 土层获取土样, 每个样方 7 钻, 充分混合后, 将部分土样装满铝盒并盖紧后用于土壤含水率测定 (烘干恒重法, 105 °C, 24 h), 剩余部分土样带回实验室进行后续测定。土壤样品自然风干后, 过 2 mm 筛进一步去除动植物残体和石块, 用于测定土壤理化性质和 EEA, 包括土壤 pH (电极法, 雷磁 PHS-3C pH 计, 上海, 中国)、电导率 (电极法, 雷磁 DDS-307A 电导率仪, 上海, 中国)、机械组成 (干筛法, ISSCAS, 中国科学院南京土壤研究所), 土壤脲酶 (Urease) 活性 (水解酶, 靛酚蓝比色法, pH 6.7 柠檬酸盐缓冲液, 630 nm, Solarbio BC0120)、纤维素酶 (Cellulase) 活性 (水解酶, 3,5-二硝基水杨酸比色法, pH 5.5 醋酸盐缓冲液, 540 nm, Solarbio BC0150) 和碱性蛋白酶 (Alkaline protease) 活性 (水解酶, 福林—酚比色法, pH 10.5 硼酸盐缓冲溶液, 680 nm, Solarbio BC0880)。土壤 10 cm 温度数据来源于全球高分辨率陆面模拟系统 (GLDAS)《NASA GES DISC GLDAS_NOAH025_M_2.1》数据集, 空间分辨率为 0.25° × 0.25°, 时间分辨

率为逐月^[28]。

1.4 数据处理与分析

试验数据经 Excel 2013 处理后, 采用 SPSS 25.0 软件统计分析, 方差分析与相关性分析之前对数据进行正态性检验、方差齐性检验, 并剔除异常值; 使用单因素方差分析 (one-way analysis of variance, ANOVA) 分别检验不同温度和降水梯度变化对土壤理化性质和 EEA 的显著性差异, 使用最小显著性差异法进行多重比较; 当数据方差不齐且经过转换后仍不满足方差齐性时, 使用 Welch's ANOVA 检验不同温度和降水梯度对土壤理化性质和 EEA 的显著性差异, 使用 Games-Howell 进行多重比较; 差异显著性水平均为 $\alpha = 0.05$; 使用 Pearson 相关系数分析土壤理化性质与 EEA 之间的相关性; 利用 R 语言 (R software version 4.0.3, lavaan 包) 构建结构方程模型分析环境因子对土壤 EEA 的直接和间接影响; 使用 Origin 2018 进行绘图分析。数据以平均值 ± 标准误的形式表示。

2 结果与分析

2.1 不同水热梯度下土壤基本理化性质特征

不同水热梯度下沙质草地土壤均表现为弱碱

性(表 2)。温度梯度上, 温度升高显著降低了沙质草地土壤 pH ($P < 0.05$), 其中 HT 的 pH 显著低于 MT ($P < 0.05$), LT 的 pH 与 HT 和 MT 相比差异不显著 ($P > 0.05$) (表 2)。温度增加对电导率没有显著影响 ($P > 0.05$), 但是其变化趋势与 pH 相似, 即 MT 的电导率显著高于 HT ($P < 0.05$)。随着温度增加, MT、HT 土壤含水率显著高于 LT ($P < 0.05$), MT 和 HT 含水率差异不显著 ($P > 0.05$)。降水梯度上, pH 与电导率表现出相似变化特征, 如表 3 所列, 随着降水减少 pH 与电导率极显著增加 ($P < 0.001$)。土壤含水率随降水减少显著降低 ($P < 0.01$), 与 HP 相比, MP 与 LP 含水率降幅分别为 2.09% 与 15.71% (表 2、表 3)。

不同水热条件下沙质草地土壤机械组成均表现为细砂占优势(表 4), 其次为中粗砂、极细砂, 黏粉粒含量在机械组成中占比最低。温度增加极显著影响了土壤细砂、极细砂和黏粉粒含量 ($P < 0.001$) (表 5), 细砂含量表现为 HT > LT > MT, 但极细砂和黏粉粒含量却表现为相反趋势, 极细砂含量表现为 MT > LT > HT; 黏粉粒含量表现为 MT > HT > LT。降水减少显著降低了细砂含量 ($P < 0.05$), 极显著增加了极细砂与黏粉粒含量 ($P < 0.001$), 其中与 HP 相比, LP 的细砂含量减少了 9.59%, 而极细砂与黏粉粒含量增幅达到 75.45% 与 219.12% (表 5)。

2.2 不同水热梯度下土壤胞外酶活性变化特征

如表 6 所列, 温度和降水梯度变化对沙质草地土壤脲酶 ($P < 0.001$) 和碱性蛋白酶 ($P < 0.05$) 均产生了显著影响, 对纤维素酶的影响无显著性差异 ($P > 0.05$)。其中温度变化极显著改变了土壤脲酶活性 ($P < 0.001$), 随着温度增加, 脲酶活性呈现先增加后减少的趋势, MT 脲酶活性显著高于 LT 和 HT ($P < 0.05$), 而 LT 脲酶活性均值高于 HT, 但差异不显著 ($P > 0.05$) (图 2); 相比于温度变化, 降水变化对脲酶活性的影响呈现相反的规律, 随着降水减少, 脲酶活性先减少后增加, MP 脲酶活性最低, 而 LP 脲酶活性显著高于 HP 和 MP ($P < 0.05$), 与后两者相比随着降水减少 LP 脲酶活性增幅分别为 18.24%、45.05% (图 2)。碱性蛋白酶活性在 HT、MT 显著高于 LT, 温度升高显著增加了碱性蛋白酶活性 ($P < 0.05$), 但是 HT、MT 之间碱性蛋白酶活性没有显著差异 ($P > 0.05$); 降水减少对碱性蛋白酶活性的影响较温度变

表 2 不同水热梯度下土壤理化性质
Table 2 Soil physical and chemical properties under different hydrothermal gradients

水热梯度 Hydrothermal gradient		pH	电导率 Electrical conductivity/ ($\mu\text{S}\cdot\text{cm}^{-1}$)	含水率 Moisture content/%
T	LT ₁	8.50 ± 0.04a	66.68 ± 0.94a	1.91 ± 0.17a
	LT ₂	8.03 ± 0.09b	36.34 ± 1.65b	1.37 ± 0.15b
	LT ₃	7.62 ± 0.06c	29.94 ± 1.71c	1.05 ± 0.08b
	LT	8.05 ± 0.10AB	44.32 ± 4.35AB	1.44 ± 0.12B
	MT ₁	8.00 ± 0.04c	53.92 ± 1.77b	2.94 ± 0.20a
	MT ₂	8.49 ± 0.02a	71.78 ± 2.13a	2.24 ± 0.06b
	MT ₃	8.14 ± 0.04b	34.54 ± 0.48c	1.39 ± 0.04c
	MT	8.21 ± 0.06A	53.41 ± 4.16A	2.19 ± 0.18A
	HT ₁	7.51 ± 0.04a	26.14 ± 1.02a	1.90 ± 0.06a
	HT ₂	8.33 ± 0.03b	60.58 ± 1.40b	1.88 ± 0.12a
	HT ₃	7.69 ± 0.03c	30.84 ± 1.21c	1.83 ± 0.08a
	HT	7.84 ± 0.10B	39.19 ± 4.13B	1.87 ± 0.05A
	P	HP ₁	7.36 ± 0.02a	35.36 ± 2.02a
HP ₂		6.94 ± 0.03b	23.10 ± 1.09b	1.76 ± 0.08a
HP ₃		7.39 ± 0.05a	27.40 ± 1.08b	1.80 ± 0.17a
HP		7.23 ± 0.06B	28.62 ± 1.57B	1.91 ± 0.08A
MP ₁		7.51 ± 0.04a	26.14 ± 1.02a	1.90 ± 0.06a
MP ₂		8.33 ± 0.03b	60.58 ± 1.40b	1.88 ± 0.12a
MP ₃		7.69 ± 0.03c	30.84 ± 1.21c	1.83 ± 0.08a
MP		7.84 ± 0.10A	39.19 ± 4.13A	1.87 ± 0.05A
LP ₁		7.42 ± 0.02b	39.56 ± 1.20b	1.40 ± 0.10b
LP ₂		7.48 ± 0.03b	43.02 ± 1.80b	1.66 ± 0.06a
LP ₃		8.60 ± 0.07a	56.84 ± 1.78a	1.75 ± 0.07a
LP		7.83 ± 0.15A	46.47 ± 2.17A	1.61 ± 0.06B

水热梯度中1、2、3表示同一温度或降水区域不同取样点; 同列不同大写字母表示不同温度或降水区域差异显著($P < 0.05$), 同列不同小写字母表示相同温度或降水区域不同取样点差异显著($P < 0.05$); 下同。

1, 2, 3 indicate different sampling sites in the same temperature or precipitation region. Different capital letters within the same column indicate significant differences in different temperature or precipitation regions at the 0.05 level, and different lowercase letters within the same column indicate significant differences between different sampling sites within the same temperature or precipitation regions at the 0.05 level. This is applicable for the following figures and tables as well.

化更加明显, 随着降水减少碱性蛋白酶活性显著降低 ($P < 0.01$), 表现为 HP > MP > LP (图 2)。

表 3 水热条件对沙质草地土壤理化性质的影响
Table 3 Effects of hydrothermal conditions on physical and chemical properties of the Horqin sandy grassland soils

水热梯度 Hydrothermal gradient	df	pH		电导率 Electrical conductivity		含水率 Moisture content	
		F	P	F	P	F	P
T	2	4.419	0.018	2.948	0.069	8.480	0.001
P	2	10.800	< 0.001	9.983	< 0.001	7.024	0.004

表 4 不同水热梯度下土壤机械组成
Table 4 Soil mechanical composition under different hydrothermal gradients

水热梯度 Hydrothermal gradient		中粗砂 Coarse sand (0.25 mm, 2 mm]/%	细砂 Fine sand (0.1 mm, 0.25 mm]/%	极细砂 Very fine sand (0.05 mm, 0.1 mm]/%	黏粉粒 Clay and silt (< 0.05 mm)/%
T	LT ₁	35.27 ± 1.01a	50.90 ± 1.57c	12.95 ± 1.37a	0.65 ± 0.11b
	LT ₂	29.02 ± 0.29b	64.00 ± 0.47a	6.29 ± 0.32b	0.40 ± 0.06b
	LT ₃	36.04 ± 0.60a	54.71 ± 0.68b	8.00 ± 0.31b	0.92 ± 0.08a
	LT	33.45 ± 0.92A	56.54 ± 1.57B	9.08 ± 0.88B	0.66 ± 0.07B
	MT ₁	25.44 ± 0.60c	47.88 ± 0.72b	24.26 ± 1.02a	2.35 ± 0.10a
	MT ₂	28.92 ± 0.52b	51.17 ± 0.34a	17.17 ± 0.87b	2.25 ± 0.40a
	MT ₃	35.42 ± 0.79a	52.87 ± 0.70a	10.60 ± 0.49c	0.93 ± 0.10b
	MT	29.93 ± 1.16A	50.64 ± 0.64C	17.34 ± 1.56A	1.84 ± 0.22A
	HT ₁	38.89 ± 0.67a	56.41 ± 0.67c	4.25 ± 0.14b	0.43 ± 0.11b
	HT ₂	29.34 ± 0.22b	61.38 ± 0.90b	7.44 ± 0.95a	1.91 ± 0.25a
	HT ₃	24.81 ± 0.54c	68.61 ± 0.52a	6.16 ± 0.19a	0.50 ± 0.09b
	HT	31.01 ± 1.59A	62.14 ± 1.39A	5.95 ± 0.46C	0.95 ± 0.20B
P	HP ₁	27.29 ± 0.65b	62.94 ± 0.92b	9.15 ± 1.00a	0.65 ± 0.05a
	HP ₂	23.29 ± 0.58c	68.32 ± 0.90a	7.23 ± 0.47ab	0.90 ± 0.19a
	HP ₃	33.70 ± 0.67a	61.05 ± 0.72b	5.15 ± 0.51b	0.49 ± 0.18a
	HP	28.09 ± 1.20A	64.10 ± 0.94A	7.17 ± 0.58B	0.68 ± 0.09B
	MP ₁	38.89 ± 0.67a	56.41 ± 0.67c	4.25 ± 0.14b	0.43 ± 0.11b
	MP ₂	29.34 ± 0.22b	61.38 ± 0.90b	7.44 ± 0.95a	1.91 ± 0.25a
	MP ₃	24.81 ± 0.54c	68.61 ± 0.52a	6.16 ± 0.19a	0.50 ± 0.09b
	MP	31.01 ± 1.59A	62.14 ± 1.39AB	5.95 ± 0.46B	0.95 ± 0.20B
	LP ₁	36.23 ± 0.57a	47.60 ± 0.72b	13.88 ± 0.83a	2.09 ± 0.18ab
	LP ₂	24.31 ± 1.13b	61.99 ± 0.94a	11.94 ± 0.52a	1.66 ± 0.21b
	LP ₃	21.06 ± 0.75c	64.26 ± 1.29a	11.92 ± 0.90a	2.75 ± 0.36a
	LP	27.20 ± 1.80A	57.95 ± 2.04B	12.58 ± 0.48A	2.17 ± 0.18A

表 5 水热条件对沙质草地土壤机械组成的影响
Table 5 Effects of hydrothermal conditions on the mechanical composition of the Horqin sandy grassland soils

水热梯度 Hydrothermal gradient	df	机械组成 Mechanical composition							
		中粗砂 Coarse sand (0.25 mm, 2 mm]		细砂 Fine sand (0.1 mm, 0.25 mm]		极细砂 Very fine sand (0.05 mm, 0.1 mm]		黏粉粒 Clay and silt (< 0.05 mm)	
		F	P	F	P	F	P	F	P
T	2	2.062	0.140	20.595	< 0.001	30.533	< 0.001	12.382	< 0.001
P	2	1.495	0.242	4.230	0.021	52.623	< 0.001	22.451	< 0.001

表 6 水热条件对沙质草地土壤脲酶、纤维素酶和碱性蛋白酶活性的影响

Table 6 Effects of hydrothermal conditions on urease, cellulase, and alkaline protease activities in the Horqin sandy grassland soils

水热梯度 Hydrothermal gradient	df	脲酶 Urease		纤维素酶 Cellulase		碱性蛋白酶 Alkaline protease	
		F	P	F	P	F	P
T	2	11.109	< 0.001	0.427	0.656	4.415	0.022
P	2	8.159	0.002	2.058	0.147	8.189	0.002

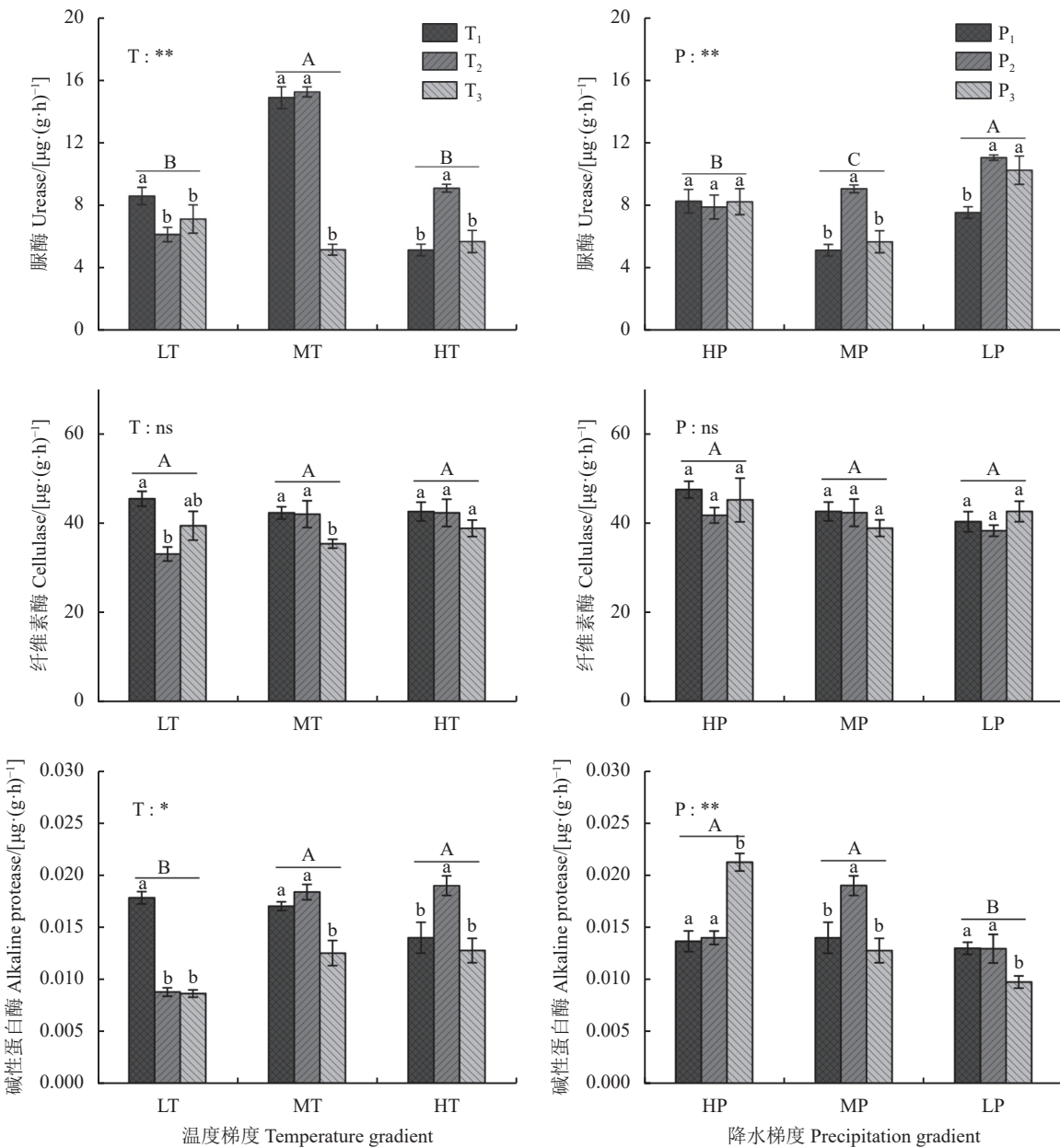


图 2 不同温度和降水梯度下沙质草地土壤脲酶、纤维素酶和碱性蛋白酶活性

Figure 2 Urease, cellulase, and alkaline protease activities in the Horqin sandy grassland soils under different temperature and precipitation gradients

*表示差异显著 ($P < 0.05$), **表示差异极显著 ($P < 0.01$), ns 表示无显著差异 ($P > 0.05$); 不同大写字母表示不同温度或降水区域之间的差异显著 ($P < 0.05$), 不同小写字母表示相同温度或降水区域不同取样点之间的差异显著 ($P < 0.05$).

* indicate significant difference, ** indicate highly significant difference, and ns indicate no significant difference; different capital letters indicate significant differences between different temperature or precipitation regions at the 0.05 level, and different lowercase letters indicate significant differences between different sampling sites in the same temperature or precipitation regions at the 0.05 level.

2.3 土壤理化性质、区域经纬度和海拔及土壤胞外酶活性的相关关系

如图 3a 所示, 区域温度变化条件下, 土壤 pH 只与电导率极显著正相关 ($P < 0.01$), 与其他环境因子没有显著相关关系; 电导率与黏粉粒含量显著正相关, 土壤温度和含水率分别与纬度和经度极显著负相关 ($P < 0.01$), 含水率与极细砂及黏粉粒显著正相关 ($P < 0.05$); 土壤机械组成部分, 细砂与极细砂含量显著负相关, 而极细砂与黏粉粒含量显著正相关 ($P < 0.05$)。脲酶活性与电导率、含水率呈显著正相关 ($P < 0.05$), 与极细砂、黏粉粒含量极显著正相关 ($P < 0.01$); 纤维素酶活性与其他因子均没有显著相关性; 与脲酶相似, 碱性蛋白酶与电导率极显著

正相关 ($P < 0.01$), 与含水率及脲酶活性显著正相关, 与经度显著负相关 ($P < 0.05$)。如图 3b 所示, 区域降水变化条件下, pH 与电导率, 电导率与黏粉粒含量均极显著正相关 ($P < 0.01$); 土壤温度和细砂含量与其他因子均无显著相关性 ($P > 0.05$), 而含水率与纬度和经度均为负相关关系, 与极细砂和黏粉粒正相关, 但未达到显著性水平 ($P > 0.05$); 极细砂与黏粉粒含量仍显著正相关 ($P < 0.05$)。脲酶活性与电导率、极细砂、黏粉粒含量正相关, 与温度、中粗砂含量负相关; 纤维素酶活性与含水率及经度正相关性, 其中与经度的相关性达显著水平 ($P < 0.05$); 与脲酶相反, 碱性蛋白酶与极细砂、黏粉粒含量负相关, 与经度显著正相关 ($P < 0.05$)。

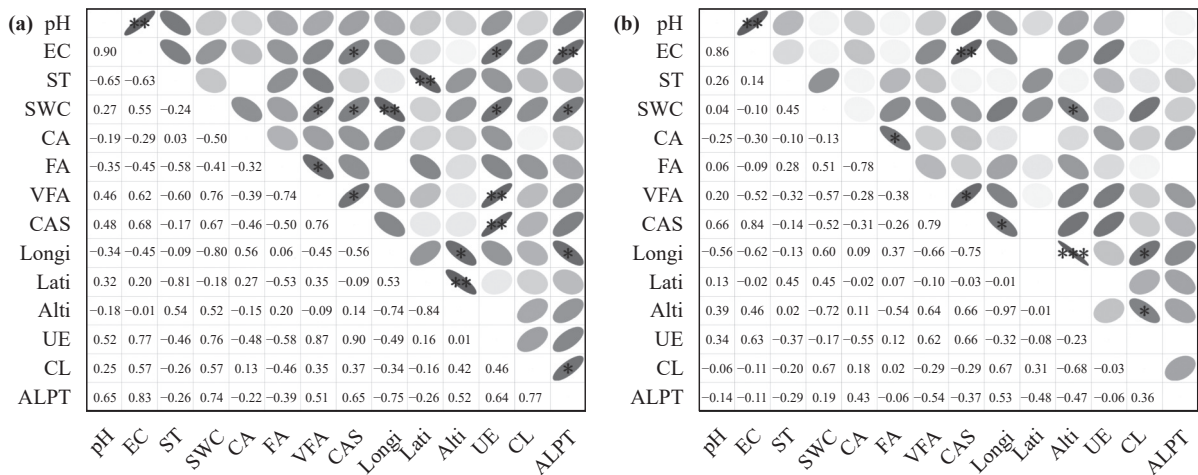


图 3 不同温度和降水梯度下土壤理化性质、区域经纬度、海拔及土壤胞外酶活性的皮尔逊相关关系

Figure 3 Pearson correlation between soil physical and chemical properties, regional latitude and longitude, and altitude and soil extracellular enzyme activity at different temperature and precipitation gradients

(a) 温度梯度, (b) 降水梯度; 椭圆方向左上右下代表正相关关系, 椭圆方向左下右上代表负相关关系; 椭圆面积越小、颜色越深代表相关性越大, 星号表示显著性, 其中*: $P \leq 0.05$, **: $P \leq 0.01$, ***: $P \leq 0.001$; EC: 电导率; ST: 土壤温度; SWC: 土壤含水率; CA: 中粗砂; FA: 细砂; VFA: 极细砂; CAS: 黏粉粒; Longi: 经度; Lati: 纬度; Alti: 海拔; UE: 脲酶; CL: 纤维素酶; ALPT: 碱性蛋白酶。下同。

(a) temperature gradient, (b) precipitation gradient. The lower left and upper right ellipse directions represent positive correlations, and the upper left and lower right ellipse directions represent negative correlations. The smaller the ellipse area and the darker the color represents, the greater the correlation. The asterisk indicates statistical significance, where *: $P \leq 0.05$, **: $P \leq 0.01$, and ***: $P \leq 0.001$. EC: electrical conductivity; ST: soil temperature; SWC: soil water content; CA: coarse sand; FA: fine sand; VFA: very fine sand; CAS: clay and silt; Longi: longitude; Lati: latitude; Alti: altitude; UE: urease; CL: cellulase; ALPT: alkaline protease. This is applicable for the following figures as well.

通过结构方程模型来检验土壤温度和含水率对土壤 EEA 的直接和间接影响。如图 4 所示, 所有预测变量共同解释了 83.4% 的土壤脲酶活性变化 ($R^2 = 0.834$) 和 38.5% 的碱性蛋白酶活性变化 ($R^2 = 0.385$)。土壤含水率对脲酶和碱性蛋白酶活性分别产生了极显著 ($P < 0.01$) 和显著 ($P < 0.05$) 的正向直

接影响, 而土壤温度对脲酶活性和碱性蛋白酶活性存在负向直接影响, 但未达显著性水平。土壤含水率通过对电导率、极细砂含量、黏粉粒含量的正向直接影响从而间接影响酶活性, 土壤温度对极细砂含量的路径系数极显著为负 ($P < 0.001$), 而极细砂和黏粉粒含量受其他环境因子的综合影响对脲酶

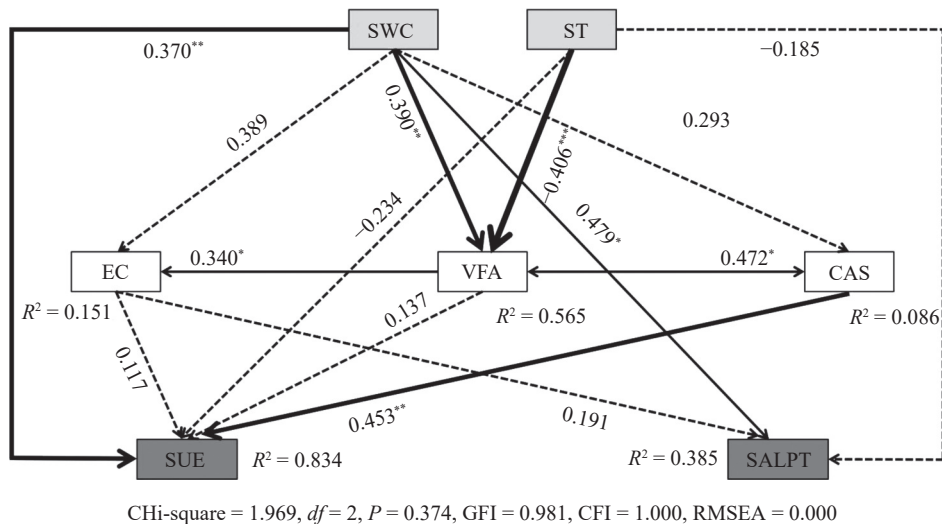


图 4 不同水热梯度下表示环境因子对土壤胞外酶活性直接与间接影响的结构方程模型

Figure 4 Structural equation models representing the direct and indirect effects of environmental factors on soil extracellular enzyme activity under different hydrothermal gradients

实线与虚线分别表示显著与不显著的路径关系。箭头粗细代表标准化路径系数的相对大小， R^2 表示此变量被解释的程度，箭头数字表示标准化路径系数，数字为正代表正相关，为负代表负相关。SUE：土壤脲酶；SALPT：土壤碱性蛋白酶。

The solid and dashed lines indicate the significant and insignificant path relationships, respectively. The thickness of the arrow indicate significant difference at the 0.05 level indicates the relative magnitude of the standardized path coefficient, and R^2 indicates the extent to which this variable is explained. The numbers on the arrows are the standardized path coefficient. A positive number indicate a positive correlation, a negative number indicates a negative correlation, and an asterisk indicates its statistical significance. SUE: soil urease; SALPT: soil alkaline protease.

活性产生直接正向影响。结构方程模型表明土壤含水率、温度和黏粉粒含量是土壤酶活性的主要影响因素。

3 讨论

3.1 不同温度梯度下土壤胞外酶活性变化

陆地生态系统碳氮生物地球化学循环通过光合等初级生产作用、呼吸作用和分解作用相互联系^[29]，土壤 EEA 可以指示碳和养分有效性，在土壤和沉积物有机质的分解过程中起关键作用^[30]。温度被认为是微生物活动最重要的变量之一，气候变暖会强烈改变微生物活动^[31]，进而改变与之密切相关的土壤 EEA。脲酶是氮矿化的近似因子^[13]，蛋白质是有机氮的最大来源^[32]，均与养分的获取和吸收有关。本研究中温度增加对土壤脲酶和碱性蛋白酶活性均产生了显著影响，EEA 明显升高。有研究表明增温对 EEA 的影响随着区域年均温的增加而增加，随着土壤温度升高，氮限制可能会逐渐增加，刺激微生物增加氮降解酶的产生^[11]，这与本研究中土壤脲酶和碱性蛋白酶活性随温度增加而升高的结果相一致(图 2)。而在本研究中随着温度升高，脲酶活

性升速趋于平缓甚至降低，可能因为增温通过刺激蒸发蒸腾和减少水分来降低土壤水分可用性^[33]，减缓酶的扩散速率从而降低 EEA。如有研究表明增温显著降低了内蒙古短花针茅荒漠草原团聚体内脲酶活性^[34]。还有研究表明增温对克氏针茅(*Stipa krylovii*) 草原脲酶活性无明显的影响^[35]。碳降解酶纤维素酶的活性可以用来跟踪土壤微生物主要碳源的变化^[36]，本研究中增温对纤维素酶活性无显著性影响(图 2)。与本研究的结果相似，青藏高原高寒草甸短期(2 年)和长期(10 年)增温对纤维素酶无显著影响，但是显著提高了土壤脲酶活性^[37]。研究表明，在酶尺度上，虽然温度可以在短期内对酶催化能力产生积极影响，但随着时间的推移，这种影响可以通过酶失活和降低底物亲和力抵消^[38]。中国北方温带草原地区土壤胞外酶的温度敏感性随着年平均气温显著上升^[39]，也有研究表明实验变暖对土壤胞外酶活性可能没有长期性影响^[40]，由于酶产生和降解的抵消作用，很难预测变暖对酶活性的影响。在微生物尺度上，短期变暖可以通过加速微生物周转速率来增加酶的催化能力，但微生物群落组成和生长的变化可能会调节长期变暖的影响^[38]。总

之土壤胞外酶活性对全球变暖的响应仍存在很大的不确定性,不同功能的土壤酶对气候变暖的反应也有所不同^[41]。

3.2 不同降水梯度下土壤胞外酶活性变化

水分变化是微生物代谢限制的最重要驱动因素之一^[42]。一般来说降水减少或蒸散量增加会导致微生物生物量和酶的产生减少,潜在的 EEA 会因干旱而降低^[11]。本研究中碱性蛋白酶活性受降水减小影响显著下降,脲酶活性随着降水减小先降低后升高(图 2),表明降水减小显著抑制了脲酶活性。地中海灌丛草地的研究表明降水减少降低了土壤蛋白酶活性^[43];还有研究表明半干旱草地降水减少胁迫下生长季中后期碳氮获取胞外酶会显著降低^[44];中国腾格里沙漠东南缘干旱显著降低了苔藓覆盖土壤中的胞外酶活性^[45]。这些研究结果均支持了本研究的结果。而短期内降水量变化对荒漠草原土壤蔗糖酶、脲酶和磷酸酶活性的影响较小^[46],本研究中土壤纤维素酶活性在降水梯度上无显著性差异(图 2),说明干旱胁迫会在一定程度上增加酶的数量,但是也会降低酶的作用效率,酶扩散速率和作用效率降低对 EEA 的抑制作用会抵消酶数量增加对酶活性的促进作用^[47]。分析表明降水减少显著提高了草地生态系统水解 EEA,如 β -1,4-葡萄糖苷酶^[48]。本研究中低降水区域脲酶活性高于中降水区域,重度干旱胁迫对脲酶活性有促进作用,可能原因为当土壤含水率较低时,原位土壤 EEA 活动也低,但是由于土壤孔隙度和团聚体变化部分空间尺度 EEA 可能表现较高^[9]。因此脲酶活性与降水减小幅度有关,重度干旱胁迫在一定程度上会促进脲酶活性以维持土壤养分的周转和循环。土壤 EEA 对降水变化的响应可能存在环境依赖性的,在不同的生境中可能表现特殊。

3.3 环境因子与土壤胞外酶活性的相关关系

研究气候变化下胞外酶整体活性的变化有助于预测陆地生态系统中与碳、氮循环相关的生物地球化学过程^[38]。分析表明,增温持续刺激碳氮磷获取相关的氧化 EEA,如多酚氧化酶,但对起水解作用的 EEA 有不同的影响,如脲酶和纤维素酶,这取决于增温幅度、持续时间或环境因素^[1]。也有研究表明区域尺度温带草原胞外酶的温度敏感性主要受

到年平均气温的直接控制^[39]。黄土丘陵区撂荒草地^[49]和黄土高原半干旱草地^[50]温度变化均显著改变了 EEA。本研究相关性分析与结构方程模型均表明温度是影响沙质草地土壤 EEA 的重要因素(图 4)。温度变化一方面可以改变土壤微生物来源酶的数量与活性,另一方面可以通过改变植物根冠比,进而影响根系分泌来源酶的数量与活性^[51]。在所有土壤理化因子中,含水率是影响 EEA 最主要的因子^[52],降水变化显著地改变了干旱荒漠区土壤 EEA,EEA 均随着水分的增加而逐渐升高^[53]。分析表明降水变化会显著影响脲酶和蛋白酶等氮水解酶^[1]。本研究发现沙质草地土壤胞外酶活性与土壤初始含水率显著正相关,结构方程模型结果也显示土壤含水率通过正向直接或间接作用影响脲酶、碱性蛋白酶活性(图 4)。说明在干旱半干旱草地生态系统碳氮的生物地球循环过程和与之相关的微生物活动主要受可用水量的控制。土壤温度和水分是影响内蒙古灌丛草地草斑不同降水处理下土壤 EEA 变化的主要因素^[54]。目前关于温带草原土壤 EEA 对全球变化因子的响应及其对土壤有机质分解调节机理的研究仍然非常缺乏。

本研究中 pH 和电导率对 EEA 最可能的影响是通过调节土壤养分的有效性^[55]进而影响酶对底物的获取能力,最终间接影响 EEA。土壤机械组成差异是造成养分差异的重要因素^[56],而有机质含量^[57]是酶活性的重要驱动因素。本研究风沙土中细砂含量最高,而随着细砂含量下降,黏粉粒含量增加,酶活性呈递增趋势。土壤中细颗粒的比例与土壤胶体呈正相关,而土壤胶体可以吸附吸收大量的有机质养分,从而使得土壤胞外酶数量和活性保持在较高水平上^[58]。另外土壤小粒径颗粒增多会形成紧密的团聚体提高有机碳的稳定性,减少有机质分解^[59],从而增加胞外酶相关底物的可用性间接影响土壤 EEA。

4 结论

通过分析不同水热梯度下土壤胞外酶活性变化特征及其与环境因子之间的相关关系,结果表明:不同水热梯度上,土壤水分和养分含量相对较低,沙质草地土壤胞外酶活性整体较低。温度升高条件下土壤脲酶活性先上升后减小,随着降水减小脲酶活性先减少后增加。同时温度升高显著增加了土壤

碱性蛋白酶活性 ($P < 0.05$), 降水减少则显著降低了碱性蛋白酶活性 ($P < 0.05$)。而自然梯度上温度增加和降水减少对土壤纤维素酶活性的影响无显著性差异 ($P > 0.05$)。土壤脲酶活性与电导率、含水率、极细砂及黏粉粒含量显著正相关 ($P < 0.05$), 与土壤温度、中粗砂、细砂含量负相关; 土壤纤维素酶活性

与含水率正相关, 与土壤温度负相关; 与脲酶相似, 土壤碱性蛋白酶与电导率、含水率及脲酶、纤维素酶活性正相关, 与土壤温度负相关。总之, 土壤含水率、温度、黏粉粒含量是沙质草地土壤胞外酶活性重要影响因素, 其中土壤含水率对胞外酶活性的直接和间接驱动作用均高于其他环境因子。

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