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青藏高原高寒沼泽化草甸群落生物量 及地下CNP对积雪增加的响应

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摘 要: 以青藏高原多年冻土区高寒沼泽化草甸为研究对象, 采用雪栅栏诱导方式模拟积雪厚度增加, 结合植物地上、地下根系以及土壤养分变化, 分析了高寒沼泽化草甸对积雪厚度增加的响应。结果表明: 积雪厚度增加后, 0~20 cm 浅层土壤温度和水分含量增加; 植物群落高度和土壤表层 0~10 cm 根系生物量显著增加, 植物群落组成和地上生物量没有变化; 地下 0~20 cm 土壤碳(C)、氮(N)、磷(P)总储量降低, 根系中 C、N、P 储量增加; 土壤表层 0~10 cm 总 N:P 比显著增加, 但是有效磷含量在 0~10 cm 和 10~20 cm 土层均显著增加。可见, 积雪厚度增加并不影响沼泽化草甸植物群落的组成和地上生物量, 仅增加植被高度; 增加土壤表层总 N:P 比意味着积雪厚度增加可能会减轻沼泽化草甸土壤中氮限制, 从而减缓沼泽化草甸的氮匮乏状况。结论可为高寒生态系统响应积雪变化研究提供样地尺度的观测数据, 并为冰冻圈生态系统应对未来气候变化的模型估算提供数据支撑。

关键词: 青藏高原; 积雪; 群落结构; CNP 储量; 生态化学计量比

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0 引言

积雪是全球气候系统的重要组成部分, 通过气候和水循环, 影响地球表面的各种生态系统^[1]。青藏高原是北半球中纬度地区积雪覆盖最广的地区之一, 1979—2010 年青藏高原积雪厚度以 $0.26 \text{ cm} \cdot (10\text{a})^{-1}$ 的速率显著增加, 尤其冬季, 增加速率达 $0.57 \text{ cm} \cdot (10\text{a})^{-1}$ ^[2]。积雪厚度增加对青藏高原高寒草地生态系统造成的影响, 是陆地生态系统应对气候变化研究的重要关注点之一, 明晰高寒沼泽化草甸对积雪变化的响应格局和生物学机制有助于客观、全面了解高寒草地生态系统对积雪增加的响应模式及其规律, 可为精准模拟预测区域生态系统与气候变化的关系提供基础数据。

积雪对植物生长影响主要表现在两方面: 一方面, 通过提前返青期和推迟枯黄期^[3], 以延长植物生长季长度^[4-6], 从而增加植物根系对养分的吸收利用积累, 影响植物生长、繁殖和物种多样性^[7-8]; 另一方面, 积雪改变土壤中养分、水分和温度^[9], 使微生物的生物量和土壤胞外酶(如纤维二糖水解酶、酚氧化酶和多氧化物酶等)活性增加, 从而影响植物生长和土壤元素循环^[10-13]。例如, 积雪的保温作用使土壤微生物保持活性, 进而维持较高的土壤微生物活性^[14], 土壤微生物对植物有效养分有储备作用, 并可调节土壤 C、N 等养分的有效性^[15]。积雪融化后, 微生物量固持的氮以可溶性氮和有机态氮的形式释放到土壤中, 可为春季植物的生长提供养分^[16], 进而影响植物生长和群落组成^[17]。目前有关

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积雪对陆地生态系统的影响大多集中在植物物候、生产力和多样性等地上部分的观测报道^[18-20],有关积雪增加对土壤养分条件影响的研究甚少,尤其是土壤P在青藏高原多年冻土区高寒草甸变化过程和机理不甚清楚。

土壤养分影响植物生长发育,对植物的生产力起着关键作用^[21]。积雪对土壤养分的影响存在三方面:一是积雪覆盖增加土壤温度和改善微生物的呼吸环境,提高微生物丰度和活性,增强了微生物对P的吸收固定,从而降低土壤微生物体内N:P比,最终降低可供植物吸收利用P的获取^[22-26];二是积雪增加导致土壤含水量增大,有利于更多的无机养分转变成溶解态,在积雪融化作用下,会加强土壤淋溶而导致养分下渗流失^[27-30];三是积雪保温作用能缓解土壤冻融循环引起的土壤氮流失^[31-32]。这些研究大多集中在阿尔卑斯山、北极^[22,27],而高寒极端环境下青藏高原积雪变化对土壤养分的影响是否也遵循这三方面的规律,目前还不清楚^[33]。

高寒沼泽化草甸是青藏高原多年冻土区分布的主要植被类型之一,本研究以其为研究对象,采用雪栅栏的方式人为诱导积雪厚度增加,调查植物群落组成结构,测定群落地上、地下生物量和土壤养分含量,测算土壤碳氮磷储量和生态化学计量比,旨在探究高寒沼泽化草甸对积雪增加的响应,从而为冰冻圈生态系统应对未来气候变化的模型估算提供数据支撑。

1 研究方法

1.1 研究区概况及试验设计

研究区域位于青藏高原腹地风火山地区(34°40′~34°48′ N, 92°50′~93°30′ E),海拔为4 680~

5 360 m,属于典型多年冻土区,研究区主要植被类型为高寒草甸和高寒沼泽化草甸,5—9月为生长季。该地区年均气温为-5.2℃,极端最高气温为23.2℃,极端最低气温为-37.7℃,年平均降水量为290.9 mm,年平均蒸发量为1 316.9 mm,平均相对湿度为57%,年平均地温为-1.5~4.0℃,多年冻土厚50~120 m,活动层厚0.8~2.5 m^[34]。

本研究以高寒沼泽化草甸(34°43.816′ N、92°53.506′ E,海拔4 778 m)为研究对象,主要以藏嵩草(*Kobresia tibetica*)为优势物种,伴生种有青藏苔草(*Carex atrofusca*)和矮火绒草(*Leontopodium nanum*)等。2009年9月,采用高为1.8 m的雪栅栏模拟积雪厚度增加,模拟积雪属于干雪。雪栅栏的安装方向主要与主风方向垂直^[7],通过研究区域条件和主风方向来确定栅栏的高度、方位^[35]。2009年9月至2010年5月野外观测发现,距离栅栏3 m处积雪最深约32 cm[图1(a)]。据此,对该处进行积雪厚度增加处理,设置8个1 m×1 m的样方,每个样方间距1~1.5 m[图1(b)]。对照组设在雪栅栏影响降雪漂移轨迹之外,距雪栅栏20 m远,有平行的8个观测样方(1 m×1 m)[图1(b)]。同时,在积雪和对照组样方内布设同步的土壤温湿度传感器(美国Decagon公司土壤水分温度电导率测量仪MG-EM50),测定土壤10 cm、20 cm深度水热变化。

1.2 样品采集与室内分析

在积雪处理第4年(2013年)8月进行植物群落特征调查:对1 m×1 m样方框内群落高度、盖度及物种丰富度进行测定统计。群落地上净初级生产力(ANPP,地上生物量峰值)采取直接获取方式,具体做法是在生物量达到峰值的8月将样方内植物齐地面刈割,60℃恒温烘干48 h至恒重,用电子分析天

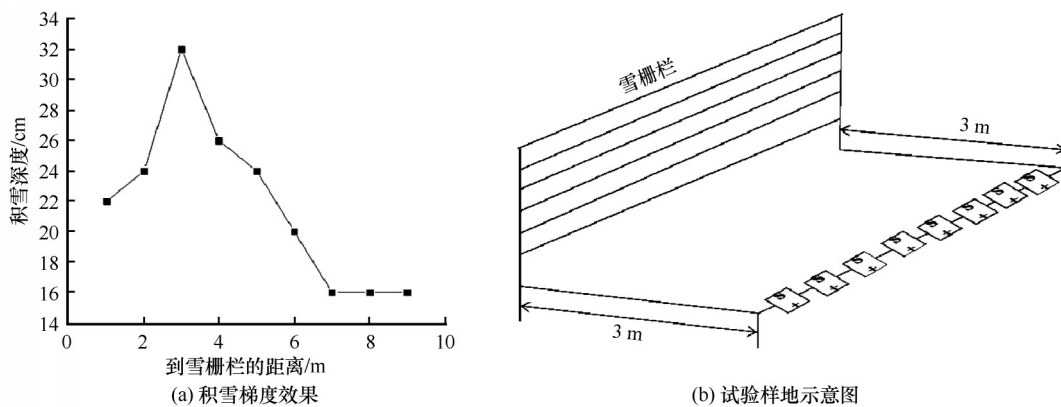


图1 风火山雪栅栏诱导积雪梯度效果和试验样地

Fig. 1 Snow depth distribution induced by snow fence in the Fenghuoshan Mountain (a) and sampling plots (b)

平称重得到地上生物量。

按照 0~10 cm 和 10~20 cm 的深度用直径为 5 cm 的根钻钻取土柱(每个样方内取 3 钻),过 16 目筛取出自然根系,洗净后置于 60 ℃ 的烘箱中恒温 48 h 获取干重,换算成单位面积上 0~10 cm 和 10~20 cm 地下生物量($\text{g}\cdot\text{m}^{-2}$)。余下的土壤自然风干后过 100 目筛后装入自封袋中以测定土壤养分。

土壤全碳(TC)的测定采用总有机碳分析仪测定,有机碳(OC)含量用重铬酸钾氧化法测定,全氮含量(TN)采用凯氏定氮法测定,全磷含量(TP)采用 $\text{HClO}_4\text{-H}_2\text{SO}_4$ 消煮-钼锑抗比色法测定,有效氮(AN)采用酸水解法测定,pH 采用电位法测定(水土比是 1:2.5),有效磷(AP)采用盐酸和硫酸溶液浸提法测定,植物全氮采用奈氏比色法测定,植物全磷采用钒钼黄比色法测定^[36]。

1.3 数据处理

本研究所有数据用 Excel 进行整理,利用 R3.2.3 软件(<http://www.R-project.org/>)进行分析和作图,采用单因素方差分析(One-way ANOVA)和 LSD 方法检验各指标处理与对照的差异显著性(显著水平均为 $P<0.05$)。

2 结果与分析

2.1 土壤温度和含水量对积雪增加的响应

雪栅栏诱导积雪增加使得土壤 0~10 cm、10~20 cm 生长季内温度分别增加 0.26 ℃ 和 0.17 ℃;土壤 0~10 cm、10~20 cm 生长季内土壤含水量分别增加 2.09% 和 0.88%(图 2)。雪栅栏诱导积雪增加使得生长季内土壤温度和土壤水分含量增加,但在不同土壤深度的变化幅度存在差异。

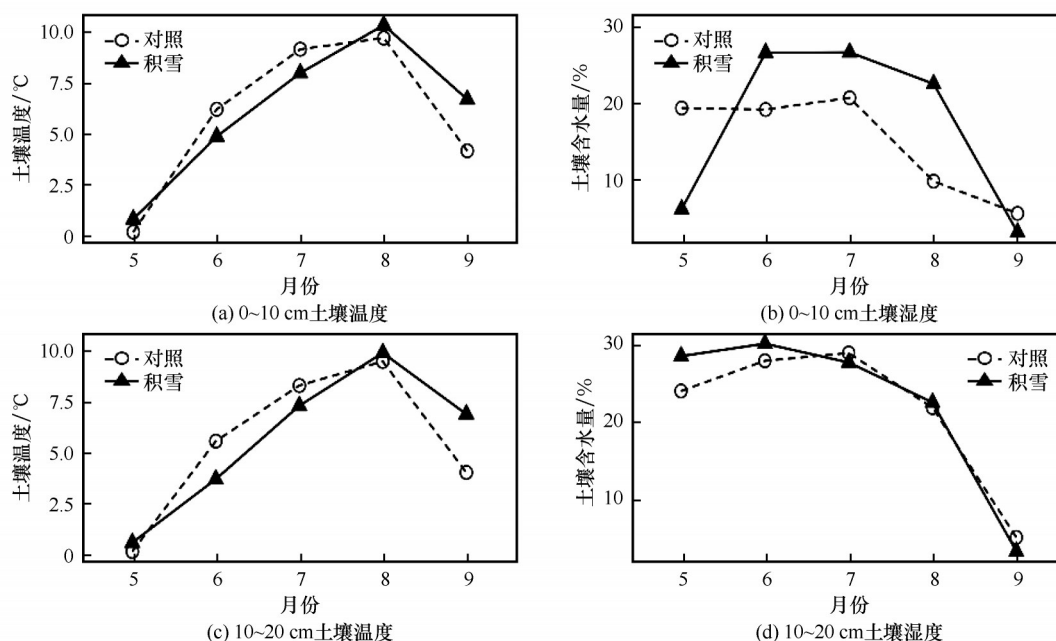


图2 高寒沼泽化草甸生长季(5—9月)土壤温湿度

Fig. 2 Monthly variations of soil temperature (left) and moisture (right) within various depth ranges in the alpine swamp meadow during growing season (from May to September) with and without snow fence

2.2 群落结构对积雪增加的响应

积雪增加使得高寒沼泽群落物种丰富度和群落盖度有增加趋势,统计检验不显著,但是积雪显著增加了群落植被高度(图 3, $P<0.05$)。

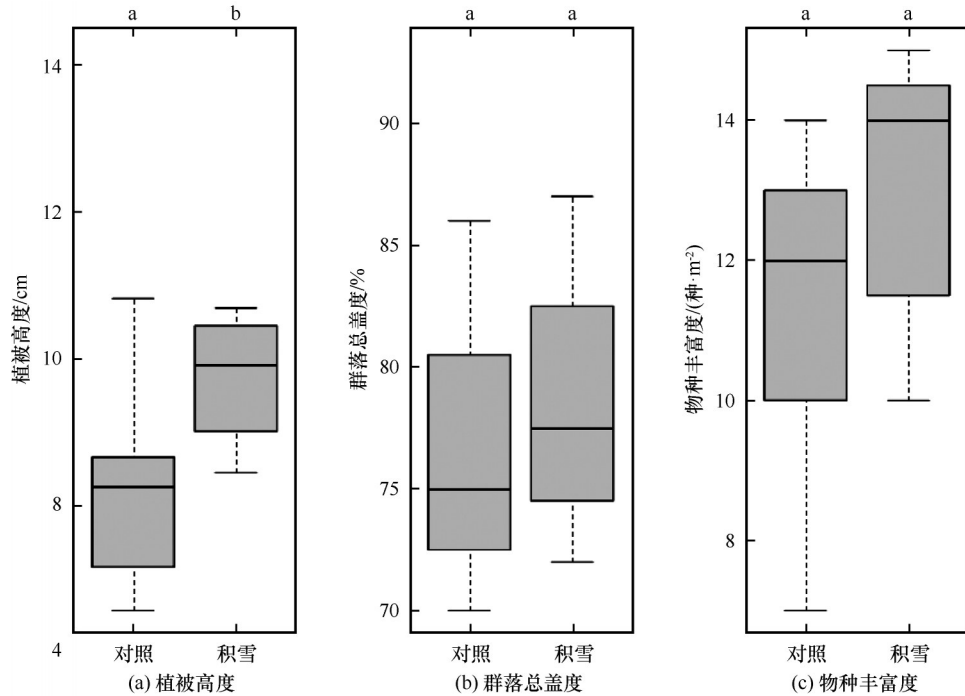
2.3 积雪对地上生物量(AGB)和地下生物量(BGB)的影响

积雪处理后 AGB 没有显著变化。无论是对照还是积雪处理,根系生物量的 86%~91% 集中在浅层土壤 0~10 cm 处。积雪显著增加了沼泽化草甸浅

层 0~10 cm 土壤中根系的生物量($P<0.05$),0~20 cm 和 10~20 cm 土层根系生物量没有显著变化(图 4)。

2.4 积雪对地下部分 CNP 储量的影响

积雪增加后,地下表层(0~20 cm)总 C、N、P 储量减少,相比于对照组,C 储量降低了 19.87%、N 储量降低了 31.84% 和 P 储量降低了 39.46%(图 5, $P<0.05$)。根系/总地下的 C、N、P 储量比中,积雪增加均显著增加了其在 0~20 cm 比例,分别增加了 6.34%、2.51% 和 1.40%,但是降低了土壤/总 C、N、



注: 不同小写字母 a、b 表示不同处理间差异显著 ($P < 0.05$); 箱线图虚线两端表示最小值与最大值; 样本数为 8

图 3 积雪对高寒沼泽化草甸植物群落特征的影响

Fig. 3 Effects of snow on vegetation height (a), coverage (b) and species richness (c) in the alpine swamp meadow without snow fence (left) and with snow fence (right)

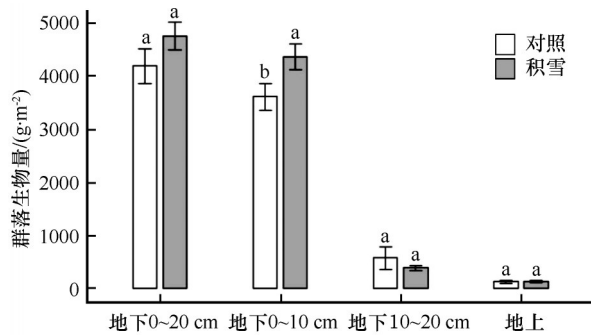


图 4 积雪对高寒沼泽化草甸群落地上、地下生物量的影响 ($P < 0.05$, $n = 8$)

Fig. 4 Effects of snow without snow fence (blank) and with snow fence (shadow) on biomass within depth range of 0~20 cm, 0~10 cm, 10~20 cm and on the surface in the alpine swamp meadow ($P < 0.05$, $n = 8$)

P 储量比 (图 5, $P < 0.05$), 分别降低了 4.22%、2.82% 和 2.20%。可见, 根系 C、N、P 储量的增加虽然不能完全缓解地下 C、N、P 储量的降低, 但是起着积极的正效应, 可以部分抵消碳汇丧失。

2.5 土壤生态化学计量特征对积雪的响应

在积雪增加的情况下, 土壤总 C、N 含量以及有机碳、有效氮含量在各层都有增加的趋势, 但统计检验不显著 ($P > 0.05$)。土壤 P 含量在各层都有减少的趋势, 统计检验不显著 ($P > 0.05$)。但是, 土壤

有效磷在 0~10 cm 和 10~20 cm 均显著增加 ($P < 0.05$) (图 6)。积雪增加对不同土壤深度碳氮比、碳磷比没有显著影响 (图 7)。然而, 0~10 cm 土层的 N:P 比受积雪厚度增加显著增加, 这可能是由于该层土壤全 N 增加, 而全 P 含量降低引起的。

3 讨论

3.1 积雪厚度增加对高寒沼泽化草甸群落的影响

在本研究中, 短期的积雪增加促进了高寒沼泽化草甸的植被高度, 对物种组成及其盖度没有影响, 地上生物量也没有变化。这可能与积雪厚度增加对植被生长的浅层土壤环境条件改变有关。浅层土壤水分和温度均增加, 这有利于高寒植被的高度生长^[37-38]。然而, 高寒沼泽化草甸总体都比较低矮, 加上有较大的空间异质性, 还有低幅度增温相对于高原环境的年际间温度变化, 并不能足以改变植物群落的生长特征, 这可能是植被的组成和地上生物量没有变化的原因。但是, 观测到积雪厚度增加显著增加了表层 0~10 cm 根系生物量, 这可能是由于根系生长对水热条件的改变比地上部分更敏感。宋海星等^[39]研究发现合适水分能够促进植物根系生长, 增加了根系吸收总面积、活跃吸收面积,

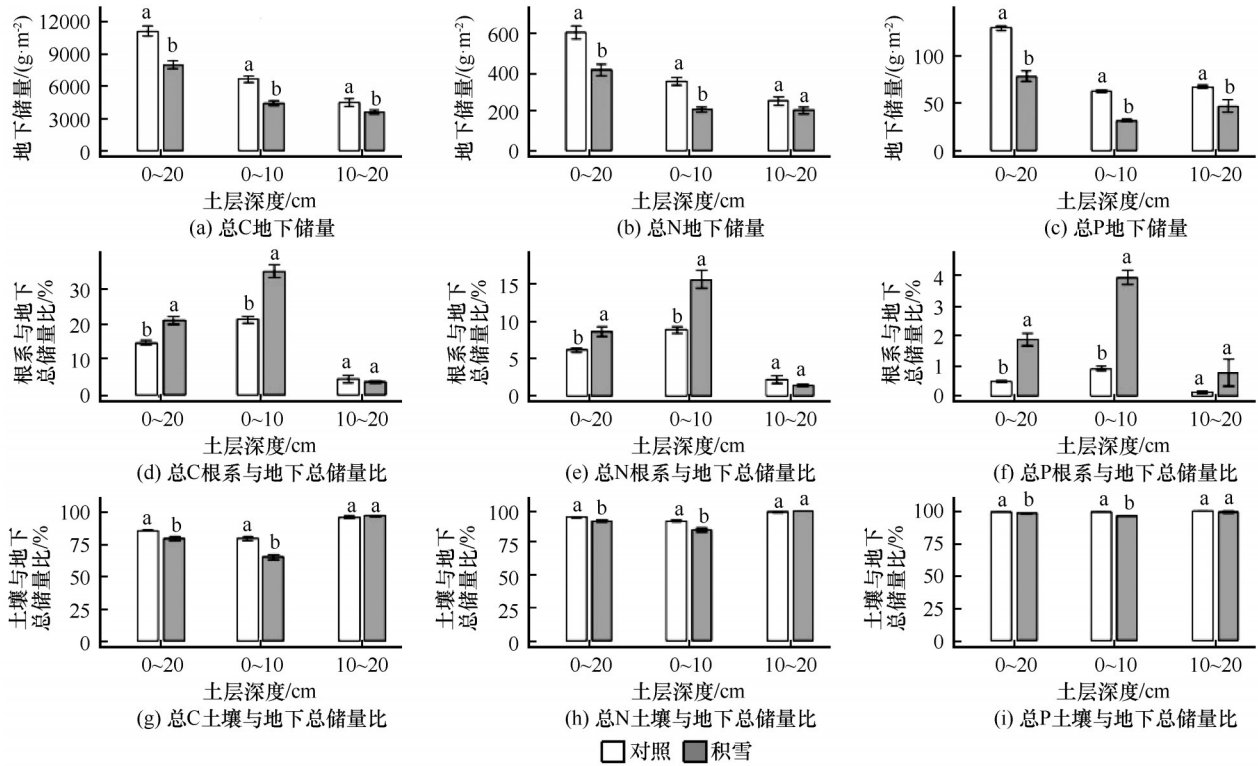


图5 积雪对高寒沼泽化草甸不同深度地下C、N、P储量的影响

Fig. 5 Effects of snow without snow fence (blank) and with snow fence (shadow) on C (a, d, g), N (b, e, h) and P (c, f, i) stocks in different depth ranges in the alpine swamp meadow

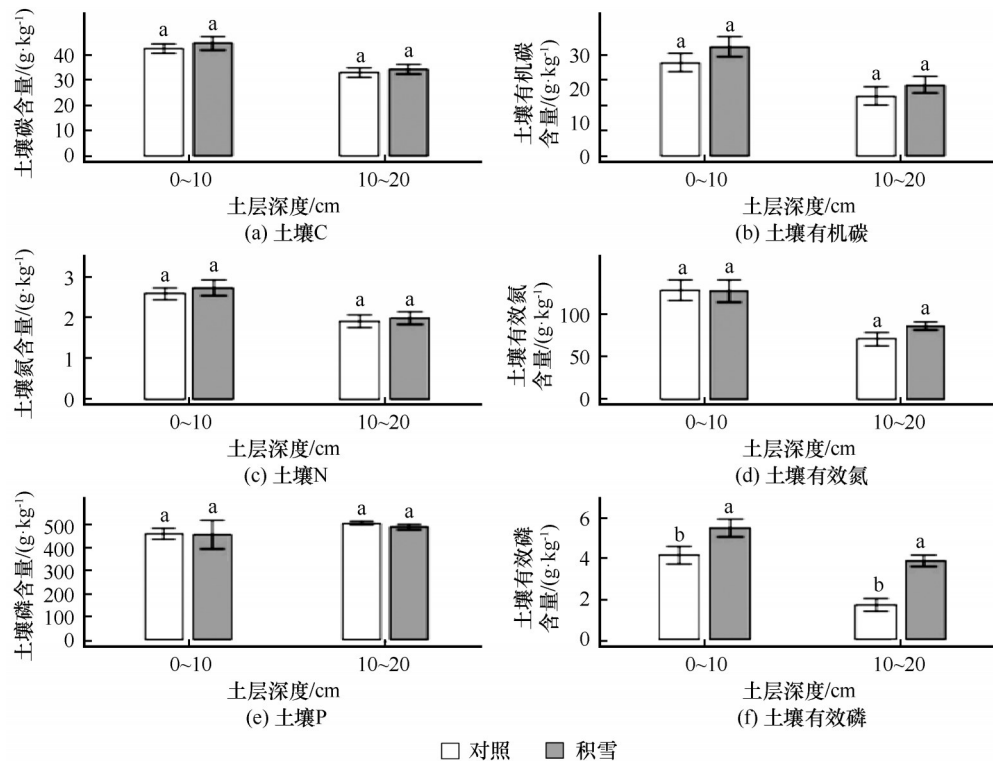


图6 积雪增加对高寒沼泽化草甸不同深度土壤C、N、P及有机碳、有效氮、有效磷含量的影响

Fig. 6 Effects of snow addition without snow fence (blank) and with snow fence (shadow) on soil C (a) and soil organic C (b), soil N (c) and soil available N (d), and soil P (e) and soil available P (f) stocks in different depth ranges in the alpine swamp meadow

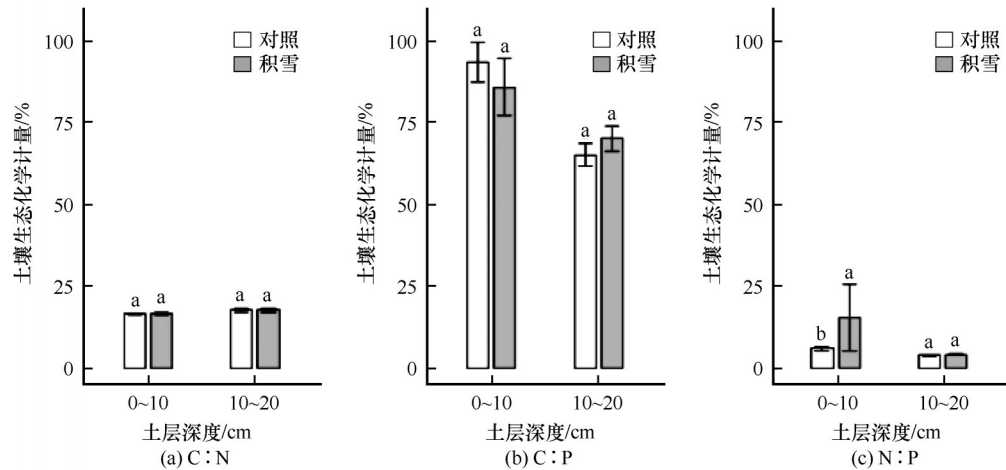


图7 积雪增加对高寒沼泽化草甸不同深度土壤碳氮比、碳磷比和氮磷比的影响

Fig. 7 Effects of snow addition without snow fence (blank) and with snow fence (shadow) on soil C:N ratio, C:P ratio and N:P ratio at the depth of 0~10 cm and 10~20 cm in the alpine swamp meadow

促进根系对土壤养分的吸收,从而提高了植物生产力。同时,在一定条件下,土壤温度的升高可促进根系的生长,但不同类型的植物对土壤温度变化的响应趋势也有较大的区别,但沼泽植被对土壤温度变化的响应趋势比草甸植被大^[40]。内蒙古温带草原模拟积雪厚度增加试验结果^[20]表明,积雪增加并没有改变草地群落地上生物量和物种组成,表明地上生物量的相对稳定;但积雪增加显著增加草地的地下生物量,归因于融雪后土壤含水量增加,使植物根系垂直分布变化,增加了植物生产力对根系的分配,从而使根系生物量增加。青藏高原的岛状多年冻土区高寒草甸模拟试验结果显示,积雪厚度增加对草甸的繁殖物候影响存在种间差异,提前了浅根且早花的莎草科小嵩草繁殖物候,对深根且晚花的杂类草没有影响,可能是由于根系长度的差异引起的土壤水分的敏感性差异^[19]。阿拉斯加的苔原研究发现,积雪厚度增加通过加深冻土的活动层厚度而改变植物群落的物种组成,灌木逐渐取代莎草科植物成为优势物种^[41]。

3.2 积雪厚度增加对青藏高原沼泽化草甸地下CNP储量的影响

积雪增加后,地下碳氮磷总储量减少,但是根系碳氮磷储量所占比值增加。积雪保温隔离了外界的不利环境,可能会减少冻融交替的幅度和频次,从而使土壤微环境朝着好的方向发展,有利于土壤微生物群落功能多样性增加、生长和活动^[42-43],此时根系自身分解相对更快,同时土壤生物变得活跃并能加快对有机质的消耗,增强了对土壤养分的利用率,因此土壤中总碳氮磷储量降低。随着积雪

厚度增加,植物生长季长度增长,加快植物根系对营养吸收和积累,从而使根系碳氮磷储量所占比值增加。但是,积雪增加后,土壤表层积雪消融后会产生淋溶作用,加快土壤养分流失^[44-45],使土层中0~20 cm碳氮磷总储量下降。其中,P储量变化最大,N储量变化次之,C储量变化最小,这可能是因为植物体内C主要是起骨架的作用,一般不直接参与植物生产活动,因此变异很小,并且通常植物组织内P元素变异性较N元素大,主要原因是有机体内N比P元素具有更强的内稳态系数,造成植物N素在应对外界环境变化时变异性更小^[46]。

3.3 积雪厚度增加对表层土壤有效磷含量及其N:P比的影响

积雪厚度增加显著提高了沼泽化草甸0~10 cm和10~20 cm的土壤有效磷储量。土壤有效磷主要来源于自然界磷的矿化和土壤中有机磷的分解^[47]。本研究中对照和积雪增加处理设置在同一研究区域,因而排除了自然界矿化差异,增加的有效磷主要是由于有机磷分解过程产生的有效磷含量差异不同造成的。土壤中磷酸酶是一类催化土壤有机磷化合物矿化的酶,其活性高低直接影响着土壤中有机磷的分解转化效率^[48]。积雪增加了土壤表层的温度和湿度,提高了土壤中磷酸酶活性^[49],从而促进土壤中有机磷转化为有效磷。该结果与其他地区的积雪试验结果一致。如古尔班通古特沙漠苔藓植被中,积雪增加显著提高了土壤中有效磷的含量^[50]。加拿大低北极中部地区的连续多年冻土积雪增加试验结果显示^[51],冬季积雪的保温和保水作用加速了土壤微生物对土壤中P的固化,而夏季

积雪融化,温度降低,微生物死亡,使得固定的微生物P被释放到土壤中,而使土壤有效磷增加。

研究结果显示,积雪增加使得沼泽化草甸表层(0~10 cm)土壤总N:P比增加,这可能是由于两个方面的原因。一是积雪可以释放 NO_3^- ^[52],增加土壤中溶解态有机氮^[53],这也是青藏高原新氮输入的长期来源^[54],二是氮沉降能减少土壤中磷含量^[55-56]。土壤N:P>16可认为是磷限制,在土壤N:P<14则是氮限制,14≤N:P≤16可能是氮磷同时限制或者都不限制^[57],本研究结果显示,无论是对照还是积雪处理N:P比均小于14,可见研究区域属于氮限制,与已经报道的研究结果一致^[58-59]。然而,积雪增加下显著提高土壤表层的N:P比说明积雪增加可能缓解研究区域的氮缺乏现状。

4 结论

(1)青藏高原沼泽化草甸积雪厚度增加,使得表层土壤(0~20 cm)在生长季节内温度和含水量增加。

(2)积雪增加促进了青藏高原沼泽化草甸土层(0~10 cm)根系生物量和植被高度的增加,但并未影响草地群落的物种组成、盖度和地上生物量。

(3)积雪增加导致了青藏高原沼泽化草甸土层(0~20 cm)地下碳氮磷总储量降低;积雪增加后,P储量降低最大,N储量次之,C储量变化最小。同时,土壤表层0~10 cm总N:P比、0~10 cm和10~20 cm土壤有效磷含量均显著增加,积雪增加可能缓解沼泽化草甸的氮限制。

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Responses of plant community biomass and below-ground CNP stocks to snow addition in alpine swamp meadow on the Tibetan Plateau

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Abstract: In this study, snow fence was employed to simulate artificial snow addition in an alpine swamp of permafrost region on the Tibetan Plateau. We aimed to investigate the responses of alpine swamp ecosystem to snow addition. Our results showed that: Increased snow would increase both soil moisture and temperature at the depth of 0~20 cm; Increased snow would increase vegetation height and root biomass at depth of 0~10 cm; Increased snow would decrease below-ground pools in total carbon (C), total nitrogen (N) and total phosphorus (P) at the depth of 0~20 cm, although the C, N, P pools had increased in the roots; Increased snow also increased soil total N:P ratio with increasing available phosphorus concentration at the depth of 0~10 cm and 10~20 cm. Our results suggested that short-term snow addition had no effected community composition and above-ground biomass, but significantly increased vegetation height. Moreover, increased N:P ratio in the soil surface had indicated that snow addition could alleviate N limitation in the study region, thereby relieve the soil N deficiency for plant growth in this area. These findings provide observation data at the plot-scale for alpine ecosystem under snow change, as well as a dataset for modeling permafrost ecosystem under future climate change.

Key words: Tibetan Plateau; snow; community structure; CNP stocks; eco-stoichiometric ratio

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