

光合产物传输方向对蓉城竹根际微生物过程的影响

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摘 要 分株间光合产物的整合作用对克隆植物适应生存环境具有重要作用, 但有关光合产物传输方向对克隆植物根际土壤微生物过程的影响尚不清楚。该研究以根状茎克隆植物蓉城竹(*Phyllostachys bissetii*)为研究对象, 通过剪除分株地上部分控制光合产物传输方向(顶向传输和基向传输), 研究光合产物传输方向对蓉城竹分株根际土壤微生物过程的影响, 其中顶向传输组是将远端分株地上部分剪除(保留地面以上20 cm), 近端分株自然生长; 基向传输组则是将近端分株地上部分剪除(保留地面以上20 cm), 远端分株自然生长。两组实验中保持根状茎连接或切断处理。测定了地上部分被剪除分株根际土壤中碳和氮有效性、微生物生物量参数以及氮转化相关土壤胞外酶活性等指标。结果表明: 光合产物顶向传输中, 根状茎保持连接的远端分株根际土壤总有机碳(TOC)、溶解性有机碳(DOC)、溶解性有机氮(DON)、铵态氮(NH₄⁺-N)、硝态氮(NO₃⁻-N)含量显著高于切断的远端分株, N-乙酰基-β-D-氨基葡萄糖苷酶(NAGase)、多酚氧化酶(POXase)和脲酶(Urease)活性显著升高, 光合产物的顶向传输对远端分株根际碳、氮有效性和根际微生物过程产生了显著性影响; 光合产物的基向传输中, 根状茎保持连接的近端分株根际与切断分株相比具有更高的微生物生物量氮(MBN)含量、Urease、POXase活性, 较低的NAGase活性和NH₄⁺-N、NO₃⁻-N含量, 但碳的有效性无显著性差异。蓉城竹分株间光合产物的非对称性传输对根际微生物过程的影响可能是对动物取食或人为砍伐等干扰的有益权衡, 这有助于理解克隆植物对生存环境的种群适应机制。

关键词 光合产物传输方向; 根际土壤; 微生物过程; 土壤酶活性

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Effects of transportation direction of photosynthate on soil microbial processes in the rhizosphere of *Phyllostachys bissetii*

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Abstract

Aims Clonal integration contributes greatly to the adaption of clonal plants to heterogeneous habitats. However, effects of transportation direction of photosynthate on microbial processes need to be further investigated in the rhizosphere. The purpose of this study is to determine the effects of directional differences in photosynthate transport on microbial processes in the rhizosphere of clonal plant *Phyllostachys bissetii*.

Methods By removing the aboveground parts of the ramets, acropetal treatment and basipetal treatment were applied in this study to control the transportation direction of photosynthate. In acropetal treatment, aboveground parts of distal ramets were cut off (with 20 cm above ground kept), and proximal ramets were left intact. While in basipetal treatment, aboveground parts of proximal ramets were cut off (with 20 cm above ground kept), and distal ramets were left intact. Rhizomes between the two ramets were either connected or severed. Carbon (C) and nitrogen (N) availabilities, and enzyme activities in the rhizosphere soils were measured.

Important findings In acropetal treatment, total organic carbon (TOC), dissolved organic carbon (DOC), dissolved organic nitrogen (DON) and soil inorganic nitrogen (NH₄⁺-N and NO₃⁻-N) content in the rhizosphere soil of distal ramets with connected rhizomes were significantly higher than those with severed rhizome. The activities of urease, polyphenol oxidase (POXase), N-acetyl-β-D-Glucosaminidase (NAGase) were significantly enhanced. Further, clonal integration had a significant effect on C and N availability, and microbial processes in the rhizosphere soil of neighbouring ramets. In basipetal treatment, clonal integration did not show a significant effect

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on C availability in the rhizosphere soil of proximal ramets, but microbial processes along with soil enzyme activities were altered accordingly. Effects of transportation direction of photosynthate on microbial processes in the rhizosphere of *P. bisetii* provides insights into the adaptation mechanisms of clonal plant populations.

Key words transportation direction of photosynthate; rhizosphere soil; microbial process; soil enzymes activities

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通过维管组织的传输, 植物实现光合产物在各器官中资源分配的权衡(平晓燕等, 2010); 根系通过根际沉积作用为土壤环境提供可利用碳源(Kuzakov, 2002; Jones *et al.*, 2009; Rajaniemi & Allison, 2009), 这些易溶性碳源促进了土壤微生物生长代谢过程, 调控土壤有机质的矿化、降解和转移、氮(N)循环等过程(Schimel & Weintraub, 2003; Trudell *et al.*, 2004; Lei *et al.*, 2014)。树木环割实验结果证实, 阻断*Fagus sylvatica*地上部分碳同化产物向根系的传输, 会削弱根际土壤碳(C)的有效性, 显著影响根际微生物过程(Koranda *et al.*, 2011)。

相比非克隆植物, 克隆植物不仅存在分株内地上部分与地下部分资源分配的权衡关系, 分株之间也存在光合产物、水分和矿质养分的整合(张称意等, 2001; Li *et al.*, 2002; 王昱生等, 2004; 彭一可等, 2013; 胡俊靖等, 2015)。对欧活血丹(*Glechoma hederacea*)、羊柴(*Hedysarum laeve*)、*Carex bigelowii*资源传输格局的同位素示踪研究表明, 光合产物在连接分株间均存在顶向传输和基向传输(Jónsdóttir & Callaghan, 1990; Price & Hutchings, 1992; 张称意等, 2001); 分株间主要的资源传输格局是顶向传输, 即年长分株向年幼分株的物质传输比从年幼分株向年长分株的物质传输要普遍得多(Pitelka & Ashmun, 1985; Marshall, 1990; Stuefer, 1996; 王长爱等, 2006; 张文军, 2014), 这在N资源的整合中尤为明显(Alpert *et al.*, 2002)。

克隆植物分株间资源传输的方向性差异对邻体分株根际微生物过程的影响尚不清晰, 现有研究结果也不尽相同。Lei等(2014)研究发现, 分株之间的克隆整合作用使得遮阴远端分株根际C、N的有效性显著增加, 微生物群落结构也发生显著性变化, 表现出较强的根际过程。在蓉城竹(*Phyllostachys bisetii*)中, 尽管克隆整合显著增加了遮阴蓉城竹分株根际C的有效性, 但根状茎切断处理并没有对遮阴分株根际细菌的群落结构产生显著性影响(薛阁等, 2018)。推测这可能与植物种类不同有关, 更与资源

类型(如C和N)不同而表现出的不同传输方向密切相关(Alpert *et al.*, 2002)。

竹林是中国森林植被的重要组成部分。竹类植物是以木本为主的克隆植物, 其克隆生长特征对异质性生境具有很强的适应能力(施建敏等, 2014)。这一方面有利于高异质性生境的植被保持和生物多样性保育(邱尔发等, 2001; 李睿等, 2003); 另一方面竹林入侵其他群落所造成的群落结构破坏、生物多样性降低、生态功能下降等负面影响日益受到关注(白尚斌等, 2013; 刘骏等, 2013; 杨清培, 2017)。

因此, 我们提出如下假设: 克隆植物分株间光合产物的传输格局使得远端分株(年幼分株)获得更多的光合碳分配, 根际可利用碳资源的增加影响根际微生物过程; 而近端分株(年长分株)获得较少或不能获得光合碳分配, 克隆整合不会对近端分株根际微生物过程产生显著影响。本研究以单轴散生型克隆植物——蓉城竹为对象, 探讨克隆分株间光合产物传输对邻体分株根际微生物过程的影响, 这对于理解竹类植物的种群适应机制具有重要的理论意义。

1 材料和方法

1.1 研究材料

蓉城竹别名白夹竹, 属禾本科刚竹属(*Phyllostachys*), 株高3–6 m, 基径约2 cm。蓉城竹为单轴散生竹, 通过竹鞭(根状茎)进行克隆生长, 鞭梢生长期6–11月, 11月后停止生长, 次年3–4月发笋, 5月出笋成竹(曾林等, 1998)。蓉城竹竹笋可用于造纸、编篾, 笋可食用, 具有重要的经济价值, 同时也是大熊猫的主食竹之一(宋会兴等, 2011)。

1.2 实验设计

实验样地位于四川省成都市邛崃市南宝山镇(103.19° E, 30.45° N), 海拔1 217 m, 年平均气温16.3 °C, 年日照时间1 107.9 h, 年降水量1 117.3 mm。2015年11月, 选取当年生、长势一致的蓉城竹分株对, 控制分株间距在(30 ± 5) cm ($n = 12$)

范围内,依据竹鞭走向分别标记分株对的近端分株和远端分株。切断分株对外围竹鞭,用双层加厚塑料膜包裹蓉城竹根部土块(大小为0.5 m × 0.5 m)与周围环境隔离,以排除外界土壤环境对实验分株对的影响。实验分顶向传输(A)和基向传输(B)两组:顶向传输组中,将远端分株地上部分剪除(保留地面以上20 cm),近端分株自然生长;基向传输组中,将近端分株地上部分剪除(保留地面以上20 cm),远端分株自然生长。两组实验中保持根状茎连接或切断处理,每处理3个重复,共12个分株对(图1)。

1.3 土壤样品收集及相关指标测定

2016年11月,按照Riley和Barber (1970)的“抖落法”,对地上部分剪除的分株根际进行土壤取样。具体操作为:将没有黏附在根上的非根际土壤抖落,紧密黏附在根上、距离根系表面1–3 mm的土壤作为根际土壤,用无菌毛刷轻轻刷下,手工捡出动植物残体、砾石等,过筛(<2 mm)后保存于干燥灭菌的自封袋中(孙悦等, 2014; Guo *et al.*, 2016),用于相关指标的测定。不能及时测量的土壤样品置于–20 °C冰箱备用。

1.3.1 根际土壤碳氮有效性

土壤总有机碳(TOC)和总氮(TN)含量采用元素分析仪(vario MACRO cube, Elementar, Langensfeld, Germany)测定;溶解性有机碳(DOC)和溶

解性有机氮(DON)用0.5 mol·L⁻¹ K₂SO₄溶液浸提,于TOC/TN分析仪(TOC-L analyzer, Shimadzu, Kyoto, Japan)中测定其含量;土壤微生物生物量碳(MBC)和生物量氮(MBN)采用氯仿熏蒸提取法(CFAP)进行提取(Witt *et al.*, 2000; Setia *et al.*, 2012),于TOC/TN分析仪中测定其熏蒸处理和未熏蒸处理后的DOC、DON含量,通过Vance等(1987)和Wu等(1990)提出的公式计算土壤微生物生物量碳(氮)含量:

$$MBC(N) = E_B / 0.45$$

其中 E_B 是进行氯仿熏蒸处理与未熏蒸处理的浸提液DOC、DON含量差值,0.45为转换系数。

土壤无机氮即铵态氮(NH₄⁺-N)和硝态氮(NO₃⁻-N),用2 mol·L⁻¹ KCl溶液浸提后分别采用靛酚蓝比色法和双波长比色法测定含量(Crepin & Johnson, 1993);同时将等量土样于40 °C恒温箱中培养7昼夜,测定NH₄⁺-N和NO₃⁻-N含量,根据以下公式(Zhou *et al.*, 2011)计算土壤样品的净矿化速率(N_{min})和硝化速率(N_{nitr}):

$$N_{min} = \frac{(NH_4^+ + NO_3^-)_{\text{培养后}} - (NH_4^+ + NO_3^-)_{\text{培养前}}}{\text{培养时间}t}$$

$$N_{nitr} = \frac{(NO_3^-)_{\text{培养后}} - (NO_3^-)_{\text{培养前}}}{\text{培养时间}t}$$

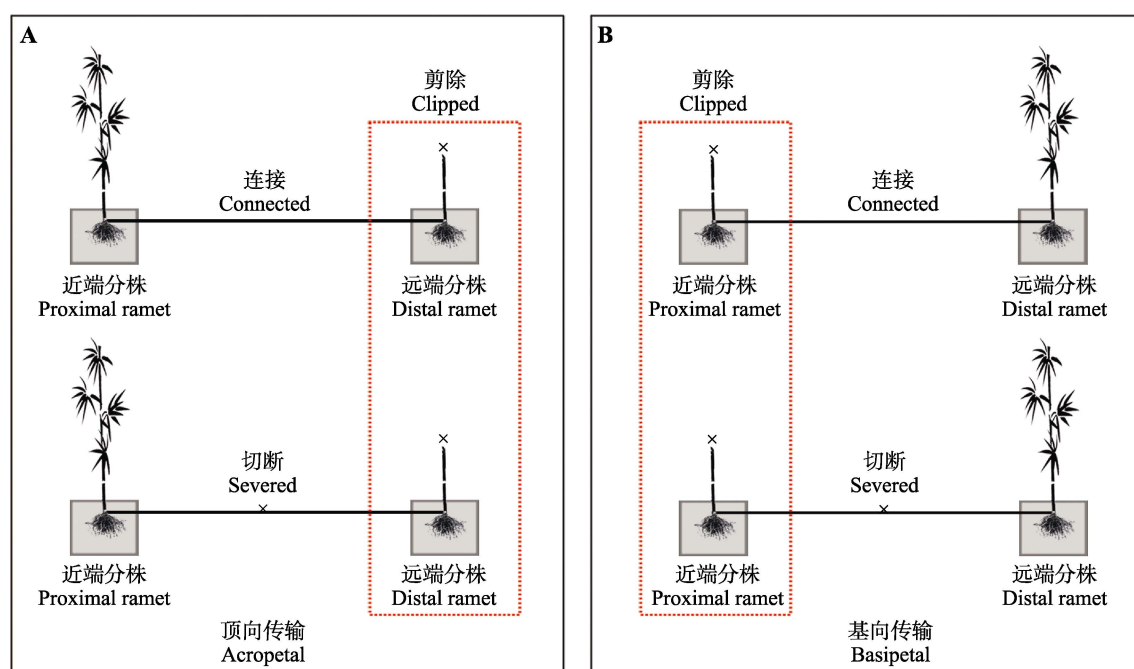


图1 实验设计图。

Fig. 1 Schematic diagram of experiment design.

1.3.2 土壤酶活性

N-乙酰基-β-D-氨基葡萄糖苷酶(NAGase)、多酚氧化酶(POXase)和脲酶(Urease)均为在根际土壤C、N转化过程中起重要作用的土壤酶,其中NAGase参与壳多糖水解,是决定土壤有机碳来源的重要因子(Smucker & Kim, 1987); POXase则对土壤腐殖质碳的形成有重要作用(关松荫, 1986); 而Urease参与土壤中有机氮向有效氮的转化过程,一定程度上反映土壤无机氮的供应能力(Gianfreda *et al.*, 2005)。本研究中NAGase采用Parham和Deng (2000)的方法,以对硝基苯酚-N-乙酰基-β-D-氨基葡萄糖苷(pNP-NAG)为底物进行测定,活性用 $\mu\text{g}\cdot\text{g}^{-1}\cdot\text{soil}\cdot\text{h}^{-1}$ 表示; Urease采用Kandeler和Gerber (1988)的方法,以尿素作为底物进行测定,活性用 $\mu\text{g}\cdot\text{g}^{-1}\cdot\text{soil}\cdot\text{h}^{-1}$ 表示; POXase采用Perucci等(2000)等的方法,以邻苯二酚为底物进行测定,活性用 $\mu\text{mol}\cdot\text{g}^{-1}\cdot\text{min}^{-1}$ 表示。

1.4 数据分析

采用IBM SPSS Statistics 19软件对数据进行正态检验,以S-W检验结果为准, p 值设置为0.05; 对数据进行方差齐性检验(Levene's test), 检验的显著性概率临界值为0.05; 通过单因素方差分析方法分析根状茎连接与否对根际土壤C、N有效性、酶活性、矿化速率及硝化速率的影响。采用OriginPro 8软件完成绘图。

2 结果

2.1 根际土壤C、N有效性

光合产物顶向传输中,根状茎连接的远端分株

根际的TOC、DOC、DON、 $\text{NH}_4^+\text{-N}$ 和 $\text{NO}_3^-\text{-N}$ 含量显著高于根状茎切断的远端分株,但TN含量差异不显著; 光合产物基向传输中,根状茎连接的近端分株根际DON、 $\text{NH}_4^+\text{-N}$ 和 $\text{NO}_3^-\text{-N}$ 的含量显著低于根状茎切断分株,而根状茎切断与否对TOC、TN和DOC含量无显著影响(表1)。

2.2 根际土壤微生物生物量特征

光合产物顶向传输中,根状茎保持连接的远端分株根际土壤MBC含量显著高于根状茎切断的分株,但切断根状茎并没有显著影响根际土壤MBN含量; 光合产物基向传输中,切断根状茎没有显著影响根际土壤MBC含量,却显著改变了根际土壤MBN含量,使得根状茎保持连接的近端分株根际土壤MBN含量显著高于根状茎切断的近端分株根际(表1)。

MBC/MBN值在两个实验中也表现出了不同的变化趋势,在光合产物顶向传输中,根状茎保持连接的远端分株根际MBC/MBN值为8.282,显著高于切断根状茎的远端分株根际; 在光合产物基向传输中恰好相反,表现为根状茎保持连接的近端分株根际MBC/MBN值显著低于切断根状茎的近端分株根际(表1)。

2.3 根际土壤酶活性

光合产物顶向传输中,根状茎保持连接的远端分株根际NAGase、POXase和Urease活性均显著高于根状茎切断的远端分株根际; 但在光合产物基向传输实验中3个酶的变化趋势并不一致: 其中Urease与POXase活性变化与顶向传输组一致,表现为根

表1 光合产物传输方向对蓉城竹根际土壤性质的影响(平均值±标准偏差)

Table 1 Effects of transportation direction of photosynthate on soil properties in the rhizosphere of *Phyllostachys bisetii* (mean ± SD)

土壤性质 Soil properties	顶向传输组 Acropetal treatment		基向传输组 Basipetal treatment	
	连接 Connected	切断 Severed	连接 Connected	切断 Severed
TOC ($\text{g}\cdot\text{kg}^{-1}$)	8.859 ± 0.139	8.221 ± 0.048**	8.513 ± 0.108	8.697 ± 0.170
TN ($\text{g}\cdot\text{kg}^{-1}$)	1.707 ± 0.149	1.560 ± 0.172	1.569 ± 0.073	1.617 ± 0.088
DOC ($\text{mg}\cdot\text{kg}^{-1}$)	62.683 ± 0.293	58.23 ± 0.621***	56.017 ± 0.180	56.163 ± 0.295
DON ($\text{mg}\cdot\text{kg}^{-1}$)	7.99 ± 0.105	6.674 ± 0.042***	7.126 ± 0.079	7.422 ± 0.041**
MBC ($\text{mg}\cdot\text{kg}^{-1}$)	20.052 ± 1.725	14.621 ± 0.719**	21.467 ± 1.156	19.238 ± 1.186
MBN ($\text{mg}\cdot\text{kg}^{-1}$)	2.456 ± 0.414	3.084 ± 0.151	2.522 ± 0.244	1.599 ± 0.138**
MBC/MBN	8.282 ± 1.225	4.750 ± 0.371**	8.551 ± 0.716	12.083 ± 1.148*
$\text{NH}_4^+\text{-N}$ ($\text{mg}\cdot\text{kg}^{-1}$)	7.206 ± 0.234	5.557 ± 0.368**	5.531 ± 0.127	6.957 ± 0.181***
$\text{NO}_3^-\text{-N}$ ($\text{mg}\cdot\text{kg}^{-1}$)	1.908 ± 0.120	1.224 ± 0.203**	1.467 ± 0.175	2.304 ± 0.441*

根状茎连接与切断分株间显著性检验表示为: ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$ 。DOC, 溶解性有机碳; DON, 溶解性有机氮; MBC, 微生物生物量碳; MBN, 微生物生物量氮; TN, 总氮; TOC, 总有机碳。

The significant differences between rhizome connected ramets and rhizome severed ramets were indicated by *** ($p < 0.001$), ** ($p < 0.01$), and * ($p < 0.05$). DOC, dissolved organic carbon; DON, dissolved organic nitrogen; MBC, microbial biomass carbon; MBN, microbial biomass nitrogen; TN, total nitrogen; TOC, total organic carbon.

状茎连接近端分株显著高于根状茎切断的近端分株; NAGase活性变化与顶向传输实验相反, 表现为根状茎连接近端分株显著低于根状茎切断的近端分株(图2)。

2.4 根际土壤N矿化、硝化速率

光合产物顶向传输中, 根状茎切断并没有对远端分株根际土壤 N_{\min} 与 N_{nitr} 产生显著性影响; 在光合产物基向传输中, 根状茎保持连接与否没有对近端分株根际 N_{\min} 产生显著影响, 但显著影响了其 N_{nitr} , 根状茎保持连接的近端分株根际 N_{nitr} 显著高于根状茎切断分株(图3)。

3 讨论

3.1 光合产物传输对蓉城竹根际C、N有效性的影响

根际沉积作用是植物根系为土壤环境提供可利用碳源的重要方式(Kuzyakov, 2002; Jones *et al.*, 2009)。在蓉城竹中, 根状茎保持连接的远端分株根

际TOC、DOC含量均显著高于根状茎切断的远端分株, 这与遮阴活血丹(*Glechoma longituba*)远端分株具有较高的DOC含量是一致的(Lei *et al.*, 2014), 暗示了地上部分被剪除的远端分株根际, 获得了近端分株光合产物的支持。而根际氮肥有效性的增加能显著增加绿竹(*Dendrocalamopsis oldhami*)的竹笋产量(曾爱平等, 2007), 意味着蓉城竹远端分株地上部分被剪除后出笋量可能增加。

光合产物基向传输中, 根状茎保持切断与否并没有显著影响近端分株根际TOC、DOC含量, 这一方面是由于植物地上部分去除会引起植物的补偿效应, 即将根系积累的碳水化合物重新输送到地上部分, 进而影响根系的沉积作用(Giese *et al.*, 2013); 另一方面, 光合产物的传输主要是顶向传输, 而基向传输中传输的量较少, 从而影响了近端分株根际C有效性(D'Hertefeldt & Jónsdóttir, 1999)。

植株根际C有效性的增加, 促进了土壤微生物生长代谢过程(赵劲松等, 2003), 加快了微生物调控

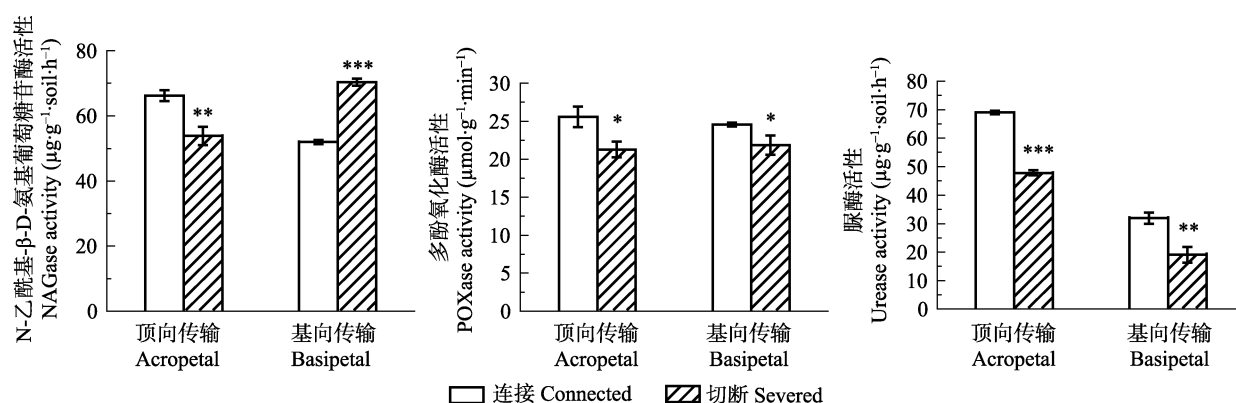


图2 光合产物传输对蓉城竹根际土壤酶活性的影响(平均值±标准偏差)。***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$ 。

Fig. 2 Effects of transportation direction of photosynthate on soil enzyme activities in the rhizosphere of *Phyllostachys bisetii* (means ± SD). NAGase, N-acetyl-β-D-glucosaminidase; POXase, phenol oxidase. ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$.

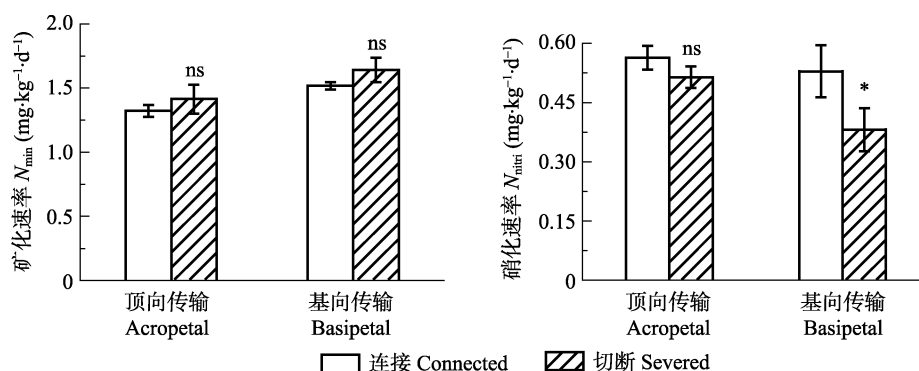


图3 光合产物传输对蓉城竹根际土壤氮素矿化速率(N_{\min})和硝化速率(N_{nitr})的影响(平均值±标准偏差)。***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$ 。

Fig. 3 Effects of transportation direction of photosynthate on soil N mineralization rate(N_{\min}) and nitrification rate(N_{nitr}) in the rhizosphere of *Phyllostachys bisetii* (means ± SD). ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$.

的N转化过程,使得根状茎保持连接的蓉城竹远端分株根际具有较高的N有效性(表1),这与对活血丹的研究结果是一致的(Lei *et al.*, 2014)。而在光合产物基向传输中,根状茎保持连接的近端分株根际 NH_4^+ -N和 NO_3^- -N浓度显著低于切断分株。同位素示踪实验发现,年龄较大的无叶分株可以保持较高的根系吸收活力,其功能特化为吸收地下资源并传递给年龄较小的具叶分株,维持年幼分株的顶端优势和生长(Jónsdóttir & Callaghan, 1990)。此外,光合产物基向传输中根状茎连接近端分株根系分泌的有机碳促进了根际土壤微生物的生长,表现出了较高的微生物生物量,但其对根际N的竞争能力远远强于微生物对营养的摄取,这种植物和微生物对N的竞争策略同时也是生态系统N循环的重要环节(Schimel & Bennett, 2004; 章晴, 2016)。因此,根际土壤N有效性同时受到植物根系吸收、土壤微生物摄取以及根际土壤N矿化硝化作用等多方面因素的影响,且根系吸收的能力与根系的生理年龄、根量等有关(钦绳武和刘芷宇, 1984; 章晴, 2016)。同时,由于光合产物在不同方向上传输量的差异,使得地上部分剪除后蓉城竹近端、远端分株根际N有效性发生了迥异变化。

3.2 光合产物传输对蓉城竹根际土壤酶活性的影响

根际区域土壤酶活性主要受到根系分泌物、根系凋落物及土壤微生物群落结构组成和土壤微生物活性等因素的影响(Toberman *et al.*, 2011)。在远端分株根际,根状茎保持连接的植株土壤酶活性显著高于根状茎断开植株。这在紫竹(*Phyllostachys nigra*)(张云和陈劲松, 2017)、活血丹(Lei *et al.*, 2014)等中也有发现,这与根状茎保持连接的远端分株根际通过整合作用获得了更多的光合碳资源,改变了土壤微生物群落结构和活性有关(Rajaniemi & Allison, 2009)。树木环割(Koranda *et al.*, 2011)以及牧草刈割(章家恩等, 2005)后土壤酶活性的变化也间接证明了我们的研究结果。

在光合产物基向传输中,根状茎连接近端分株根际土壤Urease和POXase活性依旧高于根状茎切断的近端分株,而NAGase活性恰好相反,根状茎切断近端分株显著高于根状茎保持连接近端分株。有关植物根系活力与Urease、POXase活性正相关的研究结果在烟草(*Nicotiana tabacum*)(李艳平等, 2016)、番茄(*Lycopersicon esculentum*)(吴瑕等, 2015)中均有

报道。因此我们推测土壤Urease和POXase活性变化可能与根状茎连接分株较切断分株具有更高的根系活力有关;而根际NAGase活性与土壤真菌Glomeromycota(球囊菌门)丰度显著负相关(李丽华, 2016)。球囊菌是构成陆生植物丛枝菌根的主体,需从宿主植物中获取碳及能量才能生存。由此推测,尽管在蓉城竹中光合产物基向传输的量不足以引起根际TOC、DOC浓度的显著变化,但依旧能够维持共生的丛枝菌根菌的生存,从而影响着根际NAGase活性。

3.3 光合产物传输对蓉城竹根际土壤微生物量特征的影响

土壤微生物参与了土壤有机质的转化过程,在植物养分有效性和腐殖质形成过程中发挥着重要作用(Bardgett *et al.*, 2005)。通常采用MBC/MBN来评价土壤微生物种群结构(Paul & Clark, 1989)。有研究表明,少量的根系分泌物会影响土壤微生物活性,而在根系分泌物量较大时,细菌与真菌的相对多度发生改变,影响土壤微生物群落结构(de Graaff *et al.*, 2010)。在根状茎保持连接的蓉城竹远端分株根际, MBC含量显著高于切断分株,连接和切断分株MBC/MBN差异显著,是蓉城竹生理整合作用下远端分株根际沉积作用的结果。光合产物顶向传输实验中根状茎切断与否并没有对MBN含量产生显著影响。黑杨(*Populus nigra*)、水杉(*Metasequoia glyptostroboides*)根际的添加实验表明, C/N较高的低分子量有机碳对根际土壤MBN含量没有显著影响(章晴, 2016)。

在光合产物基向传输中, MBC/MBN在保持连接的蓉城竹分株根际与根状茎切断的分株根际存在显著差异,预示着根状茎连接与否对近端分株根际土壤微生物群落组成产生了显著影响。这可能是根状茎切断后与近端分株根系共生的丛枝菌根真菌生长受限及(或)腐生真菌增多的原因(Koranda *et al.*, 2011)。

3.4 光合产物传输对蓉城竹根际土壤N矿化、硝化速率特征的影响

N矿化是土壤氮循环一个最重要的过程,微生物是土壤N矿化过程重要的参与者,土壤有机质与根际沉积物可促进微生物的矿化作用(Rajaniemi & Allison, 2009)。通过向土壤中添加易分解有机碳,发现根系分泌物的增加会加速或抑制N矿化过程,

而表现为正激发效应(Hamer & Marschner, 2005; Kuzyakov *et al.*, 2007)或负激发效应(Kuzyakov & Bol, 2006; Blagodatskaya *et al.*, 2007)。de Graaff等(2010)认为这是根系分泌物量的高低造成的结果。在我们的研究中,无论在光合产物顶向传输还是基向传输实验中, N_{\min} 都没有发生显著性变化, N_{nitri} 仅是在基向传输实验中连接分株显著高于根状茎断开分株。由于实验并没有对根系分泌物的数量进行研究,出现这一结果的机制并不清楚。此外,测定的土壤N矿化、硝化速率属于瞬时变化,不同于根际C、N有效性及土壤酶活性等具有累积效应(Zhou *et al.*, 2011);同时,土壤 N_{\min} 、 N_{nitri} 受温度、湿度等因子的影响(McMurtrie *et al.*, 2001; Zaman & Chang, 2004),季节性变化明显,对土壤 N_{\min} 、 N_{nitri} 动态的研究有助于揭示这一研究结果的详细机制。

总之,控制性实验造成的光合产物传输方向差异使得蓉城竹近端和远端分株根际C有效性产生不同变化,进而对根际土壤酶活性等微生物过程产生了不同的影响,意味着克隆植物分株间光合产物传输的非对称性。光合产物顶向传输的优势促进了远端分株根际N有效性,可能有利于受动物取食或人为砍伐等干扰影响的蓉城竹分株的再生长(如新生笋的萌发和生长)(周世强等, 2009; 魏宇航, 2013)。而根状茎保持连接的近端分株地上部分剪除后地下部分功能特化,保持较高的根系活力(Jónsdóttir & Callaghan, 1990),但其根际较低的N有效性似乎暗示了其根际存在一定的营养转移(可能供给幼嫩分株或土壤微生物)。因此,蓉城竹分株地上部分剪除形成的分株间光合产物非对称性传输,影响了根际微生物过程,这可能是蓉城竹对动物取食或人为砍伐等干扰的有益权衡,是对自身克隆片段的“取舍”,这有助于克隆植物对生存环境的适应调节。

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