酚酸和氮素交互作用下欧美杨107细根形态特征

朱婉芮¹ 汪其同¹ 刘梦玲¹ 王华田^{1,2} 王延平^{1,2*} 张光灿^{1,2} 李传荣^{1,2}

¹山东农业大学林学院, 山东泰安 271018; ²国家林业局泰山森林生态系统定位研究站, 山东泰安 271018

摘 要 树木细根生长与根际过程的关系十分密切。该研究仿生欧美杨107 (*Populus × euramericana* ‘Neva’) 人工林根际土壤酚酸沉降与氮素有效性变化, 通过设置3种酚酸梯度(0X、0.5X、1.0X, X为田间土壤酚酸含量)与3种氮素水平(缺氮0 mmol·L⁻¹、正常氮10 mmol·L⁻¹、高氮20 mmol·L⁻¹), 探究酚酸和氮素对欧美杨107细根形态的影响, 以期阐明树木根系生长对根-土界面过程的响应奠定基础。结果表明: (1)在无酚酸(0X)环境中, 缺氮和高氮均可抑制欧美杨107细根生长, 尤其对1–3级细根的影响更为显著。比根长随氮素水平升高逐渐减小, 但其他细根特征并未呈现与氮素水平的线性关系。(2) 0.5X和1.0X酚酸梯度相比, 欧美杨107的1–2级细根直径和体积随酚酸浓度增加而显著增大($p < 0.05$)。酚酸和氮素对杨树细根的影响存在交互作用, 1–2级细根直径、体积受酚酸的影响显著, 而4–5级细根长度、表面积受氮素影响显著。双因素方差分析结果表明, 酚酸和氮素对细根形态建成具有协同或拮抗效应。(3)主成分分析(PCA)和冗余分析(RDA)结果表明, 在酚酸和氮素交互效应下, 杨树1–3级、4级、5级细根之间具有显著的形态差异。第一主成分主要体现细根觅食性状特征, 可解释细根形态变异的60.9%的信息; 第二主成分主要体现细根形态构建特征, 可解释25.3%的信息。杨树细根形态变化与根序高度相关, N素影响杨树细根形态的主效应较酚酸更强。因此, 根际环境中酚酸累积和氮素有效性变化会影响杨树细根的形态构建和细根对水分、养分的吸收, 而氮素有效性是影响杨树细根生长的重要因素, 开展杨树人工林土壤养分管理是林分生产力长期维持的关键。

关键词 细根形态, 氮素有效性, 酚酸根际沉降, 杨树根序, 根土互作

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Interactive effects of phenolic acid and nitrogen on morphological traits of poplar (*Populus × euramericana* ‘Neva’) fine roots

ZHU Wan-Rui¹, WANG Qi-Tong¹, LIU Meng-Ling¹, WANG Hua-Tian^{1,2}, WANG Yan-Ping^{1,2*}, ZHANG Guang-Can^{1,2}, and LI Chuan-Rong^{1,2}

¹Forestry College of Shandong Agricultural University, Tai'an, Shandong 271018, China; and ²Taishan Forest Ecosystem Research Station of State Forestry Administration, Tai'an, Shandong 271018, China

Abstract

Aims The relationship between rhizosphere process and fine root growth is very close but still obscure. In poplar plantation, phenolic acid rhizodeposition and soil nutrient availability were considered as two dominant factors of forest productivity decline. It is very hard to separate them in the field and they might show an interactive effect on fine root growth. The objective of this study is to examine the influence of phenolic acids and nitrogen on branch orders of poplar fine roots and to give a deeper insight into how the ecological process on root-soil interface affected fine root growth as well as plantation productivity.

Methods The cuttings of health annual poplar seedlings (I-107, *Populus × euramericana* ‘Neva’) serve as experiment materials, and were cultivated under nine conditions, including three concentration of phenolic acids at 0X, 0.5X, 1.0X (here, X represented the contents of phenolic acids in the soil of poplar plantation) and three concentration of nitrogen at 0 mmol·L⁻¹, 10 mmol·L⁻¹, 20 mmol·L⁻¹, based on Hoagland solution. The roots were all separated from poplar seedlings after 35 days, and 30 percent of total fine roots of every treatment were taken as fine root samples. These fine roots were grouped according to 1 to 5 branch orders, and then the morphological traits of each group of fine roots were scanned via root analyzer system (WinRHIZO, Regent Instruments Company, Quebec, Canada) including total length, surface area, volume and average diameter. Meanwhile, the dry mass of fine root samples of every order was measured to calculate specific root length (SRL), root tissue density

(RTD). All data were analyzed via SPSS 17.0 software, and interactive effect of phenolic acids and nitrogen on roots was analyzed through univariate process module. Principal component analysis (PCA) and redundancy analysis (RDA) were conducted via Canoco 4.5 software.

Important findings Under the conditions without phenolic acids application, the fine roots growth was significantly inhibited in deficiency and higher nitrogen treatments, especially for 1–3 order roots. Only specific root length appeared decreased with nitrogen level, and other traits of fine roots did not demonstrate linear relationship with nitrogen concentrations. Compared to 0.5X phenolic acids treatment, 1.0X phenolic acids significantly promoted the diameter and volume of 1–2 order roots ($p < 0.05$). Both phenolic acids and nitrogen demonstrated influence on poplar fine root traits. However, the diameter and volume of 1–2 order roots were significantly affected by phenolic acids, while the total length and surface area of 4–5 order roots was affected by nitrogen. Two way ANOVA showed that phenolic acids and nitrogen made a synergistic or antagonistic effect on morphological building of fine roots. Furthermore, PCA and RDA indicated that the interactive effects of phenolic acids and nitrogen led to significant differences among 1–3 order, 4th order and 5th order of poplar fine roots. The PC1 explained about 60.9 percent of root morphological variance, which was related to foraging traits of roots. The PC2 explained 25.3 percent of variance, which was related to root building properties. The response of poplar roots to phenolic acids and nitrogen was closely related to root order, and nitrogen played more influence on poplar roots than phenolic acids. Thus, phenolic acids and nitrogen level would affect many properties of root morphology and foraging in rhizosphere soil of poplar plantation. But nitrogen availability would serve as a dominant factor influencing root growth, and soil nutrient management should be critical to productivity maintenance of poplar plantation.

Key words fine root morphological traits, nitrogen availability, phenolic acids rhizodeposition, poplar root order, root-soil interaction

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细根是森林生态系统中植物营养的源和库 (Bloomfield *et al.*, 1996), 也是植物与土壤密切接触的部分 (Norby & Jackson, 2000; Block *et al.*, 2006), 由此形成的根-土界面成为生态系统碳氮循环的一个重要界面 (Schweinsberg-Mickan *et al.*, 2012)。研究表明, 细根生长、死亡和周转除受树种本身的遗传控制外, 还受到土壤因素的重要影响 (Fitter *et al.*, 1996; Hodge, 2004)。细根生产与土壤氮素有效性关系的假说 (郭大立和范萍萍, 2007) 暗示细根生长与土壤氮素有效性之间可能存在非线性关系。此外, 由于土壤生态系统的复杂性, 尤其是根-土界面生物化学性质的特殊性 (Jones *et al.*, 2009), 细根生长对根际环境的响应十分复杂。例如, 由根系分泌或植物残体腐解形成的根际碳沉降显著改变了根-土界面性质 (孙悦等, 2014)。酚酸作为根际碳沉降的重要组成部分 (Rice, 1984), 其化感效应不但影响了植物生长 (Li *et al.*, 2010), 而且影响了土壤氮素循环过程 (Inderjit & Mallik, 1997; Martens, 2002)。因此, 细根生长可能受根际土壤碳-氮耦合过程的共同影响。但

迄今为止, 关于根际环境变化对细根生长的影响研究开展较少。

杨树 (*Populus*) 是我国温带地区的典型速生丰产林树种, 轮伐期 8–10 年。在生产实践中杨树人工林培育的主要模式是连作经营, 但由此导致的林分生产力下降现象非常严重 (孙翠玲等, 1995; 刘福德等, 2005)。研究表明, 杨树人工林根际存在显著的酚酸累积趋势 (谭秀梅等, 2008)。根际土壤酚酸的累积对土壤氮素有效性产生了显著抑制 (王延平等, 2013; 许坛等, 2014), 反之, 土壤氮素缺乏也促使杨树根系分泌更多的酚酸 (王延平等, 2011)。为此, 王华田和王延平 (2013) 构建了连作杨树人工林生产力衰退机理模型, 指出酚酸累积和土壤氮素有效性的耦合作用可能是导致杨树人工林生产力下降的重要原因。根系作为地上和地下生态过程联系的枢纽, 细根生长与森林生产力的关系十分密切 (Osmont *et al.*, 2007)。杨树细根形态在连作人工林代际间存在较大差异 (许坛等, 2015), 且 1–2 级细根生物量在二代人工林中显著增加。因此, 杨树人工林根际酚酸累积

和氮素有效性变化可能影响了细根形态及生物量分配,进而影响林分生产力形成。当前,关于杨树细根对酚酸和氮素的响应规律仍不清楚。本研究试图通过模拟酚酸环境并设置氮素梯度浓度以仿生欧美杨107 (*Populus × euramericana* ‘Neva’)人工林根际土壤环境,探究酚酸和氮素交互作用对杨树幼苗细根形态特征的影响,为阐明根-土界面性质改变对杨树根系生长的影响提供科学依据,同时为今后深入开展人工林根际过程与生产力衰退关系的研究奠定基础。

1 材料和方法

1.1 供试材料及试验设计

采集杨树(品种欧美杨1-107, *Populus × euramericana* ‘Neva’)一年生插穗(直径1.5 cm, 长10 cm), 水培至下端出现根原基, 将插穗转移至栽培盆(上口径20 cm, 高17 cm, 底径15 cm), 以蛭石作为基质继续培养40天以确保插穗形成根系, 选取长势一致的植株用于试验。本研究为仿生杨树人工林土壤根际环境, 设计了3个氮素水平(缺氮(0 mmol·L⁻¹)、正常氮(10 mmol·L⁻¹)、高氮(20 mmol·L⁻¹))和3个酚酸水平(0X (无酚酸)、0.5X、1.0X, X为田间土壤酚酸含量)。

氮素水平设计以Hoagland营养液为基础, 通过调节Ca(NO₃)₂·4H₂O、KNO₃和NH₄NO₃的量, 分别形成上述3个氮素浓度梯度。其中, 缺氮营养液用KCl、CaCl₂替代KNO₃、Ca(NO₃)₂维持离子平衡, 保持其他元素含量一致。酚酸溶液是依据杨树人工林土壤内测定的5种酚酸含量及各土壤对各酚酸物质的吸附率(谭秀梅等, 2008; 王延平等, 2010), 在上述3个氮素水平营养液基础上完成(表1)。试验共形成9种处理, 包括无酚酸环境时氮素的3种处理, 以及酚酸和氮素双因素影响下的6种处理。

用上述营养液浇灌杨树幼苗, 每5天一次, 每次500 mL以使盆内栽培基质完全浸润。每种处理5个重复, 共计45株苗木。实验材料培养均是在山东农业大学全自动温室内进行。

1.2 试验方法

1.2.1 杨树细根采集及根序划分

将选取的生根杨树幼苗按照上述处理分别培养35天后开始细根采集, 抖落根系附着的蛭石, 将全部根系剪下放入具有标号的自封袋, 并迅速储存在冰盒内带回实验室。首先, 从各处理中按照细根总数30%的比例随机抽取根系, 放入2–3 °C蒸馏水中反复冲洗。按照Pregitzer等(2002)和Valenzuela-Estrada等(2008)介绍的方法, 以根系生长发育顺序区分各等级的细根, 即根系分枝最先端为1级根, 其生长在2级根上, 2级根的母根为3级根, 依次类推, 一直区分到5级根。把剪下的细根按照根序进行分组, 依次放在盛有低温蒸馏水的培养皿中, 并标记好处理号及根序号。

1.2.2 细根形态特征测定

用根系扫描仪(WinRHIZO, Regent Instruments Company, Quebec City, Canada)扫描各根序细根样品, 获取细根总长度、总表面积、总体积和平均直径等形态参数。然后将扫描后的各级根序细根分别置于烘箱, 于70 °C烘干至恒质量, 放入干燥器中冷却至室温, 置于1/1000天平称量细根干质量。根据长度、体积和干质量分别计算细根比根长(m·g⁻¹)、根组织密度(g·cm⁻³)等参数。

1.3 数据处理

采用SPSS 17.0软件中的Means过程, 计算细根形态指标平均值和标准误差, 并调用最小显著差异法(LSD)分析无酚酸环境下3个氮素水平各细根形态指标的差异显著性(α = 0.05)。通过SPSS中Univariate过程对酚酸和氮素影响下各根序细根形态特征指标

表1 酚酸浓度设定
Table 1 Phenolic acid concentration setting in the treatment solutions

	对羟基苯甲酸 <i>p</i> -hydroxybenzoic acid	香草醛 Vanillin	阿魏酸 Ferulic acid	苯甲酸 Benzoic acid	肉桂酸 Cinnamic acid
林地土壤内酚酸含量 Content of phenolic acid in field soil (μg·g ⁻¹)	152.00	10.40	6.50	20.60	1.95
土壤酚酸吸附率 Absorption rate of phenolic acid in soil (%)	61.66	93.78	89.30	37.85	94.41
酚酸含量梯度 Gradient of phenolic acid content (μg·mL ⁻¹)	0.5X	123	6	4	27
	1.0X	247	11	7	54

X 为田间土壤酚酸含量。
X represents the contents of phenolic acids in the soil of poplar plantation.

进行双因素方差分析, 并采用Duncan新复极差法对交互效应显著性进行检验($\alpha = 0.05$)。采用Canoco 4.5软件的主成分分析(PCA)功能, 确定细根形态变化的主分量并计算其载荷值。将各根序细根形态变化主分量与环境因子(酚酸和氮素)结合, 采用Canoco 4.5软件的冗余分析(RDA)对细根形态与酚酸、氮素的相关性进行分析, 确定影响细根形态的主效应。

2 结果和分析

2.1 氮素对杨树细根形态特征的影响

表2显示了无酚酸添加时不同氮素水平(单因素)对杨树细根各级根序细根形态的影响。总体上, 缺氮和高氮两种水平下各根序细根总长度、总表面积、总体积小于正常氮水平, 但缺氮和高氮之间大部分未表现出显著差异。1–2级细根平均直径在正常氮水平下显著大于缺氮和高氮($p < 0.05$), 但3–5级细根平均直径未表现出显著差异。此外, 1–3级细根干质量呈现正常等氮显著高于高氮和缺氮($p < 0.05$), 而4–5级细根干质量则差异不显著。各根序细根比根长总体呈现随氮素水平升高而减小的趋势,

1–3级细根组织密度在氮素水平间差异显著, 而4–5级细根差异不显著。

2.2 酚酸和氮素对杨树细根形态的影响

从图1可以看出, 在0.5X酚酸环境中, 3种氮素水平间1–3级细根总长度的差异未达到显著水平, 但平均直径、表面积和体积的差异显著($p < 0.05$); 尤其是细根表面积在缺氮和高氮时均被显著抑制($p < 0.05$)。在此酚酸浓度下, 4级细根长度和表面积在缺氮时被显著促进, 而5级细根各形态指标均呈现正常氮水平下较大。在1.0X酚酸环境中, 细根形态参数随氮素梯度的变化与0.5X酚酸环境相似, 但是4级和5级细根形态在不同氮素水平间总体不显著。可见, 酚酸和氮素对细根长度、直径、体积等形态特征存在交互作用, 4–5级细根受这种交互作用的影响更为明显。不同酚酸浓度下杨树细根形态也存在一定差异, 例如, 高氮时, 1.0X酚酸对2级细根长度、表面积和体积具有显著促进作用, 同时3级细根表面积和体积在此酚酸浓度下也较大。该规律在正常氮水平下也有体现, 1–2级细根体积均受酚酸的显著促进。这说明, 酚酸对低级细根体积的影响较为显著, 而氮素对高级细根长度、表面积等影响较大。

表2 不同根序细根形态指标对氮素的响应

Table 2 The response of morphological traits of different order fine roots to the nitrogen treatments

根序 Root order	氮素水平 Nitrogen level (mmol·L ⁻¹)	根长度 Total root length (cm)	根表面积 Total root surface area (cm ²)	根体积 Total root volume (cm ³)	平均直径 Average diameter (mm)	根干质量 Root dry mass (g)	比根长 Specific root length (m·g ⁻¹)	根组织密度 Root tissue density (g·cm ⁻³)
1	0	534.51 ± 58.78 ^a	28.93 ± 2.11 ^a	0.13 ± 0.005 ^a	0.17 ± 0.064 ^a	0.013 ± 0.000 ^a	323.00 ± 12.66 ^a	0.114 ± 0.010 ^{ab}
	10	822.03 ± 65.15 ^b	55.41 ± 9.47 ^b	0.41 ± 0.007 ^b	0.23 ± 0.013 ^b	0.028 ± 0.002 ^b	287.53 ± 4.28 ^b	0.091 ± 0.015 ^a
	20	389.77 ± 48.70 ^a	23.55 ± 2.28 ^a	0.12 ± 0.011 ^a	0.18 ± 0.025 ^a	0.014 ± 0.002 ^a	246.51 ± 37.71 ^b	0.146 ± 0.001 ^b
2	0	716.81 ± 49.22 ^a	42.01 ± 2.90 ^a	0.19 ± 0.013 ^a	0.19 ± 0.001 ^a	0.023 ± 0.003 ^a	269.07 ± 36.03 ^a	0.113 ± 0.003 ^a
	10	871.82 ± 15.89 ^a	72.59 ± 3.10 ^b	0.26 ± 0.017 ^b	0.25 ± 0.011 ^b	0.042 ± 0.002 ^b	228.89 ± 18.80 ^{ab}	0.085 ± 0.001 ^b
	20	428.53 ± 61.70 ^b	39.30 ± 1.34 ^a	0.23 ± 0.008 ^{ab}	0.21 ± 0.006 ^a	0.023 ± 0.001 ^a	185.39 ± 10.71 ^b	0.108 ± 0.001 ^a
3	0	249.26 ± 19.75 ^a	16.37 ± 0.22 ^a	0.10 ± 0.007 ^a	0.24 ± 0.016 ^a	0.013 ± 0.001 ^a	184.68 ± 22.25 ^a	0.104 ± 0.004 ^a
	10	462.39 ± 52.25 ^b	28.30 ± 3.85 ^b	0.22 ± 0.014 ^b	0.30 ± 0.037 ^a	0.026 ± 0.000 ^b	146.59 ± 11.16 ^{ab}	0.118 ± 0.006 ^{ab}
	20	179.04 ± 16.34 ^a	16.42 ± 1.27 ^a	0.14 ± 0.026 ^a	0.29 ± 0.003 ^a	0.017 ± 0.002 ^a	111.33 ± 2.83 ^b	0.129 ± 0.005 ^b
4	0	38.28 ± 4.84 ^a	4.39 ± 0.30 ^a	0.06 ± 0.002 ^a	0.32 ± 0.016 ^a	0.006 ± 0.000 ^a	75.49 ± 7.93 ^a	0.108 ± 0.002 ^a
	10	43.26 ± 4.42 ^b	5.62 ± 0.47 ^{ab}	0.07 ± 0.009 ^b	0.42 ± 0.037 ^a	0.008 ± 0.003 ^a	63.54 ± 5.19 ^b	0.122 ± 0.005 ^a
	20	39.29 ± 4.19 ^b	4.52 ± 0.91 ^b	0.04 ± 0.011 ^a	0.39 ± 0.016 ^a	0.005 ± 0.002 ^a	60.92 ± 1.38 ^b	0.130 ± 0.003 ^a
5	0	32.85 ± 1.14 ^a	7.41 ± 0.44 ^a	0.17 ± 0.024 ^a	0.74 ± 0.018 ^a	0.032 ± 0.001 ^a	12.58 ± 1.83 ^a	0.155 ± 0.004 ^a
	10	48.15 ± 4.71 ^a	13.85 ± 1.63 ^a	0.47 ± 0.046 ^a	1.03 ± 0.056 ^a	0.043 ± 0.003 ^a	9.85 ± 1.06 ^b	0.114 ± 0.284 ^a
	20	28.24 ± 11.61 ^a	7.74 ± 4.25 ^a	0.17 ± 0.118 ^a	0.74 ± 0.136 ^a	0.024 ± 0.016 ^a	8.69 ± 0.49 ^b	0.140 ± 0.003 ^a

不同字母表示同级根序细根在不同氮水平下形态差异显著($p < 0.05$)。

Different lowercase letters indicate significant differences of fine roots morphological traits among different nitrogen treatments ($p < 0.05$).

图1 酚酸和氮素影响下杨树各根序细根形态特征(平均值±标准误差)。小写字母分别表示0.5X和1.0X酚酸环境中(X为田间土壤酚酸含量), 3种氮素水平间的差异显著性, 不同字母表示差异显著($p < 0.05$)。+, *, #分别表示缺氮(0 mmol·L⁻¹)、正常氮(10 mmol·L⁻¹)、高氮(20 mmol·L⁻¹)时, 两酚酸浓度间具有显著差异($p < 0.05$)。

Fig. 1 The fine root morphological characteristics in the interaction of phenolic acid and nitrogen treatments (mean $\pm$ SE). Different lowercase letters and capital letters represent significant difference among three nitrogen treatments under 0.5X and 1.0X phenolic acids respectively ($p < 0.05$), here X represents the contents of phenolic acids in the soil of poplar plantation. Three symbols, +, * and #, represent significant difference between two treatments of phenolic acids under nitrogen deficiency (0 mmol·L⁻¹), normal nitrogen (10 mmol·L⁻¹) and high nitrogen (20 mmol·L⁻¹), respectively.

从图2可以看出, 在0.5X酚酸环境中, 1–3级细根干质量和根组织密度在不同氮素水平间均未呈现显著差异, 而4–5级细根差异显著; 各根序细根的比根长则呈现随氮素水平升高而显著降低的趋势($p < 0.05$)。在1.0X酚酸环境中, 1–3级细根干质量和根组织密度在不同氮素水平间的差异显著, 而4–5级细根则不显著; 比根长在不同氮素水平间的差异也大部分未达到显著水平。可见, 酚酸和氮素对杨

树细根干质量、根组织密度等形态参数存在明显的交互作用。酚酸对杨树细根形态也具有一定影响, 例如, 1–3级细根干质量在正常氮、缺氮和高氮水平下均能被酚酸显著促进, 而4–5级细根受酚酸的影响不显著。这说明, 根系受酚酸的影响在低级细根中更为明显。

双因素方差分析表明, 酚酸和氮素对杨树细根形态影响的交互作用显著(表3)。虽然氮素对杨树

图2 酚酸和氮素影响下各根序细根干质量、比根长和组织密度(平均值±标准误差)。小写字母分别表示0.5X和1.0X酚酸环境中(X为田间土壤酚酸含量), 3种氮素水平间的差异显著性, 不同字母表示差异显著($p < 0.05$)。+, *, #分别表示缺氮(0 mmol·L⁻¹)、正常氮(10 mmol·L⁻¹)、高氮(20 mmol·L⁻¹)时, 两酚酸浓度间具有显著差异($p < 0.05$)。

Fig. 2 The dry mass, specific root length and root tissue density of different fine root orders under the interaction of phenolic acid and nitrogen conditions (mean $\pm$ SE). Different lowercase letters and capital letters represent significant difference among three nitrogen treatments under 0.5X and 1.0X phenolic acids respectively ($p < 0.05$), here X represents the contents of phenolic acids in the soil of poplar plantation. Three symbols, +, * and #, represent significant difference between two treatments of phenolic acids under nitrogen deficiency (0 mmol·L⁻¹), normal nitrogen (10 mmol·L⁻¹) and high nitrogen (20 mmol·L⁻¹), respectively.

1–3级细根长度、直径、表面积、体积等形态特征总体具有显著影响, 而酚酸的影响大部分不显著。此外, 4–5级细根长度、表面积和比根长受氮素的显著影响($p < 0.05$), 而受酚酸的影响不显著。但是, 在酚酸和氮素的共同作用下, 1级细根长度和表面积, 1–4级细根直径, 以及1–5级细根比根长均表现出酚酸和氮素显著的交互作用($p < 0.05$)。例如, 1级细根长度虽然受氮素的显著影响($p_N = 0.002$), 但由于酚酸

的影响不显著($p_T = 0.116$), 导致酚酸和氮素交互效应也未达到显著水平($p_{N \times T} = 0.300$), 说明酚酸和氮素对细根长度的影响可能存在主效应问题(p_N 、 p_T 、 $p_{N \times T}$ 分别表示酚酸和氮素双因素作用下, 氮素、酚酸、氮素×酚酸对细根形态影响的Duncan检验 p 值)。同样, 1级细根比根长虽然均受氮素和酚酸的显著影响($p_N = 0.018$, $p_T = 0.048$), 但是两者共同作用并未导致比根长显著变化($p_{N \times T} = 0.852$), 说明酚酸和氮

表3 酚酸和氮素对细根形态特征交互效应分析

Table 3 The interaction effect of phenolic acid and nitrogen on morphological traits of poplar fine roots

根序 Root order	处理 Treatment	根长度 Total root Length (cm)	根表面积 Total root surface area (cm ²)	根体积 Total root volume (cm ³)	根平均直径 Average diameter of root (mm)	根干质量 Root dry mass (g)	比根长 Specific root length (m·g ⁻¹)	根组织密度 Root tissue density (g·cm ⁻³)
1级 First order	<i>p_N</i>	0.002 [*]	0.000 [*]	0.000 [*]	0.000 [*]	0.009 [*]	0.018 [*]	0.001 [*]
	<i>p_T</i>	0.116 ^{ns}	0.559 ^{ns}	0.295 ^{ns}	0.201 ^{ns}	0.023 [*]	0.048 [*]	0.667 ^{ns}
	<i>p_(N×T)</i>	0.300 ^{ns}	0.394 ^{ns}	0.003 [*]	0.867 ^{ns}	0.067 ^{ns}	0.852 ^{ns}	0.008 [*]
2级 Second order	<i>p_N</i>	0.005 [*]	0.015 [*]	0.071 ^{ns}	0.001 [*]	0.001 [*]	0.000 [*]	0.009 [*]
	<i>p_T</i>	0.041 [*]	0.054 ^{ns}	0.569 ^{ns}	0.083 ^{ns}	0.002 [*]	0.715 ^{ns}	0.164 ^{ns}
	<i>p_(N×T)</i>	0.015 [*]	0.028 [*]	0.557 ^{ns}	0.424 ^{ns}	0.001 [*]	0.853 ^{ns}	0.011 [*]
3级 Third order	<i>p_N</i>	0.039 [*]	0.014 [*]	0.080 ^{ns}	0.003 [*]	0.017 [*]	0.000 [*]	0.000 [*]
	<i>p_T</i>	0.481 ^{ns}	0.011 [*]	0.046 [*]	0.164 ^{ns}	0.035 [*]	0.366 ^{ns}	0.931 ^{ns}
	<i>p_(N×T)</i>	0.004 [*]	0.012 [*]	0.086 ^{ns}	0.923 ^{ns}	0.118 ^{ns}	0.494 ^{ns}	0.023 [*]
4级 Forth order	<i>p_N</i>	0.001 [*]	0.021 [*]	0.503 ^{ns}	0.001 [*]	0.097 ^{ns}	0.000 [*]	0.052 ^{ns}
	<i>p_T</i>	0.066 ^{ns}	0.764 ^{ns}	0.406 ^{ns}	0.066 ^{ns}	0.379 ^{ns}	0.409 ^{ns}	0.521 ^{ns}
	<i>p_(N×T)</i>	0.220 ^{ns}	0.926 ^{ns}	0.070 ^{ns}	0.220 ^{ns}	0.121 ^{ns}	0.634 ^{ns}	0.819 ^{ns}
5级 Fifth order	<i>p_N</i>	0.005 [*]	0.048 [*]	0.012 [*]	0.067 ^{ns}	0.108 ^{ns}	0.002 [*]	0.222 ^{ns}
	<i>p_T</i>	0.631 ^{ns}	0.238 ^{ns}	0.111 ^{ns}	0.453 ^{ns}	0.163 ^{ns}	0.092 ^{ns}	0.876 ^{ns}
	<i>p_(N×T)</i>	0.760 ^{ns}	0.824 ^{ns}	0.552 ^{ns}	0.129 ^{ns}	0.884 ^{ns}	0.124 ^{ns}	0.569 ^{ns}

p_N、*p_T*、*p_(N×T)*分别表示酚酸和氮素双因素作用下，氮素、酚酸、氮素×酚酸对细根形态影响的Duncan检验*p*值。*，*p* < 0.05；ns，*p* > 0.05。
p_N、*p_T*、*p_(N×T)* represent the significance value of Duncan test on fine root morphological traits of nitrogen, phenolic acids, and interaction of nitrogen and phenolic acids, respectively. *, *p* < 0.05; ns, *p* > 0.05.

表4 细根形态指标的主分量载荷

Table 4 Component matrix of fine root growth indices

细根形态指标 Morphological traits of fine root	主成分 Principal component	
	1	2
根长 Total root length	0.872	0.421
根表面积 Total root surface area	0.912	0.542
根体积 Total root volume	0.239	0.916
根直径 Average diameter of root	-0.805	0.246
根干质量 Root dry mass	0.000	0.952
比根长 Specific root length	0.956	0.069
根组织密度 Root tissue density	-0.655	-0.330

素对比根长的影响可能具有补偿效应。

2.3 酚酸和氮素对杨树细根形态特征影响的主效应分析

对酚酸和氮素影响下细根形态特征的PCA分析表明，第一主成分可解释细根形态变化60.9%的信息量，其中细根长度、表面积和比根长这3个体现细根觅食特征分量的载荷值较高；第二主成分可解释细根形态变化约25.3%的信息量，体积和干质量这两个体现细根形态构建特征分量的载荷值较高(表4)。从排序图中可以看出，依据不同处理下细根形

态特征变化，可将1–3级、4级、5级细根在排序轴上清晰分离，第一排序轴(PC1)基本体现出细根形态随根序的变化(图3)，即1–3级、4级、5级细根之间均具有显著形态差异。对环境因素(酚酸、氮素)与细根形态特征的冗余分析(图4)表明：氮素向量对杨树细根形态特征影响的主效应较大，酚酸向量的影响较小(图4)。因此，本研究设置的环境梯度中，氮素(*R*² = 0.078)比酚酸(*R*² = 0.014)更能显著影响细根形态特征。此外，由于不同根序细根形态特征的显著差异，酚酸和氮素对杨树细根的影响呈现与根序的高度相关性(*R*² = 0.790)，根序向量对细根形态特征的影响也较大(图4)。同时，酚酸和氮素对细根形态特征的作用方向不同，酚酸与细根直径、体积、干质量和组织密度等形态构建特征呈现正相关，而氮素与长度、比根长等决定细根觅食性状的形态特征具有负相关性(图4)。

3 讨论

氮素对细根生长具有重要调控作用(Osmont *et al.*, 2007; Ruffel *et al.*, 2011)。关于氮素影响下树木细根特征的研究较多，陈海波等(2010)研究了不同

图3 酚酸和氮素处理下不同根序细根形态的主成分分析(PCA)。数字1-15、16-30、31-45分别表示0X(无酚酸)、0.5X、1.0X酚酸处理的各根序细根样品, 其中X为田间土壤酚酸含量。 $\diamond$ 、 $\triangle$ 和 $\circ$ 分别表示0 mmol·L⁻¹、10 mmol·L⁻¹、20 mmol·L⁻¹三种氮素水平。

Fig. 3 The principal component analysis on morphological traits of poplar fine roots under phenolic acid and nitrogen treatments. The number 1-15, 16-30 and 31-45 represent the fine root samples under 0X (no phenolic acid), 0.5X and 1.0X phenolic acids, respectively, here X represents the contents of phenolic acids in the soil of poplar plantation. $\diamond$, $\triangle$ and $\circ$ represent nitrogen deficiency (0 mmol·L⁻¹), normal nitrogen (10 mmol·L⁻¹) and high nitrogen (20 mmol·L⁻¹), respectively.

图4 杨树细根形态特征对酚酸和氮素响应的冗余分析。实线向量分别为环境因子(酚酸和氮素), 虚线向量为细根各形态参数(指标同表2)。向量越长代表环境因子主效应越强, 环境向量与根系特征向量的夹角代表它们之间的相关性。环境向量与根系特征向量同方向表明正相关, 反方向表明负相关, 垂直表明不相关。

Fig. 4 Redundancy analysis (RDA) on the effects of phenolic acids and nitrogen on morphological traits of poplar fine roots. Real vectors represent environmental factors (phenolic acids and nitrogen), and dotted vectors represent morphological traits of poplar fine roots (the same indices with Table 2). The longer vector is the more important the environmental effects. The correlation between the variables is illustrated by the angle between two vectors. Vectors pointing in nearly the same direction indicate a high positive correlation, vectors pointing in opposite directions have a high negative correlation, and vectors crossing at right angles are related to a near zero correlation.

氮素浓度下(1、8、16 mmol·L⁻¹)水曲柳(*Fraxinus mandshurica*)幼苗的细根特征, 发现1-3级细根长

度、表面积和比根长等特征值都随着氮浓度提高而增大, 低氮处理(1 mmol·L⁻¹)显著增加了水曲柳幼苗1级根的直径但降低了1-2级根的数量, 且细根直径增加与细根横切面皮层细胞直径和皮层厚度的增加有关; 而高氮(16 mmol·L⁻¹)将导致皮层细胞直径减小和皮层厚度缩窄。本研究结果表明: 缺氮(0 mmol·L⁻¹)和高氮(20 mmol·L⁻¹)均可抑制杨树幼苗各级根序细根的形态建成(表2), 尤其1-3级细根干质量低于正常氮水平(10 mmol·L⁻¹), 这可能是由于不同氮素浓度影响到根系细胞分裂并引发细根组织密度的变化所导致。4-5级细根在不同氮素水平下的形态差异大部分不显著, 这说明氮素主要影响低级细根的生长和发育。比根长是细根功能性状的重要指标, 本研究发现其随氮素水平升高而逐渐减小。因此, 氮素虽然在根系形态构建中发挥着重要作用, 但是氮素有效性与细根形态建成并不具有线性关系。大田人工林施肥试验也证实了类似的规律性, 如火炬松(*Pinus teada*)和美国黄松(*Pinus ponderosa*)人工林在施氮肥时根系表面积、直径和总长度增加, 但比根长显著减小(King *et al.*, 1997); 水曲柳和落叶松人工林施加氮肥降低了两树种低级根序的生物量、直径和比根长(刘金梁等, 2009)。丁国泉等(2010)对日本落叶松(*Larix kaempferi*)的研究表明, 施氮肥可降低1-5级细根平均根长和表面积, 增加细根直径和比根长。Kern等(2004)对美洲黑杨(*Populus deltoides*)人工林施加氮肥的研究也发现, 随着氮肥施加量的增加, 杨树细根生长量并未呈现线性增长。因此, 在杨树人工林经营过程中, 选择合适的氮素浓度适度施肥有利于杨树细根的生长, 反之则可能导致杨树细根生长受抑制, 引起林木生长量下降。氮素有效性调控根系生长机理比较复杂, 关于氮素有效性与人工林生产力的关系仍是今后应该重点关注的问题。

杨树是具有一定化感作用的树种(祝心如和王大力, 1997; 万开元等, 2005), 王延平等(2010)通过根系分泌物收集装置分离鉴定了杨树根系分泌的几种酚酸类物质。研究表明, 酚酸对植物本身具有较强的化感毒性(Rice, 1984; Li *et al.*, 2010), 且酚酸对根系生长的影响在组织解剖结构上得到了证实。如, 紫花苜蓿(*Medicago sativa*)叶片水溶性酚类物质对幼苗根系生长显著抑制, 根尖组织细胞被严重破坏以致影响根组织分化(Chon *et al.*, 2002); 苯甲酸

(benzoic acid)使芥菜(*Brassica juncea*)根尖细胞呈无规则排列并且细胞器破裂(Kaur *et al.*, 2005)。酚酸对杨树根系生长的影响在根系形态特征上表现也十分明显, 杨阳等(2010)通过模拟酚酸环境, 发现酚酸能显著抑制杨树幼苗根系生长, 酚酸处理40天的杨树幼苗平均根尖数、根长、根系表面积、根系分枝数以及根系分形维数较对照显著降低, 而幼苗根系直径则显著增大。本研究仿生田间土壤酚酸浓度设置0.5X和1.0X两种酚酸环境, 进一步发现酚酸处理显著影响了杨树1–2级细根直径和体积, 且细根体积和直径随酚酸浓度增加显著增大。在杨阳等(2010)的试验研究中, 0.5X和1.0X两种酚酸环境中杨树细根根尖数、根表面积、分枝数等特征均未呈现显著差异, 但根直径在1.0X环境中显著高于0.5X环境。本研究结果与其结论存在一致性, 同时进一步说明了酚酸对杨树细根形态影响的主效应中也体现出与根序的高度相关性(图4), 酚酸对杨树细根直径的影响主要体现在对低根序细根直径的增加。此外, 本研究为仿生杨树人工林土壤酚酸环境, 考虑到酚酸在人工林根际土壤中的累积规律, 仅选择了0.5X和1.0X两种酚酸浓度, 并未进一步设置较高浓度的酚酸环境。有研究表明, 低浓度酚酸对根系内超氧化物歧化酶和过氧化氢酶等保护酶活性具有促进作用(Devi & Prasad, 1996), 而随着酚酸浓度的提高, 酚酸诱发的伤害超出植株自我保护能力(Baziramakenga *et al.*, 1995; 吕卫光等, 2002), 并导致丙二醛等有害物质的积累(Politycka, 1996)。如果继续提高酚酸浓度, 杨树细根构型将受到严重影响, 包括细根数量显著下降, 根长和根表面积显著减少等(杨阳等, 2010)。基于此, 本研究中酚酸对杨树细根各根序形态的影响由于更符合田间土壤实际状态, 在一定程度上反映了杨树人工林细根的生长规律。

本研究结果表明, 杨树不同根序细根形态对酚酸和氮素交互作用的响应存在差异, 这说明划分根序研究细根形态是十分必要的。此外, 酚酸和氮素对细根形态的影响可能具有协同或拮抗效应, 这导致不同根序的细根形态对两者的响应规律不同。在本研究中, 虽然氮素对杨树细根形态影响的主效应大于酚酸(图4), 但是两者的交互效应对细根长度、表面积、比根长等形态参数均产生了显著影响。这说明, 酚酸及氮素有效性都无法独立成为影响细根生长的环境因子。冗余分析表明, 酚酸主要影响细

根直径、体积、干质量、根组织密度等, 这些指标较好地刻画了根系形态建成特征; 而氮素主要影响细根长度、表面积等, 这些形态与根系觅食关系密切。实际上, 伴随着根系吸收, 根际周围有效态氮将很快耗尽, 细根出现衰老而死亡, 根系只有不断生长出新细根才能拓展空间觅食氮素(Eissenstat, 1997)。因此, 细根长度受氮素有效性的影响十分显著, 比根长即是体现细根吸收功能的重要指标。同时, 伴随着细根衰老和死亡, 大量酚酸物质进入土壤, 并经由土壤胶体吸附、微生物降解等一系列过程后, 在根际土壤中形成累积(王延平和王华田, 2010)。酚酸的根际沉降一方面可与土壤养分离子发生络合、螯溶等非生物化学过程, 从而造成土壤有效养分含量下降(Chapin III, 1995), 另一方面也可能影响到土壤酶活性和微生物群落结构, 继而影响土壤养分的矿化过程(Kong *et al.*, 2008; Qu & Wang, 2008)。因此, 酚酸与氮素在根际环境中存在相互作用, 根际酚酸物质的累积可显著改变土壤养分环境(Inderjit & Duke, 2003), 使土壤的含氮量维持在很低的水平(Rice, 1984)。细根形态特征的变化在一定程度上反映出根系在根际过程交互效应下的形态构建和觅食特征, 这对今后深入研究树木根际过程对光合产物碳分配的影响机制具有重要意义。

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