施用磷对王桉幼苗生长及其氨基酸组分和含量的影响

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摘要:王桉（*Eucalyptus regnans* F. Muell.）是澳大利亚桉树中最重要的商业用材和人工造林树种之一。研究王桉的施肥与其体内氨基酸的积累和转化及与食叶虫害之间的相关性具有重要的经济和生态意义。在温室内利用 2 种不同来源的土壤对王桉幼苗进行了不同磷施用量(100 kg hm^{-2}和 200 kg hm^{-2})处理。结果显示,不同土壤和不同磷施用量对苗木生长影响显著,但均未显著影响苗木各部分的氮和磷含量水平。苗木木质部渗出液中的氨基酸含量以谷氨酰胺为主,并与苗木生长和磷施用量呈反相关。不同土壤和磷施用量对苗木组织中游离氨基酸组分和含量的影响不显著,但游离氨基酸的组分和相对水平随叶龄变化明显,尤其是精氨酸在嫩叶氨基酸总量中只占 2% ~3% ,但在老叶中占到 20% 多;精氨酸在老叶中的积累极有可能是某些蛋白质降解而精氨酸即时合成所致,因为精氨酸一般不在韧皮部转运。谷氨酰胺在树液中含量最高并与苗木生长呈反相关或许可以作为预测桉树发生食叶昆虫危害的一个有用指标。

关键词:王桉;氨基酸;苗木生长;磷
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Impact of phosphorus supply on growth and amino acid composition and concentration of *Eucalyptus regnans* F. Muell. seedlings

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Abstract: *Eucalyptus regnans* F. Muell. is one of the most commercially important timber trees in Australia. Study on the relationship between fertilizer application, amino acid accumulation and transformation and insect herbivory for eucalypts is both economically and ecologically necessary. *E. regnans* seedlings were grown with two rates of phosphorus (100 and 200 kg hm^{-2}) in two soils with different P fixation capacity. The seedlings were grown in a glasshouse with 4 replicates. Experiment results showed: (1) seedling growth was significantly affected by the different soils and P treatment; (2) N and P concentrations in plant components were not significantly different with the soil and P treatments, while N and P concentrations in leaves decreased with leaf age; (3) amino acid concentration of xylem sap was dominated by glutamine and significantly affected by P application (concentration in xylem sap of seedlings grown with 100 kg hm^{-2} was 2 times more than that with 200 kg hm^{-2}); (4) amino acid composition and concentration in leaves significantly changed with leaf age, particularly for arginine which was several-fold greater in old leaves than in young leaves. The change of arginine concentration in leaves is most likely due to some protein degradation and in situ arginine synthesis because arginine is not generally phloem sap mobile. The fact that glutamine concentration in xylem sap was dominant and inversely related to seedling growth suggests that specific nitrogenous solutes may be useful indices of the nitrogen status of *E. regnans* for insect herbivory.

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Key Words: *Eucalyptus regnans*; amino acid; seedling growth; phosphorus

氨基酸复合体是构成植物体内可溶性非蛋白氮的主要成分,可溶性非蛋白氮对植物体内的氮运输及蛋白合成具有重要作用[1]。对于许多草本植物和农作物,有关韧皮部及木质部流动液中的可溶性非蛋白氮的存储及转运,已有不少研究报道[2-4];但就木本植物而言,除去一些固氮植物而外,这方面的研究还很少。一些已有研究[5]表明,树木树液和叶片中氨基酸的组成及含量对土壤养分条件敏感。虽然对于树木体内氨基酸态氮的同化和转运的研究在增加和深入[6,7],但对桉树(*Eucalyptus*)这方面的研究尚少。

促进开展树液和叶片中氨基酸态氮研究的另一重要原因是食叶昆虫危害与树叶中可利用氮紧密相关[8,9],食叶害虫大发生往往可以极大降低桉树人工林的生长量[10]。改变树木体内的含氮量是改变昆虫与被危害树木之间关系的重要策略,有可能以此为突破口研究出控制食叶害虫的综合治理技术。植物叶片中的氮含量往往作为其昆虫适口性的一个评价指标[11,12]。

王桉(*Eucalyptus regnans* F. Muell.)是澳大利亚桉树中最重要的商业用材和人工造林树种之一[13,14]。澳大利亚的许多土壤中磷含量偏低,因此往往成为当地树木生长的制约因子[15]。在此研究中,以不同来源的土壤和不同的磷施用量作为主要处理,对王桉幼苗的生长及其树叶和树液中氨基酸的组成与含量进行了测定分析。

1 材料与方法

此试验中,包括2种不同来源的土壤和2个不同磷施用量处理(100 kg hm^{-2}和200 kg hm^{-2})。各处理为完全随机设计,4次重复。树苗栽植于墨尔本大学植物系温室中,温室温度保持在10~25℃。

土壤采集于两个林分,一个是Mt. Disappointment,其土壤磷固定能力为1500 mg kg^{-1}[16];另一个是Britannia Creek,磷固定能力为1800 mg kg^{-1},所用土壤均只采于0~10 cm的表层土,土壤气干后过筛(5 mm)。王桉种子来源于APM林木公司王桉母树林。种子先置于酸洗后的沙盘中发芽,发芽后3周将幼苗移植于填土后的花盆(直径15 cm,高17 cm)内,每盆3株。移苗5周后,按照设计开始施用磷溶液,20周内,施用磷(KH_2PO_4)分别达到100 kg hm^{-2}和200 kg hm^{-2}。平均每盆每周施用大约200 ml营养液,在需要情况下,施肥间隔期适当浇水。

移植25周后采收苗木,采收时间为最后一次施肥过后2d,树苗在离土表层约1.5 cm处切断,切断后立即在伐根上套一细塑料管,从塑料管中收集苗根渗出液,收集后冰冻保存待分析。之后,通过水洗收集所有的根。茎叶分为5部分:叶芽及相联茎顶部(Tops)、最幼嫩但全部展开的叶片(Ylefs)、最老的叶片(Olefs)、其余叶片(Ols)以及茎杆(Stems)。所有样品用冰冻法干燥后称重并磨碎(<0.5 mm)。

树叶中游离氨基酸的提取根据Atkins和Canvin[17]所述方法。叶片提取液用正离子交换管加以纯化后,用高效液相色谱柱后茚三酮衍生法进行氨基酸测定。用同样的方法分析树液中的氨基酸。所有植物组织样品煮解硝化处理后,测定其总氮和总磷含量,方法见Wang[15]。用方差分析(ANOVA)方法对试验结果进行统计分析。

2 结果

不同土壤对王桉幼苗生长的影响显著(图1,表1),生长在Britannia Creek土壤上的苗木与Mt.

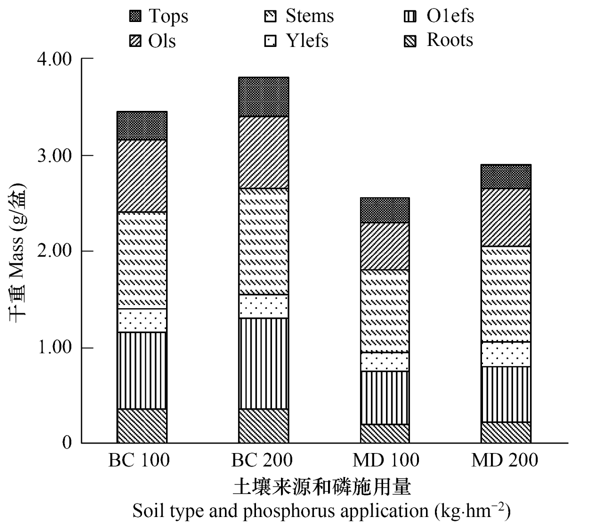

图1 不同土壤和磷施用量对王桉苗木生长的影响

Fig. 1 Effects of soil and P-application on growth of *E. regnans* seedlings

BC:来源于Britannia Creek的土壤;MD:来源于Mt. Disappointment的土壤;Tops:顶梢;Ols:其它部分;Stems:主茎;Ylefs:最嫩叶;Olefs:最老叶;Root:根 BC-soil from Britannia Creek;MD-soil from Mt. Disappointment

Disappointment 土壤上的苗木相比,生物量显著高($P<0.001$)。较高的磷施用量对苗木生长具有显著促进作用(表 1,图 1)。

不同土壤和不同磷施用量均未显著影响苗木各部分的氮和磷含量水平(表 2),但是叶片中的氮和磷含量随叶片老化而降低,顶梢内磷含量是老叶片中的 2 ~3 倍,顶梢内氮含量比老叶片中高出 30% ~40%(表 2)。

表 1　不同处理对王桉苗木生长影响的方差分析显著性检验

Table 1　Significance test (AVOVA) of treatment effects on *E. regnans* seedlings

处理 Treatment	根 Roots	顶梢 Tops	其它部分 Ols	主茎 Stems	最嫩叶 Ylefs	最老叶 Olefs
土壤 Soil	* * *	* * *	* * *	* * *	* * *	* * *
磷施用量 P application	* * *	* *	ns	* *	*	*

* * * $P<0.001$, * * $P<0.01$, * $P<0.05$, ns: 影响不显著 Not significant

表 2　不同土壤和不同磷施用量对王桉苗木中氮和磷含量(% 烘烤干重)的影响,括号内数值为标准差,方差分析表明影响均不显著

Table 2　Effects of soil and P-application on N and P concentrations (% oven dry weight) in *E. regnans* seedlings

养分 Nutrient	苗体 Component	BC# 100##	BC 200	MD 100	MD 200
氮 Nitrogen	顶梢 Tops	4.10(0.18)	3.96(0.11)	4.18(0.04)	4.41(0.34)
	最嫩叶 Ylefs	3.65(0.15)	3.44(0.18)	3.72(0.09)	3.22(0.14)
	其它部分 Ols	3.42(0.09)	3.27(0.12)	3.21(0.18)	2.95(0.11)
	最老叶 Olefs	2.89(0.11)	3.30(0.2)	2.79(0.11)	2.79(0.15)
	主茎 Stems	0.79(0.06)	0.80(0.06)	0.78(0.08)	0.79(0.04)
	根 Roots	1.48(0.11)	1.52(0.21)	1.58(0.11)	1.60(0.09)
磷 Phosphorus	顶梢 Tops	0.29(0.07)	0.30(0.07)	0.33(0.05)	0.32(0.01)
	最嫩叶 Ylefs	0.19(0.01)	0.18(0.01)	0.19(0.02)	0.18(0.01)
	其它部分 Ols	0.11(0.01)	0.12(0.02)	0.13(0.02)	0.14(0.01)
	最老叶 Olefs	0.12(0.01)	0.14(0.01)	0.11(0.02)	0.11(0.01)
	主茎 Stems	0.09(0.002)	0.08(0.003)	0.08(0.003)	0.09(0.002)
	根 Roots	0.12(0.009)	0.13(0.01)	0.14(0.01)	0.13(0.004)

BC: 来源于 Britannia Creek 的土壤; MD: 来源于 Mt. Disappointment 的土壤; ## 100、200:磷施用量($kg\ hm^{-2}$)　Standard errors given in brackets. The effects were not significant from ANOVA analysis. # BC: soil from Britannia Creek; MD: soil from Mt. Disappointment; ## 100, 200: P-application rates ($kg\ hm^{-2}$)

不同土壤对苗木木质部渗出液的氨基酸总量没有显著影响,而不同磷施用量对其影响显著(图 2),在施用磷 100 $kg\ hm^{-2}$的苗木中,其氨基酸水平是施用磷 200 $kg\ hm^{-2}$苗木的 2 倍多,这种差异恰恰与苗木生长对施用磷的反应相反。木质部渗出液中的氨基酸含量以谷氨酰胺(Glu)为主,大于 70%(图 2)。

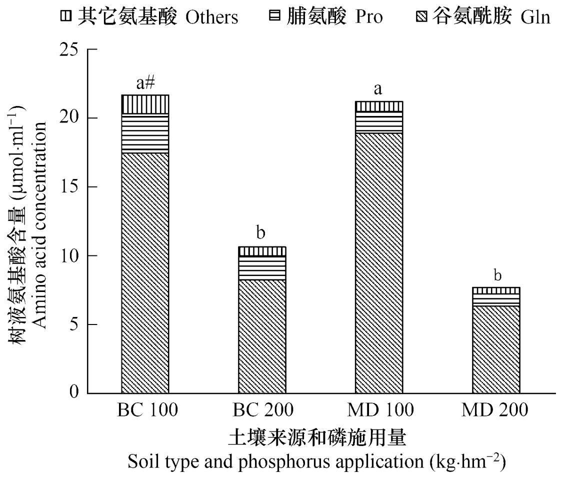

图 2　王桉苗木树液内氨基酸含量比较

Fig. 2　Comparison of amino acid concentrations in xylem sap of *E. regnans* seedlings

#: 标有不同字母表示差异显著,相同字母差异表示不显著; BC: 来源于 Britannia Creek 的土壤; MD:来源于 Mt. Disappointment 的土壤; #: different letters showing significant difference; same letters showing not significant difference. Note: BC: soil from Britannia Creek; MD: soil from Mt. Disappointment

王桉苗木组织中氨基酸含量在不同土壤和不同磷施用量处理下差异不显著(表 3),但氨基酸的组成成分和相对水平随叶龄变化显著(图 3,表 3)。如组氨酸(His)和天门冬酰胺(Asn)未在嫩叶中测出,但在老叶中出现;精氨酸在嫩叶中氨基酸总量中只占 2% ~3%,但在老叶中占到 20% 多。

3　讨论

Britannia Creek 土样采于世界上最高产的林分之一[13],在 1983 年森林火灾发生后的 10a 中,其林分自然更新的平均净初级生产量为 36 $t\ hm^{-2}\ a^{-1}$;Mt. Disappointment 土样采于生产量以及氮、磷转换率相对较低(与前者相比)的王桉林分中。所以,虽然 Britannia Creek 的土壤与 Mt. Disappointment 相比,具有较大的磷最大吸附能力(参照材料与方法部分),但是仍然可以推断,前者比后者为苗木生长提供

了较多的磷养分。结果中显示王桉幼苗生长受土壤类型和磷施用量的显著影响,充分说明其生长与土壤有效磷含量紧密相关。

表3 不同土壤和不同磷施用处理下王桉苗木老叶和嫩叶内游离氨基酸含量(μmol g^{-1} 干重)

Table 3 Concentrations (μmol g^{-1} dry weight) of free amino acids in old and young leaves of *E. regnans* seedlings grown with different P rates in different soils

项目 Item	嫩叶 Ylefs				老叶 Olefs			
	BC# 100##	BC 200	MD 100	MD 200	BC 100	BC 200	MD 100	MD 200
Asp###	0.84(0.09)	0.82(0.08)	0.75(0.11)	0.73(0.05)	0.34(0.09)	0.56(0.14)	0.41(0.11)	0.32(0.08)
Asn	0	0	0	0	0.08(0.02)	0.06(0.02)	0.05(0.03)	0.04(0.02)
Glu	0.53(0.07)	0.54(0.06)	0.48(0.03)	0.49(0.01)	0.34(0.08)	0.65(0.12)	0.56(0.09)	0.43(0.06)
Gln	0.31(0.04)	0.26(0.09)	0.35(0.05)	0.39(0.05)	0.21(0.04)	0.23(0.07)	0.24(0.02)	0.2(0.02)
Pro	0.32(0.03)	0.37(0.05)	0.36(0.09)	0.45(0.08)	0.94(0.15)	0.77(0.10)	0.65(0.16)	0.59(0.11)
Ala	1.10(0.21)	0.98(0.16)	1.04(0.17)	0.89(0.09)	0.67(0.15)	1.13(0.34)	1.09(0.13)	0.98(0.10)
g-aba	0.99(0.09)	0.97(0.15)	1.13(0.19)	0.95(0.12)	0.96(0.19)	1.11(0.17)	1.07(0.23)	0.89(0.15)
His	0	0	0	0	0.09(0.02)	0.09(0.04)	0.07(0.01)	0.09(0.01)
Arg	0.21(0.02)	0.15(0.10)	0.16(0.04)	0.19(0.02)	1.22(0.35)	1.21(0.27)	1.35(0.32)	1.53(0.32)
氨基酸总量 Total	6.75(0.98)	6.34(1.34)	6.18(1.15)	6.52(1.17)	5.56(0.53)	5.98(1.12)	6.06(0.78)	5.88(0.89)

BC:来源于 Britannia Creek 的土壤,MD:来源于 Mt. Disappointment 的土壤;## 100、200:磷施用量(kg hm^{-2});### Asp:天门冬氨酸;Asn:天门冬酰胺;Glu:谷氨酸;Gln:谷氨酰胺;Pro:脯氨酸;Ala:丙氨酸;g-aba:γ-氨基丁酸;His:组氨酸;Arg:精氨酸

BC: soil from Britannia Creek; MD: soil from Mt. Disappointment; ## 100, 200: P application rates (kg hm^{-2}); ### Asp: Aspartate; Asn: Aspargine; Glu: Glutamate; Gln: Glutamine; Pro: Proline; Ala: Alanine; g-aba: γ-aminobutyrate; His: Histidine; Arg: Arginine

括号内数值为标准差 Standard errors given in brackets

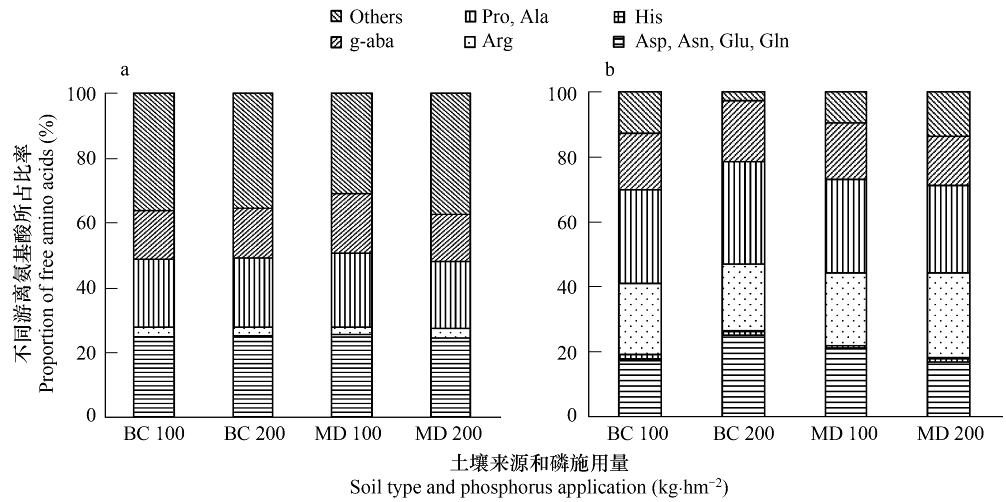

图3 王桉苗木嫩叶(a)和老叶(b)中游离氨基酸含量比较

Fig. 3 Comparison of free amino acid concentrations in young leaves (a) and old leaves (b) of *E. regnans* seedlings

BC:来源于 Britannia Creek 的土壤;MD:来源于 Mt. Disappointment 的土壤; Asp:天门冬氨酸;Asn:天门冬酰胺;Glu:谷氨酸;Gln:谷氨酰胺;Pro:脯氨酸;Ala:丙氨酸;g-aba:γ 氨基丁酸;His:组氨酸;Arg:精氨酸;Others:其它氨基酸 BC: soil from Britannia Creek; MD: soil from Mt. Disappointment. Asp: Aspartate; Asn: Aspargine; Glu: Glutamate; Gln: Glutamine; Pro: Proline; Ala: Alanine; g-aba: γ-aminobutyrate; His: Histidine; Arg: Arginine; Others: other amino acids

尽管不同土壤和不同磷施用处理对苗木生长具有显著影响(图1,表1),但植物体各部分的氮和磷含量差异并不显著(表2)。偶尔有报道,树木较高生长量与叶片中较低氮含量相伴出现,这种情况无论在林分中或在温室试验中都可能发生[18]。研究表明,人工桉树林中,林木叶片中的氮含量并不与土壤中氮含量高低相

关[19],也与树木生长量高低关系不大;同样的结果也在王桉林分中的下木和草本植物中得到证实[15]。

此试验中,树液中的氨基酸含量为谷氨酰胺单种氨基酸所主导(图 2)。尤其感兴趣的是施用磷少(100 kg hm^{-2})的苗木树液中的谷氨酰胺含量远远高于施用磷多(200 kg hm^{-2})的,这恰恰与施用磷对苗木生长的影响结果相反;那么可以据此推断,长势好的苗木谷氨酰胺含量低,长势差的含量高。这种推断可以把吸液昆虫往往在被压或生长差的植物个体上危害严重[8,12]的现象和长势差的植株木质部渗出液的较高谷氨酰胺含量联系起来。

本实验中,精氨酸在老叶中累积增加(图 3,表 3),其原因尚不清楚。有报道称,可能作为对氨离子增加的一种响应,精氨酸在植物叶片中的增加与缺磷有关[20]。但是在本试验中,王桉苗木并没有表现出缺磷症状,也没有理由推断可能缺磷。一些研究[21]表明,阻止蛋白合成或增加蛋白降解可以增加植物体内氨基酸积累。1.5-二磷酸核酮糖羧化酶/加氧酶(RUBISCO)是植物叶片中的一种主要蛋白氮,并可能对蛋白存储起一定作用[22];研究发现,在一些作物和果树的落叶过程中,与叶片中其它可溶性蛋白相比,RUBISCO 率先消失[6],还发现富含精氨酸的多种蛋白积存于悬铃木根茎之中[7]。试验结果与这样的假设相吻合,即老叶中的蛋白(或许是 RUBISCO)降解与精氨酸积累相伴而生,这很可能是所观察到的精氨酸在老叶中累积增加的原因,因为精氨酸一般不在韧皮部内流动[23]。精氨酸在树叶中的累积已被表明与病害发生及树势衰退有关[24],树叶与树液中氨基酸的增加与食叶昆虫的发生相关[11,25,26]。

桉树不仅在澳大利亚本土,而且在世界许多地区(如美国、中国)广泛栽培为人工林;为促进生长,往往进行人工施肥。同时,桉树的食叶害虫也比较严重,大大影响树木生长[10]。所以,进一步研究对桉树的施肥、其体内可溶性非蛋白氮的积累和转化与食叶虫害发生之间的相关性,对于桉树人工林的健康发展具有很重要的经济和生态意义。

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