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丛枝菌根对喜树幼苗喜树碱含量的影响

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摘要:喜树(*Camptotheca acuminata*)是我国特有的多年生亚热带落叶阔叶树种,因其次生代谢产物喜树碱具有良好的抗肿瘤活性而受到人们的广泛关注。通过温室盆栽接种试验,观察了2属6种丛枝菌根真菌对喜树幼苗喜树碱含量的影响。结果表明,接种的6种丛枝菌根真菌与喜树幼苗均形成了共生体系并且发育良好。透光球囊霉(*Glomus diaphanum*)、幼套球囊霉(*G. etunicatum*)、蜜色无梗囊霉(*Acaulospora mellea*)和光壁无梗囊霉(*A. laevis*)侵染形成丛枝菌根有利于提高喜树幼苗的喜树碱含量,地表球囊霉(*G. versiforme*)则影响不大,而木薯球囊霉(*G. manihot*)却降低了喜树幼苗的喜树碱含量。丛枝菌根形成对喜树幼苗喜树碱代谢的影响还表现在喜树碱的器官分配上,菌根幼苗根中的喜树碱比例均高于无菌根幼苗。

关键词:喜树幼苗;丛枝菌根;喜树碱;次生代谢

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Effect of arbuscular mycorrhiza on camptothecin content in *Camptotheca acuminata* seedlings

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Abstract: Mycorrhizal fungi form the most important mutualistic symbioses on earth with plants. Much research has shown that the development of arbuscular mycorrhize (AM) is correlated with plant secondary metabolism. AM fungi can directly or indirectly affect plant secondary metabolic processes. Camptothecin (CPT), a secondary metabolite in a special Chinese tree *Camptotheca acuminata*, has gained great attention for its remarkable inhibitory activity against tumor cells. The effect of AM infected with six fungi belonging to two genera on CPT content in *C. acuminata* seedlings was carried out in the present study.

The selected sterile seeds of *C. acuminata* were sown in sterilized sands in the greenhouse. After 70 days of cultivation, seedlings with similar height and crown were selected and divided into seven groups (10 pots per group). Each group of *C. acuminata* seedlings was inoculated with one of AM fungus *Glomus manihot*, *G. versiforme*, *G. etunicatum*, *G. diaphanum*, *Acaulospora mellea*, *A. laevis*, or non-mycorrhizal inoculation, namely Gm, Gv, Ge, Gd, Am, Al, or control (CK), respectively. After 3-month cultivation, the symbiotic association was observed and CPT content in the seedlings of *C. acuminata* was determined.

All *C. acuminata* seedlings inoculated with six fungi formed AM. Colonization rates of AM was over 70% in seedlings infected with 4 *Glomus* fungi (Gm, Gv, Ge, Gd), and ~50% with 2 *Acaulospora* fungi. Mycorrhizal colonization intensity of roots (M) and infected root fragments (m) were showed in Table 1. Good symbiosis systems were formed between *C. acuminata* seedlings and selected mycorrhizal fungi.

In roots, CPT contents in mycorrhizal seedlings were significantly higher than non-mycorrhizal seedlings, except Gm. CPT

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contents in Gd, Am, Al, Ge and Gv were 2.5, 2.1, 1.7, 1.6, and 1.3 times higher as CK, respectively. In the stem, CPT content was significantly higher in Al than CK, no significant difference among CK, Ge, Gd, and Am, while significantly lower in Gm and Gv than CK. In leaves, CPT contents in Al, Gd and Am were 60%, 40% and 40% higher than CK, respectively, however, CPT contents in Gm, Gv and Ge was affected little by the AM infection. CPT contents in the whole plant in Gd, Al, Am and Ge were 150%, 150%, 140% and 120% of CK, respectively, no remarkable difference between Gv and CK, whereas 23% lower in Gm than CK. As a whole, AM infection was beneficial to CPT accumulation in *C. acuminata* seedlings with *G. diaphanum*, *G. etunicatum*, *A. laevis*, and *A. mellea*, no influence with *G. versiforme*, and reduced with *G. manihot*.

AM also changed CPT allocation in different organs of *C. acuminata* seedlings. CPT ratios in all mycorrhizal roots were higher than non-mycorrhizal seedlings. In mycorrhizal root of Gv CPT ratio was the highest, 32% out of the whole plant, comparing with 15% in CK. Due to the increase of CPT allocation in roots, CPT was less distributed in stems and leaves in mycorrhizal seedlings.

Key words: *Camptotheca acuminata* seedlings; arbuscular mycorrhiza (AM); camptothecin (CPT); secondary metabolism

菌根是自然界中一种极为普遍和重要的共生现象,其中丛枝菌根是分布最为广泛的菌根类型[1],80%~90%的被子植物都能形成丛枝菌根[2]。丛枝菌根有利于植物对养分的吸收[3],从而改善植物的生长状况[4~6]。近年来,许多研究表明丛枝菌根也影响植物的次生代谢过程,导致植物的次生代谢产物发生变化[7,8],而这些次生代谢产物在植物和菌根真菌之间形成的共生关系中起着特别重要的作用[9,10]。因此,研究菌根真菌和植物次生代谢的关系具有非常重要的生态学意义。

喜树(*Camptotheca acuminata* Decne)是珙桐科(Nyssaceae)喜树属(*Camptotheca*)多年生亚热带落叶阔叶树,为我国特有树种,因其次生代谢产物喜树碱(camptothecin, CPT)具有良好的抗肿瘤活性而受到广泛关注[11]。人们已对喜树的生物学特性[12,13]、生长规律[14~17]、喜树碱的开发利用[18]、喜树碱在喜树幼苗中的分布规律[19,20],以及光强、遮荫、水渍等因子对喜树中喜树碱含量的影响[21,22]进行了一些研究工作。黄永芳等[23]以苏格兰球囊霉和地表球囊霉接种喜树幼苗,初步观察了丛枝菌根的形成及其对喜树幼苗生长的影响。有关丛枝菌根对喜树幼苗生长、养分吸收及生理代谢的影响尚缺乏深入研究。为此,通过温室盆栽接种实验,研究2属6种丛枝菌根真菌对喜树幼苗的接种效应以及幼苗次生代谢的响应,阐明丛枝菌根对喜树幼苗喜树碱含量的影响。

1 材料和方法

1.1 丛枝菌根真菌

无梗囊霉属:蜜色无梗囊霉(*Acaulospora mellea* Spain & Schenck),光壁无梗囊霉(*A. laevis* Gerdemann & Trappe);球囊霉属:木薯球囊霉(*Glomus manihot* Howeler, Sieverding & Schenck),地表球囊霉(*G. versiforme* (Karsten) Berch),幼套球囊霉(*G. etunicatum* Becker & Gerdemann),透光球囊霉(*G. diaphanum* Morton & Walker)。蜜色无梗囊霉、光壁无梗囊霉和木薯球囊霉由中国科学院南京土壤研究所林先贵研究员惠赠,地表球囊霉和幼套球囊霉由中国农业大学李晓林教授惠赠,透光球囊霉由北京市农林科学院提供。

1.2 喜树幼苗培养及接种处理

2004年3月,精选成熟饱满的喜树种子,以0.5%的$KMnO_4$浸泡消毒1 h,然后以无菌水洗去$KMnO_4$,播入121℃灭菌2 h的河沙中。幼苗开始长出侧根时移入口径20 cm、深20 cm的花盆中,盆中基质为土壤与河沙的混合物(体积比3:1,过2 mm筛,混合后121℃灭菌2 h),有机质含量1.91%,全氮含量1.04 g/kg,速效磷含量11.72 mg/kg,速效钾含量0.22 g/kg,pH 6.23。

5月末,选择长势一致的喜树幼苗分为7组(每组10盆)进行接种处理。1组作为对照(CK),不接种任何AM真菌(在花盆中加入等量灭菌处理的接种剂和10 mL各菌种混合滤液,以保证微生物区系一致);另外6组分别接种含有木薯球囊霉(Gm)、地表球囊霉(Gv)、幼套球囊霉(Ge)、透光球囊霉(Gd)、蜜色无梗囊霉(Am)和光壁无梗囊霉(Al)孢子的菌土。每盆接种剂量为30 g,菌土均匀层播于土表下8 cm的幼苗根部。

接种后的喜树幼苗置于温室中自然培养,温室为自然采光,昼夜温度自然过渡(18～28℃),湿度60%～70%。3个月后测定喜树幼苗的各项指标。

1.3 菌根侵染率统计

随机选取喜树鲜根30条,剪成长约1.0 cm的根段,采用Phillips和Hayman(1970)的染色方法染色、制片、镜检,参照盖京苹[25]的方法统计菌根侵染率、根系的菌根侵染强度和侵染根段的菌根侵染强度:

菌根侵染率(F,%)=(菌根侵染的根段数/检测的根段总数)×100%

根系的菌根侵染强度(M,%)=(侵染根长/总根长)×100%

侵染根段的菌根侵染强度(m,%)=(根系的菌根侵染强度/菌根侵染率)×100%

1.4 幼苗喜树碱含量的测定

将喜树幼苗按根、茎、叶分开,于80℃烘箱中烘干至恒重,粉碎。按照阎秀峰[26]的方法,采用Waters高效液相色谱系统测定喜树幼苗根、茎和叶中喜树碱的含量,10株重复。

以上数据用SPSS软件进行统计分析。

2 结果与分析

2.1 喜树幼苗的菌根形成情况

接种木蓄球囊霉、地表球囊霉、幼套球囊霉、透光球囊霉、蜜色无梗囊霉和光壁无梗囊霉孢子菌土的喜树幼苗,均不同程度地被侵染并形成了丛枝菌根,而对照的喜树幼苗无菌根真菌侵染,未形成丛枝菌根。实验所用球囊霉属的4种真菌(Gm、Gv、Ge、Gd)的菌根侵染率较高,均在70%以上;无梗囊霉属的2种真菌(Am、Al)的菌根侵染率稍低,但最低的Al也接近50%。

从根系的菌根侵染强度(M)和侵染根段的菌根侵染强度(m)看(表1),菌根真菌结构不仅在菌根化根系中占有较大比例,而且在幼苗整个根系中所占的比例也较大,这表明接种的6种丛枝菌根真菌与喜树幼苗形成的共生体系发育状况良好。

2.2 丛枝菌根形成对喜树幼苗喜树碱含量的影响

由图1可以看出,6种菌根真菌侵染所导致的丛枝菌根形成,均影响了喜树幼苗的喜树碱代谢。与无菌根幼苗(对照)比,多数菌根幼苗的喜树碱含量明显提高,也有差异不明显或降低的。而且,丛枝菌根形成对喜树幼苗喜树碱含量的影响有器官差异。

从根的情况看,只有Gm菌根幼苗的喜树碱含量显著低于无菌根幼苗,其他菌根幼苗均显著高于无菌根幼苗。Gd、Am、Al、Ge和Gv菌根幼苗的喜树碱含量分别达到无菌根幼苗(对照)的2.5、2.1、1.7、1.6和1.3倍。而且,菌根幼苗之间的差异也十分明显。

丛枝菌根形成对喜树幼苗茎的喜树碱含量的影响比根要弱一些,只有Al菌根幼苗的喜树碱含量显著高于无菌根幼苗,Ge、Gd、Am菌根幼苗的喜树碱含量与无菌根幼苗无显著差异,而Gm和Gv菌根幼苗的喜树碱含量则显著低于无菌根幼苗。

丛枝菌根形成对喜树幼苗叶片喜树碱含量的影响又与根、茎有所不同,Al、Gd和Am菌根幼苗的喜树碱含量显著高于无菌根幼苗,分别达到无菌根幼苗的1.6、1.4和1.4倍,而Gm、Gv、Ge菌根幼苗的喜树碱含量则与无菌根幼苗相近。

从全株的喜树碱含量看,Gd、Al、Am和Ge菌根幼

表1 接种6种丛枝菌根真菌的喜树幼苗菌根侵染率

Table 1 Colonization rate of *Camptotheca acuminata* seedlings inoculated with six arbuscular mycorrhizal fungi

处理 Treatment	菌根侵染率 Mycorrhizal colonization rate (%)	根系的菌根侵染强度 Mycorrhizal colonization intensity of root (%)	侵染根段的菌根侵染强度 Mycorrhizal colonization intensity of infected root fragment (%)
CK	0	0	0
Gm	83.18 ± 8.75	56.22 ± 5.87	67.47 ± 6.77
Gv	84.54 ± 9.03	53.30 ± 5.37	63.96 ± 6.59
Ge	88.54 ± 9.03	33.61 ± 3.31	40.33 ± 4.03
Gd	74.15 ± 8.12	41.36 ± 4.06	49.63 ± 5.13
Am	70.54 ± 6.87	56.14 ± 4.76	55.32 ± 5.71
Al	49.01 ± 5.81	26.72 ± 2.34	32.04 ± 2.95

CK,未接种丛枝菌根真菌 Non-arbuscular mycorrhizal inoculation; Gm、Gv、Ge、Gd、Am、Al,分别接种木蓄球囊霉、地表球囊霉、幼套球囊霉、透光球囊霉、蜜色无梗囊霉、光壁无梗囊霉 Inoculation with *G. manihot*, *G. versiforme*, *G. etunicatum*, *G. diaphanum*, *A. Mellea* and *A. laevis*, respectively

苗显著高于无菌根幼苗，分别达到无菌根幼苗的 1.5、1.5、1.4 和 1.2 倍，Gv 菌根幼苗与无菌根幼苗差异不显著，而 Gm 菌根幼苗则低于无菌根幼苗，为无菌根幼苗的 77%。因此，总体上看透光球囊霉、幼套球囊霉、蜜色无梗囊霉和光壁无梗囊霉侵染形成丛枝菌根有利于提高喜树幼苗的喜树碱含量，地表球囊霉则影响不大，而木薯球囊霉却降低了喜树幼苗的喜树碱含量。

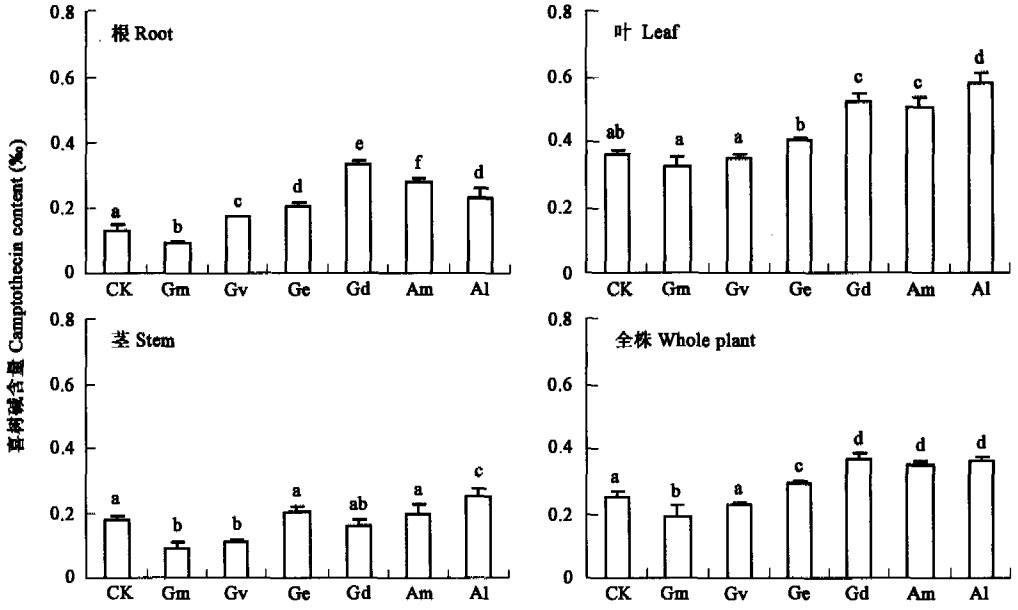

图 1 AM 真菌对喜树幼苗喜树碱含量的影响

Fig. 1 Effects of arbuscular mycorrhizal fungi on camptothecin contents of *Camptotheca acuminata* seedlings

每一小图中，具有不同字母的柱体间差异性显著（$p < 0.05$） In each panel, the bars with different letters are significantly different ($p < 0.05$)

2.3 丛枝菌根形成对喜树幼苗中喜树碱器官分配的影响

丛枝菌根形成对喜树碱代谢的影响不仅表现在喜树碱含量上，还表现在喜树碱在喜树幼苗各器官的分配上（图 2）。与无菌根幼苗相比，所有菌根幼苗根中的喜树碱比例均明显增加，其中 Gv 菌根幼苗根的喜树碱分配比例最高，占全株的 32%，而无菌根幼苗仅为 15%。由于喜树碱在根中比例增加，总体上菌根幼苗茎和叶片的喜树碱比例小于无菌根幼苗，但 Al 菌根幼苗的茎和 Gm 菌根幼苗的叶片喜树碱比例略高于无菌根幼苗。

3 讨论

植物组织中生物碱积累与环境因子有着密切的关系[21]。相关研究表明，土壤水分、光照强度、光质及土质等环境因素均明显影响喜树幼苗叶片中的喜树碱含量[21,22,27]，而生物因子调控植物组织中生物碱积累的研究相对较少。一些研究观察到丛枝菌根真菌能够直接或间接地影响植物的次生代谢过程[28,29]。魏改堂和汪洪钢[30]在不同土壤有效磷供给条件下用漏斗孢球囊霉和地表球囊霉分别接种曼陀罗（*Datura stramonium*），发现丛枝菌根真菌显著提高了曼陀罗中莨菪碱和东莨菪碱的含量。从本试验的结果看（图 1），丛枝菌根的形成影响了喜树幼苗的喜树碱代谢，一些菌根幼苗的喜树碱含量高于无菌根幼苗。

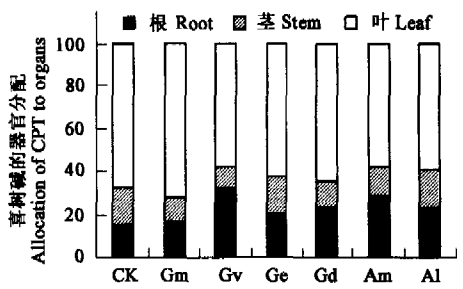

图 2 喜树幼苗中喜树碱的器官分配比例

Fig. 2 Allocation of CPT to organs of *Camptotheca acuminata* seedlings

丛枝菌根形成对喜树幼苗根中喜树碱含量的影响比茎和叶片更为明显。Rojas-Andrade 等[31]在以玫瑰红巨孢囊霉（*Gigaspora rosea*）接种牧豆树（*Prosopis laevigata*）时也发现，菌根真菌侵染的牧豆树根中葫芦巴碱

(trigonelline,一种吡啶生物碱)的含量比对照增加了1.8倍。不过在他们的结果中,无论有否菌根真菌侵染,牧豆树地上部分的葫芦巴碱含量总是恒定不变的,而喜树幼苗在菌根真菌侵染并形成菌根后,叶片的喜树碱含量也高于无菌根幼苗。

已有的一些研究结果表明,菌根真菌通过侵染形成菌根对植物次生代谢的影响,有明显的种属差异。Vierheiling等[32]用根内球囊霉(*G. intraradices*)、摩西球囊霉(*G. mosseae*)、玫瑰红巨孢囊霉分别接种到玉米(*Zea mays*)和大麦(*Hordeum vulgare*),发现不同种类的丛枝菌根真菌形成的菌根植物中其次生代谢产物Blumenin的含量有显著差异。与根内球囊霉形成菌根的大麦和玉米,Blumenin含量最高,而与玫瑰红巨孢囊霉形成菌根的含量最低。Abu-Zeyad等[33]分别用根内球囊霉和珠状巨孢囊霉(*Gigaspora margarita*)接种澳大利亚粟籽豆(*Castanospermum australe*),发现与根内球囊霉形成菌根的粟籽豆表现出更好的生长反应、更高的菌根真菌侵染率和粟籽豆碱(castanospermine,一种吲哚生物碱)含量。同时也观察到,试验的2属6种丛枝菌根真菌对喜树幼苗中喜树碱含量的影响也表现出差异。幼套球囊霉、透光球囊霉、蜜色无梗囊霉和光壁无梗囊霉提高喜树幼苗中喜树碱的含量,地表球囊霉影响不明显,而木薯球囊霉却降低了喜树碱的含量。

显然,目前观察到的只是丛枝菌根形成对植物次生代谢影响的一些表观现象,而丛枝菌根真菌在侵染植物以及与植物建立共生关系的过程中与植物次生代谢的关系是错综复杂的,需要更为深入的实验观察来洞察其关系实质,而这对于更深刻地理解植物与环境的互作本质是非常必要的。

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