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封面图说: 气候变暖下的北极冰盖——自从 1978 年人类对北极冰盖进行遥感监测以来, 北极冰正以平均每年 8.5% 的速度持续缩小, 每年 1500 亿吨的速度在融化。这使科学家相信, 冰盖缩小的根本原因是全球变暖。北极的冰盖消失, 让更大面积的深色海水暴露出来, 使海水吸收更多太阳热辐射反过来又加剧冰盖融化。由于北极冰的加速融化, 北冰洋的通航已经成为 21 世纪初全球最重要的自然地理事件和生态事件。从这张航片可以看到北极冰缘正在消融、开裂崩塌的现状。

彩图提供: 陈建伟教授 北京林业大学 E-mail: cites.chenjw@163.com

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于洋,于涛,王洋,阎秀峰. 接种后共培养时间对丛枝菌根喜树幼苗喜树碱含量的影响. 生态学报, 2012, 32(5): 1370-1377.

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接种后共培养时间对丛枝菌根喜树幼苗喜树碱含量的影响

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摘要: 在前期工作中利用蜜色无梗囊霉(*Acaulospora mellea*)和根内球囊霉(*Glomus intraradices*)从接种时期角度分析了喜树碱含量与菌根形成过程对应关系的基础上, 通过温室盆栽接种试验, 继续观察了这两种丛枝菌根真菌接种后与喜树(*Camptotheca acuminata*)幼苗的共培养时间对喜树幼苗喜树碱积累的影响。分别用两种菌根真菌每隔7 d接种一批喜树幼苗, 第5批接种7 d后采样, 获得菌根真菌与喜树幼苗共培养时间为35、28、21、14、7 d的喜树幼苗样品, 测定了菌根浸染状况和喜树碱含量。结果表明:(1)接种两种丛枝菌根真菌均促进了喜树幼苗喜树碱的积累, 表现为喜树碱含量和产量(单株幼苗所含的喜树碱量, 喜树碱含量与幼苗生物量的乘积)的显著提高。(2)从接种后共培养时间的效果看, 两种菌根幼苗各器官(根、茎、叶)及全株喜树碱含量和产量均呈现随着丛枝菌根真菌与喜树幼苗共培养时间的增加而增加的趋势。两种菌根幼苗的根和茎、根内球囊霉菌根幼苗的叶片和全株的喜树碱含量和产量, 在共培养时间增加至21 d时趋于稳定, 而蜜色无梗囊霉菌根幼苗的叶片和全株的喜树碱含量和产量在共培养时间增加至28 d时达到最高, 其后略有降低。(3)两种丛枝菌根真菌的侵染率和侵染强度同样随共培养时间的增加而增加, 至共培养28 d后无显著变化。在一定共培养时间范围内, 喜树碱含量和产量的变化与丛枝菌根真菌的侵染及菌根形成之间具有对应性。

关键词: 喜树幼苗; 丛枝菌根真菌; 喜树碱

Effect of co-cultivation time on camptothecin content in *Camptotheca acuminata* seedlings after inoculation with arbuscular mycorrhizal fungi

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Abstract: Arbuscular mycorrhizal (AM) is the most widespread form of plant symbiosis and has been found to enhance photosynthesis rate, biomass accumulation, pathogen defense, and tolerance to heavy metals and cold stress. In addition, it affects the production of plant secondary metabolites, one of which is camptothecin, an anti-cancer compound used in clinical practice. Camptothecin is a water-insoluble cytotoxic monoterpenoid derived from indole alkaloid and was initially isolated from the Chinese tree *Camptotheca acuminata* (Nyssaceae). It has gained great attention for its remarkable inhibitory activity against tumor cells. Based on our previous study on the correlation between the formation of mycorrhiza and camptothecin content in mycorrhizal *C. acuminata* seedlings, the effect of co-cultivation time on camptothecin accumulation in *C. acuminata* seedlings after inoculation with *Acaulospora mellea* and *Glomus intraradices* was investigated in the present study. Seeds of *C. acuminata* were sterilized and sown in sterilized matrix (a mixture of soil and sand) in the

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greenhouse. Seedlings with similar height and crown size were selected and divided into three groups, inoculation with arbuscular mycorrhizal fungi *A. mellea*, inoculation with *G. intraradices* and mock inoculation control. Each group was divided into five sub-groups, with an inoculation of each sub-group every seven days. The seedlings were sampled at the seventh day of the last inoculation, i. e. the co-cultivation time of each subgroup was 35, 28, 21, 14 and 7 days, respectively. Mycorrhizal colonization frequency, colonization intensity of roots and camptothecin contents and yields in *C. acuminata* seedlings were determined. The results showed that: (1) Camptothecin contents and yields in mycorrhizal seedlings increased significantly. This implies that the accumulation of camptothecin in *C. acuminata* seedlings was enhanced after inoculation with the two mycorrhizal fungi. (2) Camptothecin contents and yields in roots, stems, leaves and the whole plants increased with the co-cultivation time of *C. acuminata* seedlings with the mycorrhizal fungi. Camptothecin contents and yields in roots and stems of the two arbuscular mycorrhizal seedlings, and in leaves and whole plants of *G. intraradices* seedlings reached the highest levels after 21 days of co-cultivation, and then remained constant. While in leaves and whole plants of *A. mellea* seedlings camptothecin contents and yields were the highest on the 28th day after co-cultivation and dropped slightly thereafter. (3) Mycorrhizal colonization frequency and colonization intensity in two arbuscular mycorrhizal seedlings were enhanced with the increase of co-cultivation time till the 28th day, after which no significant differences were observed. Therefore, a significant correlation was observed between camptothecin contents and yields in *C. acuminata* seedlings and co-cultivation with arbuscular mycorrhizal fungi for up to 28 days. These results demonstrate that there is a precise correlation of camptothecin accumulation and fungal development. Our future studies will be focused on understanding of the fungal-dependent regulation of the temporal metabolic activities during mycorrhiza development and the spatial distribution of camptothecin in different tissues and cell types. Ultimately, we aim to conduct molecular genetics and engineering of camptothecin -AM fungus interactions.

Key Words: *Camptotheca acuminata* seedlings, arbuscular mycorrhiza fungi, camptothecin

喜树(*Camptotheca acuminata* Decne.)是蓝果树科(Nyssaceae)喜树属多年生亚热带落叶阔叶乔木,为我国特有树种,其次生代谢产物喜树碱(camptothecin,一种单萜吲哚生物碱)具有良好的抗肿瘤活性^[1]。以往人们对喜树碱的环境调控研究多集中在非生物因子方面^[1-4],对生物因子的关注相对较少^[5-6]。

丛枝菌根(arbuscular mycorrhiza)是一种较为普遍和重要的菌根类型,具有十分重要的生物学意义。一些研究表明,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。植物的次生代谢产物通常可分为萜类化合物、酚类化合物和含氮化合物(主要是生物碱)三大类,其中萜类化合物、酚类化合物与丛枝菌根关系的研究工作相对多些^[7-12],而植物生物碱与丛枝菌根关系的研究较少,仅见在具有药用价值的植物上。一些研究表明丛枝菌根的形成影响生物碱的含量,某些生物碱也可能在菌根真菌侵染时起到重要的作用^[13-15]。

已有研究表明,一些丛枝菌根真菌与喜树幼苗形成共生体系并影响喜树幼苗的喜树碱代谢^[16-18]。由此推测,菌根真菌的侵染及菌根形成过程应该与喜树幼苗的喜树碱含量变化具有对应性。以往工作^[19],选取了效果显著的蜜色无梗囊霉(*Acaulospora mellea*)和相关研究工作中其他学者常用的根内球囊霉(*Glomus intraradices*)^[10-12,20]接种于喜树幼苗,从接种时期角度观察了喜树碱含量与菌根形成过程的对应关系。已有研究表明,菌根真菌与植物根系的共培养时间影响菌根真菌的侵染率和侵染强度^[21-22],而且不同种属丛枝菌根真菌对喜树幼苗喜树碱含量的影响具有差异性^[16,19]。因此,继续以上述两种丛枝菌根真菌接种喜树幼苗,从接种后共培养时间角度观察了菌根真菌的侵染及菌根形成过程与喜树幼苗喜树碱含量变化的对应性。

1 材料和方法

1.1 丛枝菌根真菌

蜜色无梗囊霉(*Acaulospora mellea*)由中国科学院南京土壤研究所林先贵提供,根内球囊霉(*Glomus intraradices*)由中国农业大学李晓林提供。

1.2 喜树幼苗培养及接种处理

2009年5月中旬,精选喜树种子(采自四川省金堂县),以0.5%的KMnO₄浸泡消毒0.5 h,无菌水洗净,播入121℃灭菌2 h的细沙中催芽,待有侧根生成时栽植于直径20 cm、高20 cm已灭菌的花盆,每盆1株,盆中基质为土壤与河沙混合物(体积比例3:1,过2 mm筛,混合后121℃灭菌2 h),有机质含量2.410 g/kg,全氮含量0.052 g/kg,全磷含量0.025 g/kg,全钾含量1.030 g/kg,pH值6.59。

6月中旬,选择长势一致的喜树幼苗(苗龄35 d)分3组进行接种处理。CK(对照)组:不接种丛枝菌根真菌,10盆;Am组:接种蜜色无梗囊霉,每7 d接种1批喜树幼苗,每批接种10盆,共5批;Gi组:接种根内球囊霉,每7 d接种1批喜树幼苗,每批接种10盆,共5批。菌土穴播于土表下喜树幼苗根部,接种剂量为30 g/盆。接种后于温室(自然光照)中培养。

1.3 样品采集

第5批接种培养7 d后,即丛枝菌根真菌与喜树幼苗共培养时间为35、28、21、14、7 d,对照组与接种组同时取样。将喜树幼苗按根、茎、叶分开,分别收集。

1.4 菌根侵染率测定

随机选取喜树幼苗鲜根30条,剪成1 cm根段,采用Phillips和Hayman^[23]的方法染色、制片、镜检,按盖京苹等^[24]的方法统计菌根侵染率、根系的菌根侵染强度:

$$\text{菌根侵染率}(F,\%) = (\text{菌根侵染的根段数}/\text{检测的根段总数}) \times 100\%$$

$$\text{根系的菌根侵染强度}(M,\%) = (\text{侵染根长}/\text{总根长}) \times 100\%$$

1.5 幼苗生物量的测定

将喜树幼苗按根、茎、叶分开于80℃烘箱中烘干至恒重,称重。

1.6 喜树碱含量的测定

经80℃烘箱烘干至恒重的样品粉碎,按阎秀峰等^[25]的方法,采用Waters高效液相色谱系统测定样品喜树碱含量。

2 结果

2.1 共培养时间对丛枝菌根真菌侵染及喜树幼苗生物量的影响

丛枝菌根真菌与喜树幼苗共培养14 d以上(含14 d),喜树幼苗根系被侵染形成了丛枝菌根共生体系,而对照组(CK)喜树幼苗均无丛枝菌根真菌侵染,未形成丛枝菌根(表1)。两种丛枝菌根真菌对喜树幼苗的侵染状况不一致,总体上蜜色无梗囊霉对喜树幼苗的侵染状况明显好于根内球囊霉。从共培养时间变化看,共培养时间的增加有利于丛枝菌根的形成,但并不是时间越长越好,至共培养后期(28 d)时两种丛枝菌根真菌的侵染率和侵染强度均趋于稳定。

表1 共培养时间对喜树幼苗丛枝菌根真菌侵染的影响

Table 1 Effect of co-cultivation time on the infection of *C. acuminata* seedlings with arbuscular mycorrhizal fungi

共培养时间 Co-cultivation time/d	菌根侵染率 Mycorrhizal colonization frequency/%			根系的菌根侵染强度 Mycorrhizal colonization intensity of root/%		
	CK	Am	Gi	CK	Am	Gi
7	0	0	0	0	0	0
14	0	9.52±0.14a	7.50±0.81a	0	2.29±0.13a	1.08±0.12a
21	0	22.86±1.29b	16.22±1.34b	0	6.91±0.31b	4.69±0.24b
28	0	47.22±2.17c	38.30±1.57c	0	12.78±0.63c	8.83±0.32c
35	0	48.03±2.58c	40.00±2.39c	0	13.30±0.50c	9.11±0.31c

表中数据为平均值±标准误差($n=3$); CK:未接种丛枝菌根真菌(non-arbuscular mycorrhizal inoculation); Am:接种蜜色无梗囊霉(inoculation with *Acaulopspora mellea*); Gi:接种根内球囊霉(inoculation with *Glomus intraradices*);同一列数据中标有不同字母表示差异显著($P<0.05$)

丛枝菌根的形成对喜树幼苗生长的促进作用主要表现在根部,而对茎和叶无显著影响(图1)。由于蜜色

无梗囊霉和根内球囊霉对喜树幼苗的侵染有差异,它们所形成的丛枝菌根对喜树幼苗生长的促进作用也表现出明显的差异。蜜色无梗囊霉菌根幼苗根系生物量随共培养时间的增加而增加,至共培养 28 d 时与无菌根幼苗差异最为显著,之后与无菌根幼苗根生物量相当。根内球囊霉与喜树幼苗共培养时间的增加,对根内球囊霉菌根幼苗根系生物量无显著影响。由于蜜色无梗囊霉菌根幼苗根系生物量的增加而茎和叶生物量无明显的变化,致使全株生物量也有所增加,且与根部生物量变化相似(图 1)。

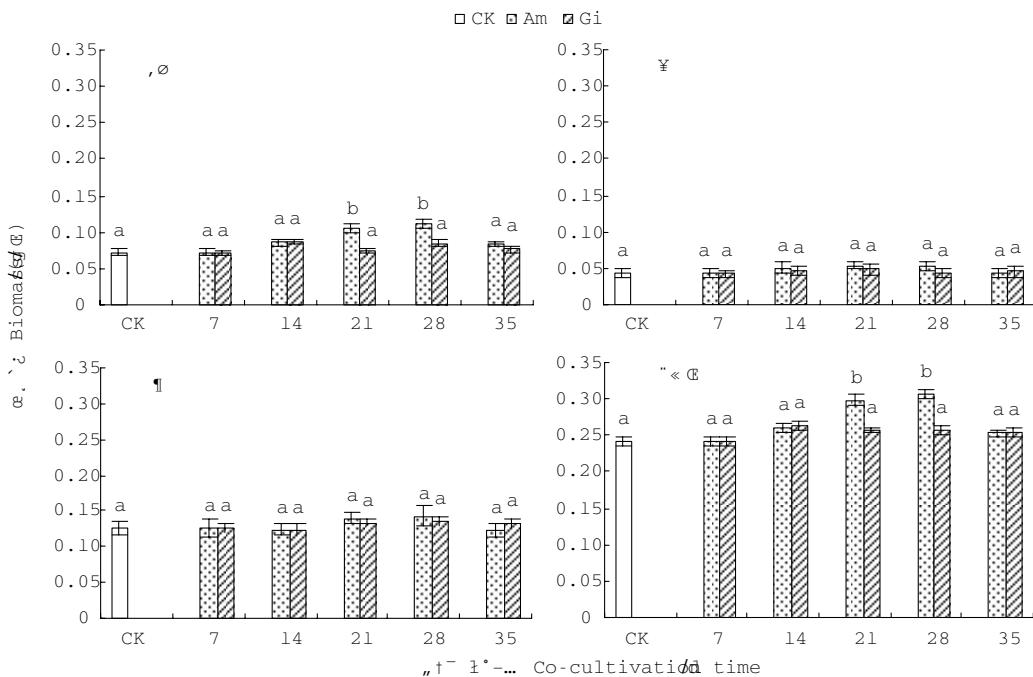


图 1 共培养时间对丛枝菌根喜树幼苗生物量的影响

Fig. 1 Effect of co-cultivation time on biomass in arbuscular mycorrhizal *C. acuminata* seedlings

每一小图中, 标有不同字母的柱体间差异性显著($P<0.05$)

2.2 共培养时间对丛枝菌根喜树幼苗喜树碱含量的影响

丛枝菌根是丛枝菌根真菌与宿主植物根系形成的共生体系,相对于宿主植物其他器官而言,丛枝菌根对根部代谢的影响最为直接。喜树幼苗丛枝菌根的形成明显提高了根喜树碱的含量,蜜色无梗囊霉与根内球囊霉菌根幼苗差异不显著。随着共培养时间的增长,菌根幼苗的喜树碱含量也显著增加,但共培养时间超过 21 d 后则无明显变化(图 2)。

丛枝菌根对喜树幼苗茎喜树碱含量的影响明显小于根,尽管茎的喜树碱含量远高于根。共培养时间较短时,菌根幼苗茎喜树碱含量与无菌根幼苗之间没有明显的差异,随共培养时间的增加(自共培养 21 d 起)菌根幼苗茎喜树碱含量明显高于无菌根幼苗。蜜色无梗囊霉与根内球囊霉菌根幼苗之间,茎喜树碱含量差异不明显(图 2)。

接种蜜色无梗囊霉与根内球囊霉于喜树幼苗,对喜树幼苗叶片喜树碱含量的影响呈现明显的不同。蜜色无梗囊霉菌根幼苗叶片喜树碱含量随共培养时间的增加而增加,至共培养 28 d 时与无菌根幼苗相比差异最为显著,为无菌根幼苗叶喜树碱含量的 1.56 倍,而后略有减少(图 2)。根内球囊霉菌根幼苗叶喜树碱含量随共培养时间的增加缓慢增加,至共培养 21 d 时与无菌根幼苗相比差异最为显著,为无菌根幼苗叶喜树碱含量的 1.29 倍,之后无显著变化(图 2)。

从全株喜树碱含量看,随共培养时间的增加,菌根幼苗全株喜树碱含量随之增加,且两种菌根幼苗之间伴随共培养时间的增加逐渐产生差异(图 2)。

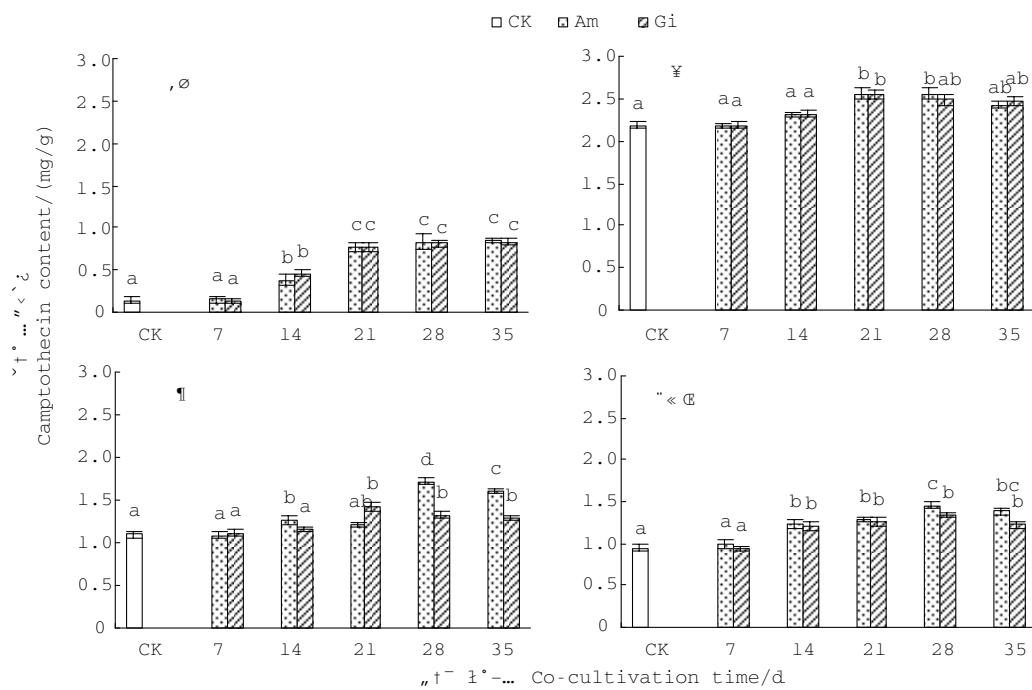


图2 共培养时间对丛枝菌根喜树幼苗喜树碱含量的影响

Fig. 2 Effect of co-cultivation time on camptothecin content in arbuscular mycorrhizal *C. acuminata* seedlings

2.3 共培养时间对丛枝菌根喜树幼苗喜树碱产量的影响

喜树碱产量(喜树碱含量与生物量的乘积)是反映丛枝菌根对喜树幼苗喜树碱代谢影响情况的另一个方面。丛枝菌根的形成明显提高了喜树幼苗根系喜树碱的产量,并且主要源于喜树碱含量的增加。两种菌根相比较,蜜色无梗囊霉菌根优于根内球囊霉菌根。伴随共培养时间的增加,菌根幼苗根喜树碱产量先明显增加,至共培养21 d时趋于稳定(图3)。

丛枝菌根对喜树幼苗茎和叶片喜树碱产量的影响与喜树碱含量相似(图2—图3)。从全株喜树碱产量来看,菌根幼苗喜树碱产量明显高于无菌根幼苗(图3)。伴随共培养时间的增加,全株喜树碱产量与根部喜树碱产量变化相似,增加幅度表现为喜树碱含量和生物量的双重作用(图1—图3)。

上述结果表明,丛枝菌根真菌与喜树幼苗共培养时间的增加,提高了幼苗喜树碱的产量,且主要源于喜树碱含量的增加。

由图4可见,丛枝菌根的形成改变了喜树幼苗喜树碱在根、茎和叶中的比例分配,并且明显提高了根中喜树碱的比例。从共培养时间变化看,蜜色无梗囊霉菌根幼苗根中喜树碱比例伴随共培养时间的增加先表现出明显的增加,而后无显著变化。不过,共培养时间对根内球囊霉菌根幼苗根中喜树碱分配比例无显著影响。

3 讨论

高克祥等^[21]用漏斗包球囊霉对苹果M₂₆组培苗进行接种实验,观察了丛枝菌根形成过程及其形态特征的变化,发现随着漏斗包球囊霉侵染时间的增加,菌根侵染率随之增加。本实验用蜜色无梗囊霉和根内球囊霉对喜树幼苗进行接种实验,观察了丛枝菌根的形成过程,发现伴随着这两种丛枝菌根真菌与喜树幼苗共培养时间的增加,菌根侵染率和侵染强度随之增加,但增加至一定共培养时间(28 d)时趋于稳定(表1)。与此过程相对应,喜树幼苗的喜树碱含量特别是根的喜树碱含量,也有随着共培养时间增加而增加的变化过程,而且也是增加至一定共培养时间时趋于稳定(图2)。因此,从丛枝菌根真菌接种后与喜树幼苗共培养时间的角度,也观察到了喜树碱含量变化与丛枝菌根真菌侵染及菌根形成过程的对应性。

从丛枝菌根真菌接种时期角度进行观察时^[19],是在喜树幼苗生长的不同时期接种丛枝菌根真菌,而在接种后相同的时间(30 d)采样进行分析,采样也是在幼苗生长的不同时期,因而幼苗喜树碱含量的差异中也

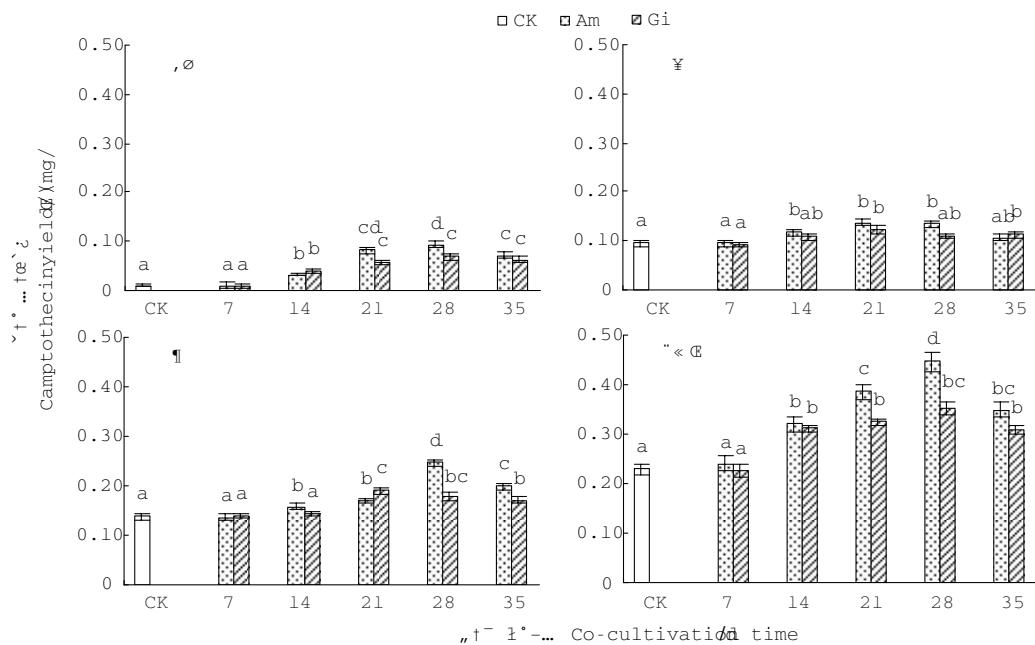


图3 共培养时间对丛枝菌根喜树幼苗喜树碱产量的影响

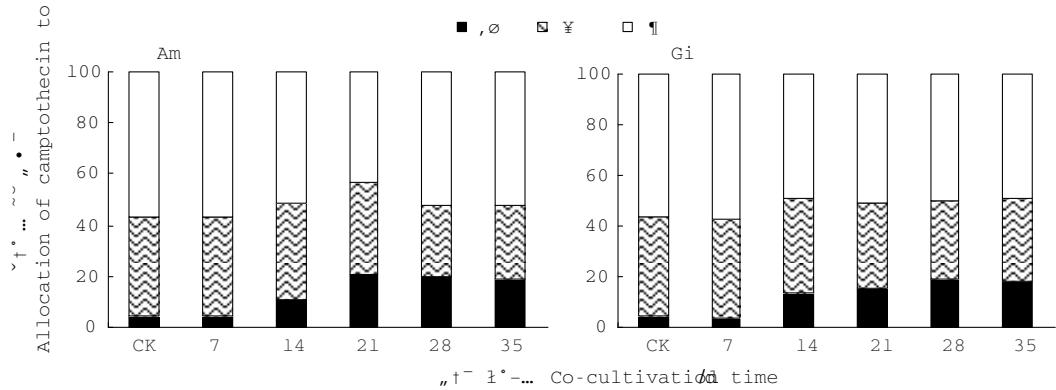
Fig. 3 Effect of co-cultivation time on camptothecin yield in arbuscular mycorrhizal *C. acuminata* seedlings

图4 共培养时间对丛枝菌根喜树幼苗喜树碱器官分配的影响

Fig. 4 Effect of co-cultivation time on camptothecin allocation to organs in arbuscular mycorrhizal *C. acuminata* seedlings

可能包含着生长时期本身对喜树碱代谢影响的因素,因为有研究表明喜树碱含量是随着喜树幼苗的生长时期而变化的^[26]。相对而言,本文从丛枝菌根真菌接种后与喜树幼苗共培养时间角度进行观察时,都是在幼苗生长的同一时期采样进行分析,从而在一定程度上避免了幼苗生长时期差异的影响,结果能更好地反映丛枝菌根真菌侵染及菌根形成与幼苗喜树碱含量的对应关系。当然,在不同的生长时期接种丛枝菌根真菌,丛枝菌根真菌侵染及菌根形成状况还是会有一些差异的。无论如何,从接种时期角度和共培养时间角度设计的实验都证实了推测,即菌根真菌的侵染及菌根形成过程与喜树幼苗的喜树碱含量变化具有对应性。两个实验都表明,喜树幼苗中的喜树碱含量伴随着菌根真菌的侵染及菌根形成的过程而增加,并且在侵染及菌根形成过程趋于稳定后不再有明显变化。

以往研究表明,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。Abu-Zeyad等^[27]分别用根内球囊霉和珠状巨孢囊霉(*Gigaspora margarita*)接种澳大利亚栗籽豆(*Castanospermum australe*),发现与根内球囊霉形成菌根的栗籽豆表现出更高的栗籽豆碱(castanospermine,一种吲哚生物碱)含量。Vierheiling等^[28]用根内球囊霉(*G. intraradices*)、摩西球囊霉(*G. mosseae*)、玫瑰红巨孢囊霉(*G. rosea*)分

别接种玉米(*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。本实验所使用的蜜色无梗囊霉和根内球囊霉，对喜树幼苗喜树碱积累的影响也表现出差异，特别是在对幼苗喜树碱产量的影响上，两种丛枝菌根真菌的表现迥然不同。蜜色无梗囊霉菌根幼苗根、茎和叶喜树碱产量高于根内球囊霉菌根幼苗，并且随着共培养时间的增加两者间的差异增大(图3)。

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