外来入侵植物对本地植物菌根真菌的影响及其机制

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摘要 菌根真菌共生是植物吸收养分的一个重要策略。外来植物可以干扰本地植物与菌根真菌的共生关系从而抑制本地植物生长, 这是近年来被发现的一种重要入侵机制, 在研究中得到日益广泛的关注。该文从以下几个方面着重综述这种入侵机制: 1) 外来植物对本地植物菌根真菌的影响, 包括菌根真菌侵染率、菌根内部结构、根外菌丝的量、菌根真菌的群落组成、非菌根真菌的影响及网络结构; 2) 外来植物对本地植物菌根真菌上述影响的机制, 包括资源竞争、化感作用和土壤肥力等生态机制以及相关的分子机制; 3) 上述两个方面随入侵时间的变化格局。尽管干扰本地植物菌根真菌是一种重要的入侵机制, 但相对其他的入侵机制(例如天敌逃逸、新武器假说等)来说, 这类机制的研究目前仍很匮乏。鉴于此, 该文提出了未来需要重点关注的几个方面: 1) 全球变化背景下, 入侵植物对本地植物菌根真菌的影响如何变化; 2) 包括这种菌根机制在内的多种入侵机制之间的关系; 3) 深入探究入侵的这种菌根机制在大的时空尺度上的变化规律。

关键词 入侵植物; 本地植物; 菌根真菌; 机制; 植物-土壤反馈

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A review on the effects of invasive plants on mycorrhizal fungi of native plants and their underlying mechanisms

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Abstract

Mycorrhizal fungi symbiosis is an important strategy for plant to uptake soil nutrients. Alien plants could thwart the symbiotic relationship between native plants and mycorrhizal fungus, and thus suppress the growth of native plants, which is an important mechanism for alien plant invasion, and has been increasingly emphasized in recent studies. In the present review, we summarized several key aspects of such mycorrhizal-related mechanism of plant invasion: 1) the impacts of alien plants on mycorrhizal fungi of native plants (i.e. mycorrhizal colonization rate, internal structures of mycorrhizal hyphae, amount of external hyphae, mycorrhizal and non-mycorrhizal composition, and mycorrhizal network); 2) mechanisms of alien-plant impacts on mycorrhizal fungi of native plants, including ecological mechanisms such as resource competition, allelopathy and edaphic fertility, as well as their molecular mechanisms; 3) variations of the above mentioned alien-plant impacts and related mechanisms at different durations of plant invasion. Despite thwarting mycorrhizal fungi of native plants is an important mechanism for alien plant invasion, researches on such mechanism are still scarce comparing to other mechanisms such as natural enemy release and new weapon hypothesis. Therefore, we proposal several research areas that need to be focused on in future studies: 1) how do global changes affect the alien-plant-invasion impacts on mycorrhizal fungi of native plants; 2) what are the relationships among different mechanisms including the mycorrhizal-related mechanism; 3) how does the mycorrhizae-related mechanism change at large spatio-temporal scales.

Key words invasive plant; native plant; mycorrhizal fungi; mechanism; plant-soil feedback

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随着全球社会经济活动的日益紧密,越来越多的植物被带入非原产地环境,快速扩散成为入侵植物。全球变化背景下,入侵植物已对当地生物多样性、社会经济以及人类健康造成重大威胁(万方浩等, 2011; 鞠瑞亭等, 2012; van Kleunen *et al.*, 2015; Pathak *et al.*, 2019)。探求外来植物成功入侵的机制是近几十年来生态和进化领域的一个重要议题,同时也是进行入侵防控的前提(Wolfe *et al.*, 2008; Catford *et al.*, 2009; Lau & Schultheis, 2015; Wan *et al.*, 2019)。外来植物可以通过多种途径成功入侵当地生态系统(Catford *et al.*, 2009)。例如,在入侵地由于缺乏有效天敌,入侵种可以将原来分配到天敌防御上的资源(如碳和氮)用于生长繁殖而促进入侵(Blossey & Notzold, 1995; Feng *et al.*, 2009; Zhao *et al.*, 2020);入侵种也会具有较高的表型可塑性,能更好地适应环境资源的波动(Richards *et al.*, 2006);它们还会产生一些特殊的化感物质,抑制本地植物生长(Callaway *et al.*, 2008; Zheng *et al.*, 2015)。

除了这些被广泛关注的途径,近年来还发现一类重要的间接途径,即入侵植物能通过干扰本地物种的共生关系(如植物-传粉昆虫和根系-菌根真菌等)而抑制本地植物的生长(Mitchell *et al.*, 2006; Pringle *et al.*, 2009; 张桂花等, 2009; Wilson *et al.*, 2012)。陆地生态系统中80%以上的植物都与菌根真菌共生,这是陆地上最古老和最重要的共生关系之一(Martin *et al.*, 2017; Brundrett & Tedersoo, 2018; Steidinger *et al.*, 2019; Tedersoo *et al.*, 2020)。在这种共生关系中,植物为菌根真菌提供碳源,菌根真菌为宿主植物提供稀缺养分(如磷和氮等),并帮助宿主防御病害,适应胁迫环境(如干旱和重金属污染等)(Parniske, 2008; Bonfante & Genre, 2010; Kohler *et al.*, 2015; Delavaux *et al.*, 2017)。因此,如果外来植物能干扰或破坏本地植物根系与菌根真菌的共生关系,就可以抑制本地植物生长,促进自身入侵。近年来,一些研究报道了入侵植物这方面的作用(Stinson *et al.*, 2006; Callaway *et al.*, 2008; Vogelsang & Bever, 2009; Dickie *et al.*, 2017),表明对本地植物共生菌根真菌的干扰是外来植物一种重要的入侵机制。

本文围绕入侵植物对本地植物菌根真菌的影响和机制,综述近年来国内外在这方面的进展,并做了相关的评论和展望。我们首先分析入侵植物对本地植物菌根真菌侵染程度、菌根内部结构、根外菌丝特征、真菌群落组成及真菌网络的影响;之后综合分析这些影响背后的生态和分子机制,涉及资源竞争、土壤养分、化感作用、信号识别及转导等;最后探讨外来植物入侵时间或强度的效应。

1 入侵植物对本地植物菌根真菌的影响

1.1 本地植物菌根真菌侵染程度

早在21世纪初,Stinson等(2006)就注意到了外来入侵植物对本地植物菌根真菌侵染的影响。他们发现在原产地欧洲,葱芥(*Alliaria petiolata*)对其邻近植物菌根真菌侵染率的影响不显著;但在入侵地北美显著降低了本地植物*Acer saccharum*、红枫(*Acer rubrum*)和*Fraxinus americana*丛枝菌根真菌(AMF)的侵染率,下降幅度分别是30%、14%和42%(Stinson *et al.*, 2006; Callaway *et al.*, 2008)。Stinson等(2006)的研究引起了广泛关注,他们的工作被认为是一种潜在的外来植物入侵的新机制。之后人们选取不同的入侵植物和本地植物体系来检验这种入侵机制的广泛性。例如,生长在英国的本地植物长叶车前(*Plantago lanceolata*)、百脉根(*Lotus corniculatus*)和红车轴草(*Trifolium pratense*)也会受到入侵植物类似的影响,在虎杖(*Fallopia japonica*)入侵时菌根真菌侵染率分别下降了20%、24%和20%,而外来植物凤仙花(*Impatiens glandulifera*)对本地植物侵染率抑制程度弱一些,下降幅度分别为12%、11%和19%(Tanner & Gange, 2013)。狗牙根(*Cynodon dactylon*)的入侵使匈牙利的小花蝇子草(*Stipa borysthena*)的AMF侵染率降低25%(Endresz *et al.*, 2013)。在我们检索到的国内外32篇相关文献中(AMF文献有27篇),有44%的文献报道入侵植物显著降低了本地植物AMF侵染率(降低18.9%),也有一部分文献报道本地植物AMF侵染率未有变化甚至是增加的现象(增加9.5%)(表1)。例如,海岸松(*Pinus pinaster*)和绢毛荣桦(*Hakea sericea*)入侵到夏威夷后当地植物群落的AMF侵染率均未发生改

表1 入侵植物对本地植物菌根真菌感染率和根外菌丝的影响
Table 1 Effects of invasive plants on the mycorrhizal fungi colonization rate and extraradical mycelium of native plants

参考文献 Reference	实验方式 Study type	入侵植物 Invasive plant	本地植物 Native plant	菌根类型 Mycorrhizal type	菌根真菌感染率的变化 ^b Variation of mycorrhizal fungi colonization rate ^b (%)	菌丝长度平均值的变化 Variation of average mycelium length (m g ⁻¹ soil)	菌丝长度平均值的变化 ^c Variation of average mycelium length ^c (m)
Allsopp & Holmes, 2001	野外取样 Field sampling	海岸松 <i>Pinus pinaster</i>	本地植物群落 ^a Native plant community ^a	AMF	ns		
Bai <i>et al.</i> , 2012	盆栽 Potted plant	绢毛荣桦 <i>Hakea sericea</i>	本地植物群落 ^a Native plant community ^a	AMF	ns		
Baohanta <i>et al.</i> , 2012	温室试验 Greenhouse experiment	大花金鸡菊 <i>Coreopsis grandiflora</i>	须苞石竹 <i>Dianthus barbatus</i>	AMF	+16.50		
		<i>Pinus patula</i>	<i>Uapaca bojeri</i>	EMF	-44.40		
Bennett <i>et al.</i> , 2011	温室试验 Greenhouse experiment	赤桉 <i>Eucalyptus camaldulensis</i>	<i>Uapaca bojeri</i>	EMF	-57.40		
		绒毛草 <i>Holcus lanatus</i>	加拿大蓬 <i>Erigeron glaucus</i>	AMF	+6.47		
Cantor <i>et al.</i> , 2011	温室试验 Greenhouse experiment	葱芥 <i>Alliaria petiolata</i>	本地植物群落 ^a Native plant community ^a	AMF			-0.004
Chen <i>et al.</i> , 2020	野外取样 Field sampling	<i>Eupatorium catarium</i>	华泽兰 <i>Eupatorium chinense</i>	AMF	-29.07		
	花园实验 Garden experiment	鬼针草 <i>Bidens pilosa</i>	田菁 <i>Sesbania cannabina</i>	AMF	-29.75		
Endresz <i>et al.</i> , 2013	野外取样 Field sampling	拂子茅 <i>Calamagrostis epigejos</i>	<i>Festuca vaginata</i>	AMF	-20.38		
		狗牙根 <i>Cynodon dactylon</i>	<i>Stipa boryshevica</i>	AMF	-10.18		
Gaggini <i>et al.</i> , 2019	田间试验 Field experiment	<i>Impatiens glandulifera</i>	<i>Festuca vaginata</i>	AMF	-27.03		
Gornish <i>et al.</i> , 2020	田间试验 Field experiment	<i>Cenchrus ciliaris</i>	<i>Stipa boryshevica</i>	AMF	-32.84		
Grove <i>et al.</i> , 2012	温室试验 Greenhouse experiment	<i>Cytisus scoparius</i>	本地植物群落 ^a Native plant community ^a	AMF	-0.11		-0.23
Guo, 2020	盆栽 Potted plant	<i>Xanthium strumarium</i>	花旗松 <i>Pseudotsuga menziesii</i>	EMF	-15.37		
Carlson <i>et al.</i> , 2014	野外取样 Field sampling	葱芥 <i>Alliaria petiolata</i>	大豆 <i>Glycine max</i>	AMF	ns		
Lekberg <i>et al.</i> , 2013	野外取样 Field sampling	<i>Centaurea stoebe</i>	本地植物群落 ^a Native plant community ^a	EMF	-35.13		
		乳浆大戟 <i>Euphorbia esula</i>	本地植物群落 ^a Native plant community ^a	AMF	+39.00		
		旱雀麦 <i>Bromus tectorum</i>	本地植物群落 ^a Native plant community ^a	AMF	+47.10		
Liang <i>et al.</i> , 2016	温室试验 Greenhouse experiment	互花米草 <i>Spartina alterniflora</i>	本地植物群落 ^a Native plant community ^a	AMF	-27.30		
Lutgen & Rillig, 2004	田间试验 Field experiment	<i>Centaurea maculosa</i>	芦苇 <i>Phragmites australis</i>	AMF	-11.66		
Maltz <i>et al.</i> , 2016	野外试验 Field experiment	<i>Brassica nigra</i>	本地植物群落 ^a Native plant community ^a	AMF	-10.36		
Mumme & Rillig, 2006	田间试验 Field experiment	斑点矢车菊 <i>Centaurea maculosa</i>	本地植物群落 ^a Native plant community ^a	AMF	-3.18		
Pakpour & Klironomos, 2015	盆栽 Potted plant	<i>Brassica nigra</i>	本地草本植物群落 ^a Native herbaceous plant community ^a	AMF	-0.76		
Ruckli <i>et al.</i> , 2014	温室试验 Greenhouse experiment	<i>Impatiens glandulifera</i>	本地植物群落 ^a Native plant community ^a	AMF	-34.46		
Ruckli <i>et al.</i> , 2016	野外试验 Field experiment	<i>Impatiens glandulifera</i>	<i>Acer pseudoplatanus</i>	AMF	-21.70		
Sanon <i>et al.</i> , 2009	野外取样 Field sampling	<i>Amaranthus viridis</i>	本地植物群落 ^a Native plant community ^a	EMF	-48.37		
Sanon <i>et al.</i> , 2009	野外取样 Field sampling	<i>Amaranthus viridis</i>	本地植物群落 ^a Native plant community ^a	AMF	-11.10		
		<i>Acacia senegal</i>	<i>Acacia senegal</i>	AMF	-42.40		
		<i>Acacia seyal</i>	<i>Acacia seyal</i>	AMF	-26.90		

表 1 (续) Table 1 (Continued)

参考文献 Reference	实验方式 Study type	入侵植物 Invasive plant	本地植物 Native plant	菌根类型 Mycorrhizal type	菌根真菌侵染率的变化 ^b Variation of mycorrhizal fungi colonization rate (%)	菌丝长度平均值 的变化 ^c Variation of average mycelium length (m ⁻¹ soil)	菌丝长度平均值 的变化 ^c Variation of average mycelium length ^c (m)
Sanon <i>et al.</i> , 2009	野外取样 Field sampling	<i>Amaranthus viridis</i>	<i>Acacia nilotica</i> <i>Fabaceae albida</i>	AMF AMF	-23.50 -53.90		
Sanon <i>et al.</i> , 2012	温室试验 Greenhouse experiment	<i>Amaranthus viridis</i>	本地植物群落 ^a Native plant community ^a	AMF		-2.40	
Shannon <i>et al.</i> , 2014	温室试验 Greenhouse experiment	<i>Ligustrum vulgare</i> 忍冬 <i>Lonicera maackii</i>	本地植物群落 ^a Native plant community ^a	AMF	-6.65		
Gaya Shivega & Aldrich-Wolfe, 2017	温室试验 Greenhouse experiment	牛奶子 <i>Elaeagnus umbellata</i>	本地植物群落 ^a Native plant community ^a	AMF	-3.91		
Stinson <i>et al.</i> , 2006	田间试验 Field experiment	节毛飞廉 <i>Carduus acanthoides</i> 葱芥 <i>Alliaria petiolata</i>	本地植物群落 ^a Native plant community ^a <i>Oligoneuron rigidum</i>	AMF AMF	+14.18 +2.18		
Tanner & Gange, 2013	野外取样 Field sampling	虎杖 <i>Fallopia japonica</i>	红枫 <i>Acer rubrum</i> <i>Acer saccharum</i>	AMF AMF	-31.43 -13.80		
Trautwig <i>et al.</i> , 2017	田间试验 Field experiment	白茅 <i>Imperata cylindrica</i>	美国白蜡木 <i>Fraxinus americana</i>	AMF	-41.83		
Wilson <i>et al.</i> , 2012	温室试验 Greenhouse experiment	臭根子草 <i>Bothriochloa bladhii</i>	长叶车前 <i>Plantago lanceolata</i> 百脉根 <i>Lotus corniculatus</i>	AMF AMF	-17.23 -12.09		
Wolfe <i>et al.</i> , 2008	野外取样 Field sampling	葱芥 <i>Alliaria petiolata</i>	红车轴草 <i>Trifolium pratense</i>	AMF	-11.01		
Yang <i>et al.</i> , 2019	田间试验 Field experiment	黄香草木犀 <i>Melilotus officinalis</i>	长叶车前 <i>Plantago lanceolata</i> 百脉根 <i>Lotus corniculatus</i>	AMF EMF	-19.77 -24.31		
		黄香草木犀 <i>Melilotus officinalis</i>	红车轴草 <i>Trifolium pratense</i>	AMF	-20.00		
		黄香草木犀 <i>Melilotus officinalis</i>	火炬松 <i>Pinus taeda</i>	AMF	-7.91		
		黄香草木犀 <i>Melilotus officinalis</i>	<i>Andropogon gerardii</i>	AMF	-33.75		
		黄香草木犀 <i>Melilotus officinalis</i>	<i>Schizachyrium scoparium</i>	AMF	-26.75		
		黄香草木犀 <i>Melilotus officinalis</i>	本地松树群落 ^a Native pine community ^a	EMF	-3.27 ^d		
		黄香草木犀 <i>Melilotus officinalis</i>	狗尾草 <i>Setaria viridis</i>	AMF	+4.81		
		黄香草木犀 <i>Melilotus officinalis</i>	黄香草木犀 <i>Melilotus officinalis</i>	AMF	+0.27		
		黄香草木犀 <i>Melilotus officinalis</i>	三种本地植物混种	AMF	+5.00		
		黄香草木犀 <i>Melilotus officinalis</i>	狗尾草 <i>Setaria viridis</i>	AMF	+2.88		
		黄香草木犀 <i>Melilotus officinalis</i>	黄香草木犀 <i>Melilotus officinalis</i>	AMF	+5.77		
		黄香草木犀 <i>Melilotus officinalis</i>	藜 <i>Chenopodium album</i>	AMF	+11.38		
		黄香草木犀 <i>Melilotus officinalis</i>	三种本地植物混种	AMF	+3.33		
		黄香草木犀 <i>Melilotus officinalis</i>	Three native plants mixed	AMF	+19.14		
		黄香草木犀 <i>Melilotus officinalis</i>	狗尾草 <i>Setaria viridis</i>	AMF	+3.97		
		黄香草木犀 <i>Melilotus officinalis</i>	黄香草木犀 <i>Melilotus officinalis</i>	AMF	+4.12		
		黄香草木犀 <i>Melilotus officinalis</i>	藜 <i>Chenopodium album</i>	AMF	-4.35		
		黄香草木犀 <i>Melilotus officinalis</i>	三种本地植物混种	AMF	+4.12		
Zhang <i>et al.</i> , 2017	盆栽 Potted plant	三叶鬼针草 <i>Bidens pilosa</i> <i>Flaveria bidentis</i>	狗尾草 <i>Setaria viridis</i>	AMF	-3.22		

表 1 (续) Table 1 (Continued)

参考文献 Reference	实验方式 Study type	入侵植物 Invasive plant	本地植物 Native plant	菌根类型 Mycorrhizal type	菌根真菌感染率的变化 ^b Variation of mycorrhizal fungi colonization rate (%)	菌丝长度平均值的变化 Variation of average mycelium length (m·g ⁻¹ soil)	菌丝长度平均值的变化 ^c Variation of average mycelium length ^c (m)
Zhang <i>et al.</i> , 2018a	田间试验	Field experiment	<i>Ambrosia artemisiifolia</i>	AMF	-29.79		
			三叶鬼针草 <i>Bidens pilosa</i>	AMF	-19.70		
Zhang, 2019	盆栽	Potted plant	<i>Xanthium strumarium</i>	AMF	-11.70		
			苍耳 <i>Xanthium sibiricum</i>	AMF	-6.34		
			狗尾草 <i>Setaria viridis</i>	AMF	-14.85		
			稗草 <i>Echinochloa crusgalli</i>	AMF	-7.90		
			黄花蒿 <i>Artemisia annua</i>	AMF	-16.68		
		<i>Solanum rostratum</i>	苍耳 <i>Xanthium sibiricum</i>	AMF	-19.45		
			狗尾草 <i>Setaria viridis</i>	AMF	-16.64		
			稗草 <i>Echinochloa crusgalli</i>	AMF	-8.15		
			黄花蒿 <i>Artemisia annua</i>	AMF	-8.95		
		<i>Ambrosia trifida</i>	苍耳 <i>Xanthium sibiricum</i>	AMF	-18.76		
			狗尾草 <i>Setaria viridis</i>	AMF	-18.25		
			稗草 <i>Echinochloa crusgalli</i>	AMF	-4.42		
			黄花蒿 <i>Artemisia annua</i>	AMF	-13.94		
		<i>Amaranthus retroflexus</i>	苍耳 <i>Xanthium sibiricum</i>	AMF	-19.37		
			狗尾草 <i>Setaria viridis</i>	AMF	-21.73		
			稗草 <i>Echinochloa crusgalli</i>	AMF	-7.48		
			黄花蒿 <i>Artemisia annua</i>	AMF	-21.40		
			苍耳 <i>Xanthium sibiricum</i>	AMF	-20.14		
		<i>Galinsoga quadriradiata</i>	狗尾草 <i>Setaria viridis</i>	AMF	-18.42		
			稗草 <i>Xanthium sibiricum</i>	AMF	-2.54		
			黄花蒿 <i>Artemisia annua</i>	AMF	-13.25 ± 2.10	-3.82 ± 1.68	-0.12 ± 0.11
平均值±标准误差(所有物种) Mean ± SE (all species)							
平均值±标准误差(不同菌根类型) Mean ± SE (different mycorrhizal types)					-11.55 ± 2.25	-3.82 ± 1.68	-0.12 ± 0.11

+; 促进作用; -, 抑制作用。a, 文献中未明确具体的植物物种; b, 文中感染率变化=本地植物未入侵时感染率-入侵后本地植物感染率; c, 文献中未标明测量菌丝长度的范围; d, 此处感染率变化=EMF感染根质量/总根质量。ns, 差异不显著 ($p > 0.05$)。
+, positive effect; -, negative effect. a, specific plant species not identified in the paper; b, change of the infestation rate = infestation rate of native plants under conditions without alien plant invasion - infestation rate of native plants under conditions after alien plant invasion; c, range of mycelium length measurements not indicated in the paper; d, change of the infestation rate = EMF infested root mass/total root mass. ns, no significant difference ($p > 0.05$).

变(Allsopp & Holmes, 2001); 而乳浆大戟(*Euphorbia esula*)的入侵使本地植物AMF侵染率由原来的40%提高到79%, 入侵植物*Centaurea stoebe*使本地植物侵染率提升了1.2倍(Lekberg *et al.*, 2013)。

相对于AMF, 外生菌根真菌(EMF)对外来干扰的抵抗能力更强(Chen *et al.*, 2020), 但研究表明外来入侵植物能抑制本地植物EMF的侵染程度(Wolfe *et al.*, 2008)。例如, 葱芥入侵后本地植物群落(红松(*Pinus resinosa*)和白松(*Pinus strobus*))的EMF侵染率降低约75% (Carlson *et al.*, 2014)。我们整理搜集文献的相关数据发现, 入侵植物对EMF侵染率平均降低30%, 相对高于入侵植物对AMF的平均抑制程度(11.6%)(表1)。这表明菌根类型是影响入侵植物对本地植物菌根真菌干扰程度的重要因素。不过, 我们也注意到, 相比于AMF, 涉及入侵植物对本地植物EMF共生关系影响的研究较少。Grove等(2017a)综述的112篇相关文章中, 82%的文章阐述了入侵植物对本地AMF植物的影响, 只有18%的文章探讨了入侵植物对本地EMF植物的影响, 而且这种影响的程度在不同研究中有较大的差异。因此, 未来需要扩大对EMF植物的关注, 以检验入侵植物对本地植物EMF的抑制效果是否普遍高于对本地植物AMF的抑制性。截至目前, 除AMF和EMF这两种常见的菌根类型外, 我们还未见到入侵植物对其他一些生长在特殊环境中的重要菌根类型, 如杜鹃类菌根(ERM)、兰科菌根(ORM)等影响的报道。这可能是由于这些菌根类型生长在特殊的环境中, 例如杜鹃花科植物多生长于土壤贫瘠和干旱等恶劣环境中, 外来植物很难成功入侵到类似环境; 而兰科植物是常见的观赏花卉, 入侵植物在其生存环境中经常被园艺工人拔除, 导致研究者们忽略了入侵生物的存在。因此, 未来研究需要探讨不同菌根类型对入侵植物响应的差异和机制。

尽管入侵植物对本地植物菌根真菌影响的这些差异性被报道, 但是很少有研究者关注这些差异背后的原因。我们推测这可能至少与以下几个方面有关: 1)本地植物和菌根真菌共生关系的强弱。例如, 有两个本地植物A和B, 如果A的菌根真菌侵染率远高于B (或者说A对菌根真菌的依赖性远超过B)(Eissenstat *et al.*, 2015; Bergmann *et al.*, 2020), 那么入侵植物对A的菌根真菌侵染率的影响要超过B。2)入侵植物的竞争力和化感作用的大小。例如, 张

海艳(2019)研究发现竞争力较强的入侵种(*Xanthium strumarium*、*Solanum rostratum*、*Ambrosia trifida*、*Amaranthus retroflexus*和*Galinsoga quadriradiata*)对本地植物苍耳(*Xanthium sibiricum*)菌根真菌的影响反而较小, 这可能是由于入侵种的化感物质较弱。3)土壤养分的高低。例如, 张海艳(2019)研究发现入侵植物*S. rostratum*在低养分的情况下对本地植物菌根真菌的影响更显著, 这可能是低养分情况下本地植物的菌根真菌对入侵植物的竞争力和化感作用更敏感所致。

以往研究大多只关注具有单共生关系的本地植物(只受菌根真菌侵染), 而对具有双共生关系的本地植物(根瘤菌和AMF共同侵染, 如豆科植物)的研究很少。我们团队的研究发现, 入侵植物*X. strumarium*抑制了本地植物苍耳(单共生关系)的AMF侵染率(张海艳, 2019), 但没有改变本地植物大豆(*Glycine max*)(双共生关系)的AMF侵染率(郭小城, 2020)。这可能是物种本身的差异所致, 但也不排除根瘤的存在改变了菌根真菌对入侵植物的响应, 需要进一步研究。这里只涉及一种豆科植物, 我们还不清楚别的豆科植物以及其他双共生体系中菌根真菌对外来入侵植物的响应是否有差异。

1.2 本地植物菌根内部结构和功能

外来植物入侵后, 本地植物菌根真菌侵染率有时没有受到显著影响(Allison *et al.*, 2006), 但这并不等于外来入侵植物不影响本地植物与菌根真菌的共生关系, 菌根的内部结构和功能可能发生了显著变化。丛枝菌根内部存在多种结构, 包括泡囊、丛枝、菌丝环以及根内菌丝(图1)。这些不同真菌结构具有不同的功能, 例如泡囊可以存储真菌脂质及其他成分, 丛枝和菌丝环是植物与菌根真菌之间进行碳和养分交换的部位, 根内菌丝可以帮助真菌在根内定殖并在菌丝内部运输养分(Johnson *et al.*, 2003; Smith & Read, 2008)。菌根真菌的这些内部侵染结构会受到环境的影响。Lugli等(2019)研究表明, 土壤中磷的多少会改变丛枝菌根内部结构, 进而影响菌根功能。入侵植物可以提高入侵地的土壤养分含量(Pattison *et al.*, 2016; Zhang *et al.*, 2018a), 例如Liao等(2008)的meta分析表明, 入侵植物可以使入侵地的土壤养分平均增加30%。入侵地土壤养分的提升可能会导致本地植物菌根真菌侵染的改变, 包括侵染率和菌根内部结构两个方面。然而, 目前有

图1 丛枝菌根内部结构概念图(改编自Johnson等(2003))。A, 丛枝; C, 菌丝环; IH, 根内菌丝; V, 泡囊。

Fig. 1 A conceptual diagram of the internal structures of arbuscular mycorrhizae in root tissues (adapted from Johnson *et al.*, 2003). A, arbuscules; C, coils; IH, intraradical hyphae; V, vesicles.

关外来入侵植物对本地植物菌根真菌内部结构影响的研究很少, 在未来研究中需要加强。

1.3 本地植物根外菌丝特征

菌根的根内菌丝延伸至根外形成根外菌丝, 根外菌丝直接参与土壤养分的吸收。外来入侵植物在对本地植物菌根真菌侵染率、真菌内部结构产生影响的同时, 也会对根外菌丝产生影响(Lutgen & Rillig, 2004; Luo *et al.*, 2019)(表1)。例如, Mummey和Rillig (2006)研究发现, 外来植物斑点矢车菊(*Centaurea maculosa*)的入侵使本地植物的AMF根外菌丝长度降低24%; Gaggini等(2019)发现, 凤仙花入侵一年使本地植物根外AMF菌丝生物量降低30%–80%。总体来说, 相对于菌根真菌侵染率, 有关根外菌丝特征对入侵植物响应的研究较少, 且相关研究中对根外菌丝的量化标准也不统一, 有的使用菌丝长度, 有的则使用菌丝生物量, 不利于将来进行整合分析。我们推荐使用菌丝长度这一指标, 因为其易于测定且成本低。入侵植物除了影响本地植物根外菌丝的长度和生物量外, 还可能会进一步影响根外菌丝与吸收功能密切相关的一些生理特征。例如, 1)根外菌丝分泌蛋白水解酶的能力, 这些水解酶往往参与分解土壤有机质和生物残体, 释放其中的养分(Martin *et al.*, 2008; Zhang *et al.*, 2019)。2)转运蛋白将土壤养分转运至菌丝内的效率(Bonfante & Genre, 2010; 田磊等, 2016; Jiang *et al.*,

2017; Zhang *et al.*, 2018b)。

1.4 本地植物菌根真菌群落组成

入侵植物除了影响本地植物菌根真菌的侵染率、根内和根外菌丝的结构与功能外, 还可能改变其菌根真菌的组成。有研究发现, 外来植物入侵会使本地植物原有的AMF被其他种类的AMF替代(Hawkes *et al.*, 2006; Barto *et al.*, 2011; Jordan *et al.*, 2011), 或有部分AMF被替代(Burke, 2008)。Zhang等(2018c)研究发现, 外来入侵植物提高了本地植物根际土微生物群落中AMF所占比例, 这可能会提高本地植物菌根真菌中AMF比例。但也有研究发现, 外来植物入侵未改变本地植物的菌根真菌群落组成(Koch *et al.*, 2011; Meinhardt & Gehring, 2012), 如凤仙花入侵一年后本地植物菌根真菌组成未发生变化(Gaggini *et al.*, 2018)。张海艳(2019)研究发现, 一方面同一本地植物菌根真菌群落组成对不同入侵植物的响应不一致, 如入侵植物*X. strumarium*改变了黄花蒿根内菌根真菌群落组成, 而入侵植物*S. rostratum*则没有影响; 另一方面同一入侵植物对不同本地植物菌根真菌群落组成的影响也不一致, 如入侵植物*X. strumarium*改变了黄花蒿的菌根真菌群落组成, 但未改变本地植物狗尾草的菌根真菌群落组成。这表明本地植物菌根真菌群落组成对入侵植物的响应既与本地植物自身特性有关, 也与入侵植物种类有关。但目前有关入侵植物对本地植物菌根真菌群落组成影响的研究大多数集中在AMF植物, 我们对本地植物EMF和其他类型菌根真菌群落组成如何响应入侵植物的认识十分有限。

上述这些研究中, 本地植物菌根真菌群落组成都是通过变性梯度凝胶电泳(DGGE)(肖龙敏, 2018)、磷脂脂肪酸(PLFA)(席浩, 2019)和高通量测序(蒋玉玲等, 2019)等方法测定的。除此之外, 菌根真菌也可以按照其功能进行分类。例如, Kiers等(2011)将菌根真菌分为合作型真菌和寡合作型真菌, 合作型真菌*Glomus intraradices*对宿主的养分回报效率(真菌转运给植物的养分/真菌接受植物的碳之比)高于寡合作型真菌*Glomus aggregatum*。由于合作型真菌对宿主具有更高的养分回报率, 我们推测共生真菌中以合作型真菌为主的本地植物可能受外来植物的影响更大。尽管这种推测有待验证, 但我们认为这种基于真菌功能的真菌群落组成研究是未来研究中值得关注的方向, 这将有助于我们深入

了解入侵植物对菌根真菌的影响及外来植物入侵机制。

1.5 本地植物菌根真菌网络

同种植物常常能与多种菌根真菌共生,即使是单个根尖也往往被多个特定的菌根真菌类群感染(Sepp *et al.*, 2019)。这些菌根真菌之间由于不同强度和方向(包括正和负)的相互作用形成复杂的菌根真菌网络,该网络的连接性、模块性往往用来评判真菌网络结构的稳定性(图2)(Bennett *et al.*, 2013; de Vries & Wallenstein, 2017)。Sepp等(2019)将植物分为专性菌根植物(只依赖菌根吸收养分)和兼性菌根植物(除菌根外还通过其他方式吸收养分,如豆科植物的根瘤),他们发现专性菌根植物真菌网络的连接性更强。理论上,不同的菌根真菌可能构成不同的网络结构,而相同的菌根真菌群落组成也可能构成不同的网络结构。目前研究者往往关注胁迫环境对菌根真菌网络的影响以及同一环境下不同菌根类型的真菌网络之间的差异(Toju *et al.*, 2018; 杨思琪等, 2019)。例如, de Vries等(2018)发现, 干旱情况下真菌共生网络的复杂性和稳定性均有所降低; 在AMF和EMF植物共存的系统中, AMF网络与宿主植物的连接性更强, EMF网络与宿主植物的专一性(共生伙伴偏好性)更强(杨思琪等, 2019)。菌根真菌网络的研究方兴未艾, 而菌根真菌网络对入侵植物响应的研究尚属空白。由于入侵植物会显著改变本地植物菌根真菌的组成和相对多度(Zhang *et al.*, 2018c; 张海艳, 2019), 我们推断这些都会影响到真菌网络的连接性和模块性; 由于EMF对环境干扰的抗性强于AMF, 我们预测入侵植物对AMF网络结构的影响高于EMF网络。当然这里的预测仅仅是一些初步的想法, 未来还需要全面和深入的实验验证。

1.6 本地植物非菌根真菌

外来植物入侵不仅会影响本地植物菌根真菌, 也会影响其非菌根真菌(NMF), 包括致病真菌、寄生真菌、一些对植物可能无害的内生真菌以及在极端环境下可以帮助植物生存的有益内生菌(Hawkes *et al.*, 2006; Meinhardt & Gehring, 2012; Hill *et al.*, 2019)。有研究根据微生物之间的互作关系将本地植物根内微生物分为两类: 促进型和拮抗性。促进型微生物的存在能为其他微生物甚至是病原菌的感染提供便利条件, 而拮抗性微生物不仅会抑制互惠微生物, 还会抑制致病菌的入侵(Li *et al.*, 2019)。菌根

图2 菌根真菌网络结构概念图(改自de Vries和Wallenstein (2017))。不同颜色的圆圈表示不同的模块(如不同种类的丛枝菌根真菌), 各模块的连接点用红色圆圈表示, 线粗细表示连接性强弱, 黑线表示正相关, 蓝线表示负相关。

Fig. 2 A conceptual diagram of the mycorrhizal fungal network structure (adapted from de Vries & Wallenstein, 2017). Circles with different colors indicate different modules (i.e., different mycorrhizal fungal communities). Module connections are indicated by red circles. Thicker lines indicate stronger mycorrhizal fungi connections. The black lines indicate positive correlations, and the blue lines indicate negative correlations.

真菌与NMF之间也存在拮抗关系(Bufford *et al.*, 2019; Sarkar *et al.*, 2019)。例如, 根中AMF感染增加会使NMF的感染下降(Maherali & Klironomos, 2007; Liang *et al.*, 2015; Barnes *et al.*, 2018); EMF也能有效抵抗病原菌的感染(Chen *et al.*, 2019)。

Hawkes等(2006)发现, 外来植物旱雀麦(*Bromus tectorum*)入侵使两种本地植物的AMF丰富度降低, 而NMF所占比例增加。如果这些NMF属于致病菌, 那么旱雀麦入侵将使本地植物的生长受到双重抑制: 一是AMF丰富度减少带来植物养分吸收的降低; 二是致病真菌所占比例增加对植物的危害(Meinhardt & Gehring, 2012)。这说明入侵植物可以通过影响本地植物NMF间接影响菌根真菌与本地植物生长间的关系(图3)。因此, 入侵植物不仅可以直接影响本地植物菌根真菌的组成和丰富度等, 还可以通过改变NMF中有益真菌与有害真菌的组成或/和比例, 进而间接影响本地植物菌根真菌的感染率、菌根内部真菌结构、根外菌丝、真菌群落组成及真菌网络等(图3)。在研究入侵植物对本地植物菌根真菌影响时, 我们应充分考虑到NMF的变化, 并查明这些NMF的“身份”(致病真菌、寄生真菌、无害真菌, 还是有益真菌)。

2 入侵植物影响本地植物菌根真菌的机制

2.1 生态机制

入侵植物可以通过多种生态机制影响本地植物

图3 外来入侵植物对本地植物菌根真菌影响的概念图(改自Grove等(2017a))。实线箭头表示改变; 虚线箭头表示存在未知的关系。

Fig. 3 Conceptual illustration showing how invasive plants affect the symbiotic mycorrhizal fungi in native plant roots (adapted from Grove *et al.*, 2017a). Solid arrows indicate change; dotted arrows indicate possible relationships.

的菌根真菌(Grove *et al.*, 2017a), 目前国内外相关研究主要集中在物种竞争、土壤养分变化和化感作用3个方面。如表2所示, 入侵植物往往具有较强的资源(光和养分等)竞争能力。例如, *Solanum carolinense*有着强大的无性繁殖能力可以快速扩散(魏雪苹等, 2020)。入侵植物还可以抑制本地植物光合作用(Funk & Vitousek, 2007; van Kleunen *et al.*, 2010; Huang *et al.*, 2020), 光合产物的减少可能会抑制本地植物菌根真菌侵染(Fellbaum *et al.*, 2012)(图3)。入侵植物往往具有较强的养分竞争力和大量的根系分泌物(Liao *et al.*, 2008; Grove *et al.*, 2017b; 韩雪等, 2020; Huang *et al.*, 2020)(表2)。入侵植物还可以通过凋落物和根系分泌物等改善和提高土壤养分(Zhang *et al.*, 2018b; Pérez Castro *et al.*, 2019), 形成植物和土壤之间的正反馈(Zhang *et al.*, 2018c, 2020; Zhao *et al.*, 2019, 2020), 进而降低本地植物(如*Solidago decurrens*和*Andropogon gerardii*)菌根真菌的感染率, 改变菌根真菌的群落组成(陆建忠等, 2005; Johnson *et al.*, 2010)(图3)。入侵植物还可以通过化感作用对本地植物菌根真菌产生直接影响(Thorpe *et al.*, 2009; Soudzilovskaia *et al.*, 2015)(图

3)。入侵植物产生的化感物质(如类黄酮和芥子油苷等)能抑制菌根真菌孢子萌发、生长和侵染, 从而抑制依赖这些真菌的本地植物的生长(Callaway & Aschehoug, 2000; Callaway & Ridenour, 2004; Prati & Bossdorf, 2004; Callaway *et al.*, 2008)。这些化感物质也可能通过抑制本地植物的生长(Zheng *et al.*, 2015), 从而降低植物对菌根真菌碳的供应, 进而抑制菌根真菌侵染。此外, 外来植物所分泌的化感物质可能也会影响本地植物的非菌根真菌, 进而对本地植物菌根真菌产生间接影响(图3)。实际上, 本地植物菌根真菌的变化可能是多种机制共同作用的结果(Grove *et al.*, 2017a, 2017b)。不同入侵植物对本地植物菌根真菌的影响机制可能不同, 而不同本地植物菌根真菌对每种机制的响应可能也有差异, 这使得不同外来植物入侵对不同本地植物菌根真菌的影响可能呈现出不同的趋势。

2.2 分子机制

植物与菌根真菌形成共生关系是一个复杂的信号转导过程。目前已经证实, 丛枝菌根的形成始于根系与AMF之间的信号交流(Gutjahr & Parniske, 2013; Tian *et al.*, 2019)。首先, 根系(如, 莲刺参

表2 外来植物入侵的生态机制
Table 2 Ecological mechanisms of alien plant invasion

生态机制 Mechanism of ecology	举例 Example	参考文献 Reference
物种竞争 Species competition	与农作物(如高粱(<i>Sorghum bicolor</i>)、玉米(<i>Zea mays</i>))相比, 入侵植物 <i>Parthenium hysterophorus</i> 具有快速早期生长的能力。 Compared with crops (such as <i>Sorghum bicolor</i> and <i>Zea mays</i>), the invasive plant <i>Parthenium hysterophorus</i> can grow much more rapidly in their early stage.	Bajwa <i>et al.</i> , 2016
	比较夏威夷19对入侵植物和本地植物的资源利用效率, 发现入侵植物具有较高的碳同化率、光利用效率、瞬时氮利用效率和瞬时能量利用效率。 Comparing the resource utilization efficiency for 19 paired invasive-native plants in Hawaii, invasive plants are observed to have higher carbon assimilation rate, light use efficiency, instantaneous nitrogen and energy use efficiency.	Funk & Vitousek, 2007
	比较47对入侵植物和非入侵植物对草食性动物的抵抗能力及养分含量发现, 入侵植物拥有更高的叶氮含量, 受到食草动物的损伤较小。 Comparisons among 47 paired invasive and non-invasive plants for leaf herbivore-resistance and nutrient content show that invasive plants have higher leaf nitrogen content and less damage by herbivores.	Huang <i>et al.</i> , 2020
	比对125种入侵植物和196种非入侵植物的生理性状发现, 入侵植物在生长率、养分分配及抗逆性更有优势。 Comparing physiological traits of 125 invasive with plants 196 non-invasive plants show that invasive plants have more advantages in growth rate, nutrient allocation and stress resistance.	van Kleunen <i>et al.</i> , 2010
	外来植物 <i>Solanum carolinense</i> 具有较强的抗寒能力和无性繁殖能力。 Exotic plant, <i>Solanum carolinense</i> , has strong ability for cold resistance and asexual reproduction.	Wei <i>et al.</i> , 2020
化感物质 Allelochemical	气候变暖及氮沉降的增加可以增强入侵植物 <i>Solidago canadensis</i> 叶片的资源获取能力。 Climate warming and increased nitrogen deposition can enhance leaf resource acquisition of an invasive plant, <i>Solidago canadensis</i> .	Zhou <i>et al.</i> , 2019
	入侵植物白羊草(<i>Bothriochloa ischaemum</i>)的渗滤液抑制本地植物 <i>Andropogon gerardii</i> 和 <i>Schizachyrium scoparium</i> 发芽及生长。 The leachate of an invasive plant, <i>Bothriochloa ischaemum</i> , inhibits germination and growth of the native plants, <i>Andropogon gerardii</i> and <i>Schizachyrium scoparium</i> .	Greer <i>et al.</i> , 2014
	入侵植物水烛(<i>Typha angustifolia</i>)根系分泌的酚类物质抑制了本地植物 <i>Bolboschoenus fluviatilis</i> 的生长发育。 Phenolic compounds secreted by roots of an invasive plant, <i>Typha angustifolia</i> , inhibit growth and development of a native plant, <i>Bolboschoenus fluviatilis</i> .	Jarchow & Cook, 2009
	<i>Solidago canadensis</i> 入侵分泌的化感物质抑制了本地植物莴苣(<i>Lactuca sativa</i>)种子萌发和幼苗生长。 Allelochemicals secreted by the invasion of <i>Solidago canadensis</i> inhibit seed germination and seedling growth of a native plant, <i>Lactuca sativa</i> .	Hu <i>et al.</i> , 2020
	外来植物 <i>Solanum carolinense</i> 含有龙葵碱及草酸盐结晶。 The exotic plant <i>Solanum carolinense</i> contains solanine and oxalate crystals.	Wei <i>et al.</i> , 2020
土壤养分变化 Soil nutrient variation	<i>Parthenium hysterophorus</i> 可以分泌帕台宁、咖啡酸、香草酸等化感物质帮助自身入侵。 <i>Parthenium hysterophorus</i> can secrete parthenin, caffeic acid, vanillic acid and other allelochemicals to facilitate its invasion.	Shi & Adkins, 2018
	氮沉降会增强 <i>S. canadensis</i> 入侵初期分泌的化感物质对本地植物莴苣种子萌发和幼苗生长的抑制程度。 Nitrogen deposition can enhance the inhibition of the allelochemicals secreted by <i>S. canadensis</i> at its initial invasive stage on seed germination and seedling growth of a native plant, <i>Lactuca sativa</i> .	Hu <i>et al.</i> , 2020
	分析94篇文章发现, 入侵植物增大了植物、土壤和土壤微生物中的碳和氮库大小。 Analysis of 94 published papers show that invasive plants increase the size of carbon and nitrogen pools in plants, soils and soil microorganisms.	Liao <i>et al.</i> , 2008
	与本地植物 <i>Artemisia californica</i> 、 <i>Salvia mellifera</i> 、 <i>Salvia apiana</i> 、锦鸡儿(<i>Calochortus splendens</i>)和 <i>Dichelostemma capitatum</i> 相比, 外来植物 <i>Centaurea stoebe</i> 、 <i>Hirschfeldia incana</i> 和 <i>Bromus madritensis</i> 可以通过加快凋落物分解改善土壤养分。 Compared with native plants such as <i>Artemisia californica</i> , <i>Salvia mellifera</i> , <i>Salvia apiana</i> , <i>Calochortus splendens</i> and <i>Dichelostemma capitatum</i> , exotic plants, like <i>Centaurea stoebe</i> , <i>Hirschfeldia incana</i> and <i>Bromus madritensis</i> , can increase soil nutrient level by increasing litter decomposition.	Pérez Castro <i>et al.</i> , 2019
	入侵植物 <i>Mikania micrantha</i> 分泌的化感物质绿原酸和β-石竹烯加快了土壤有机氮的矿化过程。 Allelochemicals secreted by the invasive plant, <i>Mikania micrantha</i> , such as chlorogenic acid and β-caryophyllene accelerate mineralization of soil organic nitrogen.	Yu <i>et al.</i> , 2020
	入侵植物通过凋落物改变了根际微生物土壤群落和养分循环, 形成植物-土壤正反馈调节。 Invasive plants can form a positive plant-soil feedback via its litter decomposition which could change rhizosphere soil microbial communities and nutrient cycling.	Zhang <i>et al.</i> , 2018c
	杂草 <i>Coryza canadensis</i> 入侵的土壤中有有效氮和有机质含量增加。 The content of available nitrogen and organic matter increases in the soil invaded by <i>Coryza canadensis</i> .	Zhang <i>et al.</i> , 2020
	与非入侵地土壤相比, <i>Eupatorium catarium</i> 入侵后土壤氮含量提高4.32 mg·kg ⁻¹ 。 Compared with non-invasive soils, soil nitrogen content increases by 4.32 mg·kg ⁻¹ after invasion by <i>Eupatorium catarium</i> .	Zhao <i>et al.</i> , 2019
	<i>Ambrosia trifida</i> 在入侵地的土壤-植物反馈高于原产地。 <i>Ambrosia trifida</i> has a greater plant-soil feedback in invaded ranges than that in its native ranges.	Zhao <i>et al.</i> , 2020

(*Lotus japonicus*)分泌独脚金内酯等信号分子, 促进AMF孢子萌发和菌丝分枝, 增加菌丝与根系接触的概率(Akiyama *et al.*, 2005)。之后, 从枝菌根真菌分泌多种信号分子(即菌根因子, 如LCOs、CO4/CO5和PsMiSSP10b), 被根系相应的受体识别后激活钙离子信号通路, 进而形成侵染线, 激活菌根真菌的侵染过程(Maillet *et al.*, 2011; Martin *et al.*, 2017; Plett *et al.*, 2020)(图4)。例如, 水稻AMF分泌脂壳寡糖(LCOs)和短链壳寡糖(CO4/CO5)因子, 能被水稻中LysM受体样激酶的异源体(包括OsMYR1/OsLYK2和OsCERK1)识别(He *et al.*, 2019)。但在豆科植物中, AMF释放的LCOs和CO4/CO5因子, 被NFR1/LYK3识别(Zhang *et al.*, 2015)。在上述过程中, 菌根真菌除了产生小分子分泌蛋白(MiSSPs)来识别宿主之外, 也会产生植物细胞壁分解酶(PCWDEs)(Martin *et al.*, 2008, 2017; Kohler *et al.*, 2015)来破坏宿主植物的细胞壁, 为共生关系的建立扫除“障碍”。而根与菌根真菌之间关系的核心在于两者对于碳(脂类和糖)和养分的交换(Jiang *et al.*, 2017), 这种物质交换过程涉及一系列脂类合成酶以及养分转运蛋白。例如, 丝裂原活化蛋白激酶(MAPKs)在植物和AMF信号沟通中起到重要作用; STR转运蛋白负责紫花苜蓿(*Medicago truncatula*)中脂肪酸的转运(Bonfante & Genre, 2010; 田磊等, 2016; Bravo *et al.*, 2017)。入侵植物可以通过影响酶和这些转运蛋白干

扰本地植物菌根真菌侵染进而影响本地植物生长。如Bravo等(2017)发现, 紫花苜蓿根系脂质合成酶(*FatM*和*RAM2*)突变后, AMF的侵染率降低, 这两个酶调控植物对菌根真菌所需脂质的供应。因此, 对根与菌根真菌物质交换过程的影响也可能是入侵植物干扰本地植物菌根真菌的一个重要的分子机制, 是未来研究中值得进一步关注的领域。

3 入侵时间的影响

已有研究证实外来植物的成功入侵受入侵时间的影响(Catford *et al.*, 2019)。在入侵植物对本地植物菌根真菌影响的相关研究中, 大多数研究都是在某个特定的入侵时间或入侵阶段进行的, 不同入侵时间和阶段的对比还较缺乏(Grove *et al.*, 2017a), 更不了解外来植物入侵对本地植物菌根真菌的影响是否也具有时间效应。另一方面, 相关研究中入侵时间序列的跨度较短。例如, Ruckli等(2016)比较研究了*I. glandulifera*入侵3和15个月时, 本地EMF植物青冈(*Fagus sylvatica*)的菌根真菌侵染率分别降低33%和66%。入侵植物的这种影响在一定入侵年限之后可能会有较大改变(Lankau *et al.*, 2009; Dostál *et al.*, 2013)。Grove等(2017b)研究发现, 入侵植物*Cytisus scoparius*对本地植物花旗松(*Pseudotsuga menziesii*)菌根真菌的影响在入侵3–31年间保持稳定。不过研究者也承认, 入侵更长时间之后

图4 植物与菌根真菌共生关系分子模式图(参考Martin等(2017))。根系分泌信号分子(①), 促进土壤中丛枝孢子(②)的萌发和菌丝分枝; AMF分泌的菌根因子(③)被根系上的受体(④)识别并激活钙离子信号通路(⑤), 进而形成侵染线(⑥); 菌根真菌菌丝侵入根细胞后, 与根系进行碳-养分交换, 这中间涉及一系列酶和转运蛋白(⑦)的共同作用。

Fig. 4 Conceptual model for the symbiotic relationship between plants and mycorrhizal fungi (adapted from Martin *et al.*, 2017). Roots secrete signaling molecules (①) promote germination of AMF spores (②) and mycelium branching in the soil; mycorrhizal factors secreted by AMF (③) are recognized by receptor proteins in root cells (④), and then activate the calcium signaling pathway (⑤) to initiate formation of the mycorrhizal fungi (⑥). After that, the carbon and nutrient exchange between mycorrhizae and root cells also requires a series of enzymes and transport proteins in the root-mycorrhiza interface (⑦).

*C. scoparius*的这种影响也可能减弱。随着入侵时间延长,本地植物与土壤微生物会对入侵植物做出适应性响应,从而消除入侵植物带来的负面影响(类延宝等,2010)。我们推测,随着入侵时间的持续,外来植物对本地植物菌根真菌的影响会减弱,且入侵植物影响菌根真菌的机制,如前述的植物竞争(Hawkes, 2007; Yelenik & D'Antonio, 2013)、土壤养分(Grove *et al.*, 2017b)及化感作用(Lankau *et al.*, 2009; Li *et al.*, 2017; 胡文杰等, 2020)等均会随入侵时间的延长而发生变化,这些变化的方向和程度的差异,最终可能会导致入侵的时间效应在入侵种间出现差异。我们建议通过连年栽培入侵植物,驯化土壤以构建入侵时间序列(Flory & D'Antonio, 2015)。这种连年栽培实验,一方面可以直接观测入侵植物种群的长期动态;更重要的是,我们可以系统地检验入侵植物对本地植物菌根真菌影响的上述几种机制(竞争、化感以及对土壤养分的调节等)的机制的作用及动态变化。这些研究能够为不同入侵阶段的外来植物的防控和管理提供针对性的措施。

4 展望

外来植物通过干扰本地植物菌根真菌获得竞争优势是一种重要的入侵机制。尽管如此,相对于其他入侵机理,我们对外来植物入侵与本地植物菌根真菌间关系的认识仍然十分匮乏(Jordan *et al.*, 2011; Gaggini *et al.*, 2018; 孙建茹等, 2019)。这主要表现在:1)目前入侵植物对本地植物菌根真菌影响的研究结果存在较大差异。一方面可能是由于所选植物类群有限选材范围较为狭窄(Allsopp & Holmes, 2001; Endresz *et al.*, 2013; Lekberg *et al.*, 2013);另一方面菌根内部结构、根外菌丝相关功能蛋白和真菌网络结构的研究相对较少,还无法得到普遍结论(Toju *et al.*, 2018; Lugli *et al.*, 2019; Luo *et al.*, 2019);此外研究者们经常忽略非菌根真菌(如病原菌)在外来植物入侵中起到的作用(Hawkes *et al.*, 2006; 初亚男等, 2018)。2)相对于生态机制,入侵植物如何影响本地植物菌根真菌与宿主根系的相互识别、侵染及养分交换的分子机制研究较少(He *et al.*, 2019; Stefanowicz *et al.*, 2019)。3)我们还不清楚外来植物长时间入侵时本地植物菌根真菌的响应(Dombrowski *et al.*, 2017; Grove *et al.*, 2017b)。

此外,我们认为在入侵植物影响本地植物菌根

真菌相关研究中,未来还应该重点关注(但不仅仅局限于)以下几个方面:1)全球变化(如全球变暖、氮沉降、干旱、火灾及虫害等)如何调节外来植物对本地植物菌根真菌的影响,尤其需要关注多种全球变化因子在多个水平时的交互作用。2)同时关注入侵植物对本地植物菌根真菌影响的多种生态机制(资源竞争、化感作用和土壤养分调节等)和分子机制(菌丝对土壤养分的吸收、转运以及和植物之间进行的碳-养分交换),以及这些机制之间的相互关系。3)以往的研究往往局限于有限的空间范围和较短的时间,未来的研究更需要探究在较大的时间(数十年甚至上百年)和空间(热带、亚热带和温带)尺度上研究入侵植物对本地植物菌根真菌影响的变化趋势以及相应的生态和分子机制。

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