•综述•

外来入侵植物的根系觅养行为研究进展

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摘要: 土壤养分分布具有高度空间异质性, 植物的根系觅养行为是其在土壤养分异质性的一种适应。不同植物为了适应养分异质性会产生不同的根系觅养行为, 通过调整自身的根系觅养范围、觅养精度和觅养速度来更好地吸收利用土壤中的养分。外来植物与本地植物的竞争是决定其成功入侵的重要因素, 土壤养分等环境因素会影响它们之间的竞争关系。近年来, 外来入侵植物的觅养行为逐渐受到人们的关注, 关于入侵植物根系觅养行为的研究成果陆续出现: (1) 总体来看, 外来入侵植物具有较强的根系觅养能力, 但根系觅养范围与觅养精度之间的权衡关系还不确定; (2) 营养异质性会影响入侵植物与本地植物之间的竞争, 反过来, 二者之间的竞争也会影响根系觅养行为对营养异质性的响应; (3) 丛枝菌根真菌(arbuscular mycorrhizal fungi, AMF)能够提高入侵植物的根系觅养能力, 外来植物入侵能够改变入侵植物对AMF的偏好性, 形成AMF对入侵的正反馈作用, 而本地植物与AMF的相互作用也会影响入侵植物的竞争力。未来还应加强营养异质环境下种间竞争和AMF共生对入侵植物根系觅养行为的影响机制研究, 以及全球变化背景下入侵植物根系觅养行为的变化与机制方面的研究, 可以更深入地认识外来植物的觅养行为在其成功入侵中的作用, 并为利用营养调控来防控入侵植物提供理论依据。

关键词: 根系觅养; 外来入侵植物; 营养异质性; 丛枝菌根真菌; 竞争; 根系分布

Advances in root foraging behavior of exotic invasive plants

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Abstract: Nutrient distribution within soils is highly spatially heterogeneous, forcing plant root foraging behavior to adapt to heterogeneous soil nutrients. By adjusting root foraging scales, foraging precision and rate, plants can maximize soil nutrients. Successful invaders are heavily influenced by soil nutrients and other environmental conditions (e.g. water content, light, etc.) as successful invasion depends on the successful competitive interaction of an exotic species with a native species. In recent years, the foraging behavior of exotic invasive plants has attracted more attention, and studies are increasing worldwide. To date, foraging behavior studies have found: (1) Invasive plants have increased root foraging abilities compared to native plants, although the trade-off between foraging scale and precision are uncertain. (2) Soil nutrient heterogeneity influences the competitive outcome between invasive and native plants, as competition alters root foraging strategy. (3) Arbuscular mycorrhizal fungi (AMF) facilitate root foraging of invasive plants, and invasive plants experience positive feedbacks with invasion by altering their AMF preference. Additionally, the interaction between AMF and native plants can influence the competitive ability of invasive plants. Further studies are necessary to understand the relationship between interspecific competition and AMF on root foraging behavior of invasive plants in heterogeneous nutrient conditions. Due to global change, root foraging strategies and related mechanisms of invasive species may be altering. Increased research on root foraging behavior in successful exotic plant invasions can provide a greater understanding of these mechanisms and a theoretical basis for control and management of invasive plants through nutrient regulation.

Key words: root foraging; exotic invasive plants; soil nutrient heterogeneity; arbuscular mycorrhizal fungi; competition; root distribution

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土壤养分分布具有高度的空间异质性(Farley & Fitter, 1999; Levine et al, 2016), 植物为了适应土壤养分异质性, 一般会通过根系形态和生理上的一系列可塑性变化来探寻、获取、利用养分, 即植物根系的觅养行为(foraging behavior) (Hutchings & de Kroon, 1994)。植物根系的觅养行为主要包括根系的觅养范围(foraging scale)、觅养精度(foraging precision)与觅养速度(foraging rate) (Rajaniemi & Reynolds, 2004; de Kroon & Mommer, 2006)。觅养范围是指植物根系在富营养斑块中延伸的广度, 通常用富营养斑块内根系的生物量或根系密度(单位体积土壤中根的长度)表示; 觅养精度指植物根系对不同斑块的选择性, 通常用富营养斑块和贫营养斑块中根系生物量或根系密度的比值来表示; 觅养速度指根系到达富营养斑块的时间(Rajaniemi & Reynolds, 2004)。

植物根系的觅养行为主要是由激素调控。例如在低磷(P)环境下, 拟南芥(*Arabidopsis thaliana*)通过诱导生长素合成关键酶的表达来增加生长素的合成, 进而调控根毛伸长及次生根的生长实现植物根系觅养(Bhosale et al, 2018); 在缺氮(N)条件下, 添加硝酸盐能瞬时上调植物体内生长素受体信号的表达, 增加初生根尖端的生长素累积和敏感性, 促进植物根生长和养分吸收(Giehl & von Wiren, 2014)。这些研究表明, 植物在营养缺乏的环境中主要通过调节生长素的合成来调控根系觅养行为, 进而达到吸收养分的目的。

外来生物入侵被认为是仅次于生境破坏导致全球生物多样性下降的第二大因素, 严重威胁着生态系统健康(Ehrenfeld, 2010; Vilà et al, 2011)。外来植物之所以能够成功入侵, 一方面与其生长速度快、繁殖能力强、竞争力强、化感作用强以及高效的资源捕获与利用能力(Callaway & Aschehoug, 2000; Funk & Vitousek, 2007; van Kleunen et al, 2010)等特性有关, 另一方面与入侵地的养分、温度、光照等环境因素有关(Bradley et al, 2010; Zhang et al, 2017b; Broadbent et al, 2018)。入侵物种到达新生境后, 一般先占领条件较为适宜的环境, 成功建群后再逐渐往外扩散。

高的表型可塑性是许多外来植物成功入侵的原因之一(Richards et al, 2016)。面对土壤营养异质性环境, 外来入侵植物通常能够更快地将根生物量

分布在富营养斑块, 以提高其营养吸收能力, 优先获取资源并降低其他物种的可利用资源, 从而获得生长优势并成功入侵(Drenovsky et al, 2008; James et al, 2009)。近年来, 人们越来越关注外来入侵植物的根系觅养行为(Keser et al, 2014; Chen et al, 2018), 本文主要从外来入侵植物的根系觅养特性及权衡关系(trade-off)、入侵植物的直接根系觅养行为与竞争、广义的根系觅养行为(丛枝菌根真菌(arbuscular mycorrhizal fungi, AMF)与植物的养分吸收) 3个方面来综述相关研究进展, 并讨论未来的研究方向。

1 外来入侵植物的根系觅养特性及权衡关系

土壤养分异质性给外来入侵植物提供了更多利用资源的机会, 有利于其入侵(Davis & Pelsor, 2001; Melbourne et al, 2007)。Drenovsky等(2008)比较了4种本地植物和4种外来入侵植物的根系觅养能力, 结果发现入侵植物的地上、地下生物量是本地植物的2–3倍, 且在营养异质性处理中入侵植物的根系密度高达60 km/m³, 显著高于本地植物(约30 km/m³); 而在均质营养条件下, 入侵植物的根系密度为30 km/m³左右, 不考虑根生物量很小的2种本地植物, 其余2种本地植物的根系密度也只有15 km/m³左右, 远低于入侵植物。James等(2009)研究了3种入侵非草本植物、3种本地丛生禾草与3种本地非草本植物的根系觅养行为, 结果显示入侵植物的根系密度大于本地的草本和非草本植物, 即入侵植物根系觅养范围较大。无论是在营养异质性土壤还是在营养均质性土壤中, 入侵植物的氮吸收速率都高于本地植物。他们认为, 入侵植物的氮吸收速率、相对生长速率和根生物量之间存在正相关关系, 但与根系觅养精度不存在明显的正相关关系(James et al, 2009)。这在一定程度上说明在营养异质性的土壤中, 入侵植物的氮吸收速率与根生物量能够同步增加, 进而促进植物根系觅养范围的增加。

Keser等(2014)利用线性混合模型分析了菊科、伞形科、禾本科、玄参科、唇形科和石竹科的6对入侵植物和外来非入侵植物对异质性土壤的不同反应。研究发现, 异质性土壤中入侵植物根系总生物量要高于外来非入侵植物, 且入侵植物在营养异质性条件下富营养斑块中的根生物量显著高于贫营养斑块, 而外来非入侵植物的根生物量分配则没有显著变化。近期研究发现, 外来入侵植物薇甘菊

(*Mikania micrantha*)和白花鬼针草(*Bidens pilosa* var. *radiata*)表现出较大的觅养范围和较低的觅养精度,而与之伴生的本地植物鸡屎藤(*Paederia scandens*)、夜香牛(*Vernonia cinerea*)则表现出较高的觅养精度和较小的觅养范围(Chen et al, 2018)。然而, Keser等(2015)分析了24种入侵植物和外来非入侵植物的根系觅养特征,发现入侵植物的觅养范围与外来非入侵植物没有显著差别,而用根直径作为根系觅养特性的分析指标时,入侵植物比非入侵植物具有更强的根系觅养能力,这说明采用不同的指标对根系觅养特性进行分析计算有可能会得到不同的结论。

一般来说,植物根系觅养范围和觅养精度之间存在权衡关系,植物会根据自身与环境的情况来选择更适宜植物生长的根系觅养策略(Campbell et al, 1991)。Kembel等(2008)用整合分析(meta-analysis)的方法研究发现,当物种数量比较少时,觅养范围和觅养精度之间呈现明显的负相关关系(即存在权衡关系),而当物种数量较多时,二者之间的相关关系消失,说明物种数量的多少会影响觅养范围和精度之间的权衡关系。然而, Grime (2007)认为植物根系的觅养范围与觅养精度之间并不存在权衡关系。近期研究发现,在营养异质性环境下,入侵植物与本地植物之间存在“觅养范围-觅养精度”的权衡关系:入侵植物薇甘菊和白花鬼针草的根系觅养范围较大,精度较小,本地植物夜香牛与鸡屎藤则刚好相反(Chen et al, 2018)。

总体来看,有些入侵植物是通过较大的觅养范围来提高养分的吸收能力从而达到快速生长,有些通过提高觅养精度来增强与本地植物竞争养分的能力,有些入侵植物的觅养范围和觅养精度都优于本地植物。植物根系的觅养范围与觅养精度之间是否存在权衡关系目前还不清楚,入侵植物与本地植物的觅养范围与觅养精度的权衡关系是否有差异值得关注,需要进一步的研究。

2 入侵植物的根系觅养行为及其竞争能力

入侵植物与本地植物之间的竞争关系是决定外来植物能否成功入侵的关键(Levine et al, 2004; 万方浩等, 2011; Golivets & Wallin, 2018)。外来入侵植物直接与本地植物竞争养分、水分、光照等资源(Lopez-Zamora et al, 2004; Gioria & Osborne, 2014; Hulvey & Teller, 2018),而养分、光照、温度等环境

因素也会影响入侵植物和本地植物之间的竞争(Suding et al, 2004; Bradley et al, 2010; Verlinden et al, 2014; Broadbent et al, 2018)。

土壤营养异质性会影响植物间的竞争,同时植物也能根据土壤营养分布状况与邻体植物的信息来调整自身的根系分布(Cahill et al, 2010; Mommer et al, 2012)。Zhou等(2012)通过对空心莲子草(*Alternanthera philoxeroides*)的研究发现,土壤营养异质性并没有改变其种内竞争的强度,这可能是因为同种植物相互识别并且避免种内竞争,在进化上更为有利。单独种植的苘麻(*Abutilon theophrasti*)根系分布对土壤营养的分布没有响应,但是与同种植物共植且两植株之间存在富营养斑块时,它们的根系会倾向于重叠,进而加剧其种内竞争(Cahill et al, 2010)。黑麦草(*Lolium perenne*)与草地早熟禾(*Poa pratensis*)的根系觅养行为只有在两者竞争时才显现出来,单独种植时觅养行为并不明显(Hodge et al, 1999; Hodge, 2004, 2006)。

在营养异质性的土壤中,两种植物竞争能力的相对大小通常会影响到其根系觅养行为:竞争能力较强的植物其觅养行为并不受土壤营养异质性的影响,但竞争能力较弱的植物在存在竞争时,会减少富营养斑块中的根系分布,而增加贫营养斑块中的根系生物量及营养吸收速率,以补偿富营养斑块中的高竞争压力(Mommer et al, 2012)。

可见,营养异质性会影响植物之间的竞争关系,反过来邻体植物的竞争也会影响入侵植物对营养异质性的响应,进而影响到其根系的觅养行为。营养异质性条件下植物根系觅养行为与植物竞争之间的相互作用更值得关注。

3 广义的根系觅养行为——AMF与植物的养分吸收

3.1 AMF促进植物的养分吸收能力

大多数陆地植物(尤其是草本植物)能与AMF共生(Smith & Read, 2008; 何新华等, 2012; van der Heijden et al, 2015), AMF不仅可以帮助植物捕获磷(van der Heijden et al, 2003; Hodge, 2004; Cheng et al, 2019),还可以帮助植物捕获氮(Leigh et al, 2009)和钾(K)等养分(Estrada et al, 2013)。研究发现,接种AMF后植物体内的钾含量显著高于未接种AMF的植物(Estrada et al, 2013), AMF处理的植株体内的磷

和氮含量分别是未受AMF处理的25倍和10倍(van der Heijden et al, 2003)。尿素循环代谢臂(catabolic arm of the urea cycle)可以使真菌在碳损失最小的条件下将氮转移到宿主植物,说明植物通过AMF共生能够有效地将土壤中大量的氮转移到根系(Govindarajulu et al, 2005)。AMF还可以从有机物质中捕获氮并将其转移到植物体中(Leigh et al, 2009)。

3.2 AMF在入侵植物根系觅养中的作用

外来入侵植物与土著AMF共生,有助于其对氮和磷的吸收,从而有利于其入侵(Reinhart & Callaway, 2006; Harner et al, 2010; 于文清等, 2012; Zhang et al, 2017a)。Bunn等(2015)用整合分析的方法研究了67篇论文中70种本地植物和55种入侵植物与AMF共生的情况,结果表明入侵植物与本地植物的AMF丰度没有显著差异,但在78%的研究中与入侵植物共生的AMF群落和与本地植物共生的AMF群落明显不同,并且入侵植物会降低本地植物的AMF侵染率,说明入侵植物与本地植物的竞争明显改变了它们与AMF的相互作用。然而,在美国半湿润草地的研究发现,菌根侵染率与入侵植物地上生物量没有显著的正相关关系,而与本地植物呈显著正相关,说明植物的菌根依赖性(mycorrhizal dependence)可能在入侵植物与本地植物的竞争中起重要作用(Siellaff et al, 2019)。Elizabeth等(2009)发现入侵北美的贯叶连翘(*Hypericum perforatum*)种群比在原产地欧洲的种群AMF侵染率低,说明贯叶连翘通过降低根部对AMF的依赖性达到入侵繁殖的目的。Zhang等(2010)发现加拿大一枝黄花(*Solidago canadensis*)的入侵促进了AMF中地球囊霉(*Glomus geosporum*)的生长,而抑制了摩西球囊霉(*G. mosseae*)的生长,入侵引起的地球囊霉的增加可以促进外来植物的生长,而摩西球囊霉的减少则不利于本地植物的生长,最终加拿大一枝黄花通过AMF对其入侵产生正反馈作用,说明有些入侵植物能够改变自身与本地植物对AMF的偏好性,形成入侵的正反馈。

3.3 AMF的碳转移作用及AMF对本地植物养分竞争的影响

由于AMF为植物提供养分的前提是需要宿主植物提供更多的碳源为代价,即宿主通过AMF共生间接觅养需要更高的碳成本,因此宿主植物要权衡

是否付出更多的碳成本而通过AMF共生体来获取养分(Treseder et al, 2018)。然而,研究发现AMF还会影响植物个体之间的碳转移,AMF不仅能够通过共生体促进入侵植物斑点矢车菊(*Centaurea maculosa*)的生长,而且能够间接地将邻近的本地植物伊达霍恩斯羊茅(*Festuca idahoensis*)的C转移到入侵植物斑点矢车菊(Carey et al, 2004)。

本地植物与土著AMF之间的共生互利会帮助本地植物吸收养分,提高本地植物对外来入侵植物的竞争力和抵抗力(Kisa et al, 2007; Dickie et al, 2017)。近期研究表明AMF可以促进本地植物金盏银盘(*Bidens biternata*)对磷的吸收进而提高其与外来入侵植物白花鬼针草的竞争力(Cheng et al, 2019)。可见,本地植物与AMF的相互作用不容忽视,其相互作用会影响本地植物对入侵植物的抵抗力。

3.4 土壤养分对植物与AMF共生关系的影响

植物通过AMF共生影响其对养分的捕获吸收,反过来土壤养分可以直接或间接影响植物的AMF侵染、菌根共生体系发育、产孢和分布,土壤养分还会改变AMF与宿主植物之间的关系(Johnson, 2010; Dickie et al, 2017; 向丹等, 2017; Treseder et al, 2018)。在养分限制的条件下,菌根真菌为宿主提供养分的有益作用大于宿主为菌根真菌提供碳源的成本,菌根真菌与宿主植物形成互利共生关系(Bever et al, 2010; Johnson et al, 2010)。在养分充足的条件下,菌根真菌为宿主提供养分的有益作用小于宿主为菌根真菌提供碳源的成本,菌根真菌与宿主植物形成寄生关系(Schulz & Boyle, 2005)。添加养分会降低植物AMF的侵染,养分充足时植物更倾向于通过根系而不是通过AMF吸收养分(Eissenstat et al, 2015)。

4 研究展望

入侵植物的根系觅养行为是非常复杂的生理过程,不同植物会产生不同的根系觅养行为适应营养异质性,入侵植物与本地植物的竞争会影响植物根系的觅养行为,其中还包含着自身以及与环境因素之间的权衡。目前,关于外来入侵植物根系觅养行为的研究还处于起步发展阶段,还有许多需要研究解答的问题。

首先,营养异质环境下本地植物的竞争对入侵植物根系的觅养能力有何影响?入侵植物根系直

接觅养与植物-AMF共生吸收养分之间有何关联,二者对外来入侵植物的竞争力有何影响,作用机制是什么?

其次,全球气候变化(气温升高、大气CO₂浓度升高、氮沉降、极端气候变化事件等)及其他环境因素(如光照、土壤水分等)会改变植物-微生物之间的相互作用,未来应加强全球变化背景下入侵植物根系觅养行为的变化与机制方面的研究,进一步探究根系觅养行为与AMF等土壤微生物的相互作用。

外来入侵植物的根系觅养行为是一个复杂的过程,相关研究的数量和深度还远远不够,需要我们更多关注和探讨,更好地阐明外来植物的觅养行为、入侵力、竞争力对环境变化的响应及其机制,为外来入侵植物的管控和入侵地的恢复提供依据。

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