

植物功能性状与外来植物入侵

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摘要: 揭示影响外来植物入侵性的功能性状及其生态机制是入侵植物生态学的核心任务之一。本文综述了植物功能性状与外来植物入侵性的研究进展, 通过分析植物功能性状对外来植物入侵的贡献以及外来植物的不同入侵阶段对其功能性状的需求, 探讨植物功能性状与外来植物入侵的相关性及其入侵机理。迄今研究较多的影响外来植物入侵性的功能性状主要包括形态性状、生长性状、生理性状、繁殖性状、种子性状、克隆性状、表型可塑性和遗传变异等。这些功能性状对外来植物入侵的贡献随着入侵阶段的不同而变化。在传播到达阶段, 种子性状对入侵具有重要影响; 在定居建群阶段, 与植物抗逆性和适应性相关的生理性状和繁殖性状发挥主要作用; 在扩散入侵阶段, 克隆性状和影响植物竞争能力的生理性状对植物成功入侵具有重要贡献。由于植物入侵性是其功能性状和环境因素互作的结果, 且功能性状的作用随环境因素和入侵阶段不同而异, 因此, 结合外来植物入侵阶段, 并考虑功能性状与环境因子的互作, 是入侵生物学中植物功能性状研究的发展趋势。

关键词: 外来植物, 生物入侵, 入侵性, 植物功能性状

The relationship between functional traits and invasiveness of alien plants

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Abstract: Understanding the functional traits and ecological mechanisms associated with successful invasions of alien plants is a key role of the field of invasion ecology. Through literature review and analysis of plant functional traits contributing to successful plant invasions and the demands for functional traits at different invasion stages, we discuss the relationships between the functional traits and invasiveness of alien plants as well as related ecological mechanisms. Functional traits that have been studied in relation to their invasions mainly include seed characters, and morphological, developmental, physiological, clonal and propagation characteristics, as well as genetic variation and plasticity of phenotype. The impacts of these functional traits on invasion success vary from one stage to another. At the introduction stage, plant invasions are mainly affected by seed characters. At the establishment stage, stress-tolerance related physiology and propagation traits exert important influences. At the explosion stage, clonal characters and physiological traits related to competitive ability largely contribute to invasion success. Because plant invasions result from interactions between plant functional traits and environmental features, further studies on plant invasions

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should consider both the effects of invasion stage and specific environmental variables on invasion success.

Key words: alien plants, biological invasions, functional traits of plants, invasiveness

外来种(alien species)是指由于人类有意或无意的活动被带到其自然演化区域以外的物种(Richardson *et al.*, 2000)。外来种中只有少数会形成入侵和造成危害(Mack *et al.*, 2000)。入侵植物(invasive alien plants)是指能在传入生境中自然生长繁殖并稳步扩展分布区的外来植物(Richardson *et al.*, 2000; Pyšek *et al.*, 2004)。外来种入侵(生物入侵)不仅使生物多样性降低,还威胁着全球的生态环境和经济发展(Pimentel *et al.*, 2000, 2005; Rudgers & Orr, 2009)。外来种一旦入侵成功,要彻底根除往往极为困难,即使清除成功也往往已造成极大的损失(Zavaleta *et al.*, 2001)。因此,在引种前对外来植物的入侵性进行分析与判别,对避免或减少入侵植物的危害是至关重要的(Goodwin *et al.*, 1999)。

什么样的环境容易被入侵和什么样的物种容易形成入侵是生物入侵生态学的两个核心问题(Alpert *et al.*, 2000; Pyšek *et al.*, 2009)。虽然人们对外来入侵植物的特性已进行了很多的研究,并发现它们具有某些非入侵植物所不具有的功能性状(Pyšek & Richardson, 2007; Mason *et al.*, 2008; Pyšek *et al.*, 2009),但目前仍无法对其入侵性进行有效预测(Alpert *et al.*, 2000; Hawkes, 2007; van Kleunen *et al.*, 2010)。

越来越多的研究案例表明,植物入侵性往往是一系列功能性状和环境因子综合作用的结果(Pyšek & Richardson, 2007; Abhilasha & Joshi, 2009; Dawson *et al.*, 2009),而且在植物入侵的不同阶段可能对植物功能性状的需求不同(Dawson *et al.*, 2009; Pyšek *et al.*, 2009)。在外来植物引进的初期,人类活动引起的繁殖体压力(propogule pressure)具有至关重要的作用;而在植物入侵的中后期,植物功能性状则发挥更加重要的作用(Dehnen-Schmutz *et al.*, 2007; Flory & Clay, 2009; Pyšek *et al.*, 2009)。因此,系统地分析植物功能性状对外来植物不同入侵阶段的影响具有十分重要的意义。本文通过综合分析外来植物在入侵过程不同阶段对植物功能性状的需求,探讨植物入侵性与其功能性状的关系和机理,并对植物功能性状与入侵性关系的研究热点进

行了展望。

1 植物入侵过程中不同阶段的划分

生物入侵的阶段划分一直存在争议,根据不同的研究目的可以有不同的划分(Williamson & Fitter, 1996; Liebhold & Bascompte, 2003; Williamson, 2006)。本文将植物入侵过程分为传播到达、定居建群和扩散入侵三个阶段,分别定义如下:

(1)传播到达阶段:外来植物在人类有意或无意活动的影响下到达其自然演化区域以外的地区并成活。

(2)定居建群阶段:外来植物在新地区成活后,在自然状态下通过与当地生态因子相互作用实现定居和建群。

(3)扩散入侵阶段:外来植物在新地区定居建群后,经过或不经潜伏期,通过自身繁殖和当地物种的竞争等,不断扩大分布区造成生物入侵。

2 生长和形态性状

植物的生长和形态性状通过影响植物的传播、定居建群和竞争能力,进而影响植物的入侵性。这些根、茎、叶等器官的形态性状都可通过影响植物的生理生态特性而影响其入侵性。有研究表明,入侵植物的个体可能比较大,但这个结论仅仅在无竞争的环境下成立(Blumenthal & Hufbauer, 2008),因为有些入侵植物是由于善于传播和占据因干扰而产生的新生态位而实现入侵(Burns & Winn, 2006)。植物相对生长速度(relative growth rates, RGR)是区别入侵植物与非入侵植物的重要性状之一(Grotkopp *et al.*, 2002),但也不尽然(Bellingham *et al.*, 2004)。在高养分下具有较高相对生长速度的外来植物容易入侵,而在低养分下没有这个规律。因此,单纯的相对生长速度不能有效解释外来种为何能与本地植物有效竞争,要解释植物入侵性需要考虑更多的植物功能性状(Smith & Knapp, 2001)。

在形态方面,有的入侵植物的茎具有缠绕特性,能绞杀本地物种,例如恶性入侵植物薇甘菊(*Mikania micrantha*);有的入侵植物在叶片特征方

面能促进其竞争和入侵,例如较大的比叶面积(specific leaf area, SLA)。虽然单纯的比叶面积不能有效解释外来种能与本地植物有效竞争的原因(Smith & Knapp, 2001),但已有研究显示比叶面积与植物入侵性的关系最大(Lake & Leishman, 2004),整合分析(meta-analysis)也显示入侵植物的比叶面积显著大于非入侵植物(van Kleunen *et al.*, 2009)。

在生物入侵的传播到达阶段,外来植物主要借助人类活动实现传播。人类有意引进的物种主要受到物种应用价值的影响,无意引进的物种则主要受到物种隐匿和传播能力的影响,例如毒麦(*Lolium temulentum*)通过隐匿在小麦种子中实现传播(李振宇和解焱, 2002)。因此种子的形态性状对某些外来入侵植物的传播具有重要意义。

在定居建群阶段,植物的生长和形态性状通过影响植物的生存和竞争能力而影响植物的入侵性,作为植物资源有效利用的重要指标,比叶面积和相对生长速度可能是外来入侵植物和非入侵植物的重要区别之一(Pyšek *et al.*, 2009; van Kleunen *et al.*, 2009)。在扩散入侵阶段,植株高度、比叶面积等均具有重要作用,这些性状都能通过提高植物的竞争能力而提高其入侵性。

3 生理性状

植物的生长、繁殖和竞争等均与其生理性状密切相关,因此,植物的生理性状对其适应能力和入侵性具有重要影响。例如,入侵植物的光合速率高能促使其在竞争和入侵中获胜(郑丽和冯玉龙, 2005; Feng, 2008; Feng *et al.*, 2009)。因为植物光合作用主要受水分和氮含量的限制,入侵植物的光合系统往往具有较高的水分利用效率和氮利用效率,使其在与本地种的竞争中处于优势地位(郑丽和冯玉龙, 2005; Feng *et al.*, 2009)。

在植物入侵的不同阶段,生理性状的影响显著不同。在传播到达阶段,植物生理性状的影响较小;在定居建群阶段,外来植物的生理性状决定了它能否在新生境中生存和繁殖;在扩散入侵阶段,外来植物的生理性状决定了它的入侵能力。一般认为植物生理特性和生态抗逆性均对外来植物的入侵性具有重要影响(Ashton & Lerdau, 2008)。但少数研究发现入侵植物的抗逆性未必就强(Garcia-Serrano *et al.*, 2009)。van Kleunen等(2009)通过大量研究案例

的整合分析显示,入侵植物的生理相关指标(如光合速率、呼吸速率、水分利用效率和氮素利用效率等)显著大于非入侵植物。

4 繁殖性状

4.1 种子繁殖性状

植物的种子繁殖性状对它的传播、定居建群和竞争能力均具有重要影响,例如花的形态、颜色与味道、花期、结实率等。自花受精和无融合生殖有利于入侵植物克服阿利效应(Allee effect)而实现入侵(Cheptou, 2007; van Kleunen & Johnson, 2007)。对甘松茅(*Nardus stricta*)和紫茎泽兰(*Eupatorium adenophorum*)等入侵植物的研究显示,通过无融合生殖的方式能产生大量种子,确保入侵植物在缺乏传粉者的情况下实现入侵(鲁萍等, 2005; Kissling *et al.*, 2006)。风媒植物更容易实现入侵,虫媒植物在到达新分布区后往往由于缺乏合适的传播媒介而影响其入侵能力(Gassó *et al.*, 2009)。因此植物繁殖性状对植物入侵性的影响,尤其是植物克隆繁殖特性与植物入侵性的关系,一直受到广泛的关注(Liu *et al.*, 2006)。

花期长短对某些外来植物的入侵性也具有影响,开花时间较长不但可以积累更多的光合产物以获得更大的定居潜力(colonization potential) (Baker, 1974),还能与本地种竞争传粉昆虫(Moragues & Traveset, 2005)。但花期较长也会因为繁殖成本高而影响生长,不利于入侵植物克服恶劣的环境。因此花期长是否有利于入侵会因生境特点和入侵阶段不同而异:在入侵的初期可能是不利的,而在入侵的扩散竞争阶段则可能有利于入侵。

种子性状是影响外来植物成功入侵的主要功能性状之一。外来入侵植物的远距离传播主要依靠种子完成(Tiebre *et al.*, 2007)。种子的大小、形态、数量、寿命和传播方式对植物的传播扩散具有直接影响。在传播到达阶段,种子大小、数量和萌发力对外来植物克服逆境,适应新的生态环境并形成入侵具有重要作用。一般地,入侵植物的种子比本地植物的种子更大更多,这能增强其远距离传播和入侵的能力(Daws *et al.*, 2007; Abhilasha & Joshi, 2009; Dawson *et al.*, 2009)。在入侵的后期,种子萌发能力与植物的入侵性正相关(Daws *et al.*, 2007; Mason *et al.*, 2008)。入侵植物种子的萌发效率高,

且萌发环境条件要求低,这是入侵种能够实现入侵的一个重要因素(López-García & Maillet, 2005)。

此外,种子性状对入侵性的影响还因为种子的传播方式而异,风媒外来植物中种子小容易入侵,而以动物为传播媒介的外来植物则是种子较大更容易形成入侵(Dawson *et al.*, 2009)。

在传播到达和定居建群阶段,种子繁殖性状对于其克服小种群的阿利效应具有重要影响;而在扩散入侵阶段,种子繁殖性状的影响因具体的环境而不同。

4.2 克隆繁殖性状

植物的克隆性对异质生境具有独特的适应能力,主要由于其具有克隆整合、表型可塑、风险分摊、觅食行为和克隆分工等特性(Pyšek, 1997; Yu *et al.*, 2004; 董鸣和于飞海, 2007)。植物入侵种中有相当一部分能够克隆繁殖,其危害严重性与其克隆生长习性直接相关(Baker, 1974; Liu *et al.*, 2006; Liu *et al.*, 2008)。在入侵植物的建群初期,种群较小的时候,克隆繁殖方式可能对它的繁殖保障和克服阿利效应具有重要意义。

有性繁殖能产生新的基因型并通过种子长距离传播占据新生境,而克隆繁殖则通过分株生长占据新的生境。部分入侵植物以克隆繁殖产生的克隆片段为主要传播方式(Wang *et al.*, 2008),尤其是湿地入侵植物主要通过克隆繁殖体实现传播(Wang *et al.*, 2008; Okada *et al.*, 2009)。另外,克隆植物的克隆构型对其入侵性也具有重要的影响,密集型克隆植物更容易形成入侵和造成危害(Cannas *et al.*, 2003)。

在传播到达阶段,由于克隆分株往往不能像种子一样远距离的传播(Pyšek, 1997),所以,克隆植物在入侵的传播阶段可能处于劣势。Pyšek(1997)发现,在欧洲中部的本地植物中,克隆植物占69.4%,非克隆植物只占30.6%;而在外来植物中,克隆植物只占36.2%,非克隆植物的比例高达63.8%。外来植物中克隆植物的比例小于本地植物中克隆植物的比例。大尺度区域分布格局研究显示,中国主要入侵植物中克隆植物和非克隆植物的分布格局没有显著差异(Liu *et al.*, 2005),这说明克隆繁殖方式对中国入侵植物的远距离传播没有显著影响。

在定居建群和扩散入侵阶段,克隆性对植物入侵性具有重要贡献。如薇甘菊的茎萌生苗比其种子

实生苗的成活率要高,生长速度也快(胡玉佳和毕培曦, 1994)。克隆性对入侵性的贡献可能主要表现在外来植物到达新入侵地以后,克隆性能增强外来植物的竞争和适应能力。在缺乏传粉媒介的情况下,依然能确保其产生大量个体,保障繁殖和克服阿利效应。

5 表型可塑性

表型可塑性是生物界中普遍存在的现象,是生物在没有遗传变异的情况下适应环境的一种机制(Bradshaw, 1965; Sultan, 2004)。植物表型可塑性涉及植物的形态特性、生理特性和繁殖特性等。表型可塑性较强的物种具有更强的适应性,能在更广泛的环境下生长和繁殖(Brock *et al.*, 2005)。对于外来入侵植物而言,表型可塑性可以通过改变植物的形态、生长、生物量分配和生理特性等来获取资源,占据生境,增强其入侵能力(Brock *et al.*, 2005; Richards *et al.*, 2006; Hulme, 2008)。例如,表型可塑性较强促进了互花米草(*Spartina alterniflora*)成功入侵(Richards *et al.*, 2005),使得喜旱莲子草能够在陆地到水域等多种生境形成入侵(Geng *et al.*, 2007)。

植物表型可塑性是预测入侵植物的重要指标,大约50%的入侵植物的入侵性与其表型可塑性有关(Ren & Zhang, 2009),因此基于物种的生物学特性建立模型能辅助预测外来种的入侵性(Rejmánek, 2000)。植物表型可塑性对入侵性的影响主要表现在定居建群和扩散入侵阶段,因为表型可塑性能增强植物对多样环境的耐受性和适应性(Williams *et al.*, 1995),增强其资源捕获与利用能力,使之表现出快速生长和繁殖的特性,提高其竞争力(Prentis *et al.*, 2008)。

6 遗传变异性

在物种入侵的初期,奠基者效应(founder effect)导致植物遭受繁育及传粉限制,基因流下降,稀有等位基因丢失,发生遗传漂变,使种群内遗传变异下降,种群间遗传分化增大(Husband & Barrett, 1991; Amsellem *et al.*, 2000)。案例研究显示入侵物种在入侵过程中会经历严重的遗传多样性丢失(Tsutsui & Case, 2001),尤其是对高度近交或自交的入侵物种来说(Novak & Mack, 2005)。Dlugosch和Parker(2007)分析了69个入侵物种,发现等位基

表1 植物功能性状在外来植物不同入侵阶段的贡献
Table 1 The effects of plant functional traits on the different stages of exotic plant invasions

植物功能性状 Functional traits	传播到达阶段 Introduction stage	定居建群阶段 Establishment stage	扩散入侵阶段 Explosion stage
生长和形态性状 Traits of growth and morphology	√	√	√
生理性状 Physiological traits	/	√	√
种子繁殖性状 Propagation traits	√	√	√
克隆繁殖性状 Clonal traits	/	√	√
表型可塑性 Phenotypic plasticity	*	√	√
遗传变异性 Genetic variation	*	/	*

√: 主要作用; /: 次要作用; *: 无作用或不确定
√ Dominant effect; / Subordinate effect; * Uncertain or no effect

因丰富度(allelic richness)呈正态分布, 其中15.5%的物种发生了遗传变异的丢失。

但近来一些研究表明, 有些成功入侵的物种遗传多样性并未下降(Bossdorf *et al.*, 2005; Jahodová *et al.*, 2007; Roman & Darling, 2007)。导致这一现象的机制有多种, 例如有些入侵物种具有多个起源的重复引进(Walker *et al.*, 2003; Koehler-Santos *et al.*, 2006; Jahodová *et al.*, 2007), 有些入侵物种未受到遗传瓶颈的影响(Jahodová *et al.*, 2007), 另外快速进化、漂变与杂交也起了重要作用(Palumbi, 2001; Lavergne & Molofsky, 2007; Jahodová *et al.*, 2007; Barrett *et al.*, 2008)。入侵物种旱雀麦(*Bromus tectorum*) (Novak & Mack, 2005)、豚草(*Ambrosia artemisiifolia*) (Genton *et al.*, 2005)、薇甘菊(李钧敏等, 2007)、大花金鸡菊(*Coreopsis grandiflora*) (Liang *et al.*, 2008)、独活(*Heracleum mantegazzianum*)、翅茎西番莲(*Passiflora alata*) (Koehler-Santos *et al.*, 2006)等均由于在入侵地具有多个起源, 从而具有较高的遗传多样性(Jahodová *et al.*, 2007)。

遗传多样性对入侵性的贡献主要体现在外来植物定居建群后能促进它对多样环境的适应。较高的遗传多样性有利于形成入侵能力较强的新基因型(Lavergne & Molofsky, 2007; Marrs *et al.*, 2008)。但研究显示, 很多入侵植物, 尤其是具有克隆性的入侵植物的遗传多样性很低(Xu *et al.*, 2003; Ye *et al.*, 2003)。例如, RAPD 技术揭示出凤眼莲(*Eichhornia crassipes*)具有很低的遗传变异, 整个中国的凤眼莲为单一的优势基因型组成的种群(Ren *et al.*, 2005)。喜旱莲子草遗传多样性较低(Wang *et al.*, 2005), 却对陆地到水域等多个生境具有较强的入侵能力。在入侵和扩散的过程中, 如果入侵种具有较强的表型可塑性, 则可能弥补遗传多样性低的不

足, 减小对生态型分化的依赖, 从而适应多变的异质生境。另外, 外来植物入侵后的的适应性进化也能增强其入侵性, 导致原产地与入侵地之间的遗传分化(Marrs *et al.*, 2008); 与基因型变异相关的表型可塑性则能消解不同生境带来的适合度的差异, 进一步促进入侵。因此, 无论入侵植物采取哪种策略加速入侵, 只要发生了适应性进化就可以获得各种资源, 占据多样的生境。

7 总结与展望

通过综合分析外来植物在不同入侵阶段对其功能性状的需求, 发现影响外来植物成功入侵的植物功能性状随不同入侵阶段而变化(表1)。在传播到达阶段, 影响外来植物成功入侵的功能性状主要是与种子或者繁殖体有关的性状; 而在定居建群阶段影响植物入侵性的因素是与植物抗逆性和适应性有关的生理性状和繁殖性状; 在扩散入侵阶段影响外来植物入侵性的包括克隆性状、生理性状和表型可塑性等方面, 因为这些性状都会影响植物对环境的适应能力以及与其他物种竞争的能力。

虽然植物功能性状对入侵性具有重要影响, 能解释很多外来植物的入侵性, 但对外来植物入侵性的预测还非常有限(Williamson, 2006), 很多性状只能增加实现入侵的可能性, 而难以准确预测其能否入侵(Herron *et al.*, 2007; Pyšek & Richardson, 2007)。环境因素与植物功能性状的互作才能决定植物的入侵性, 因此未来的研究应该更加关注不同环境因素对入侵植物功能性状的影响, 尤其要关注繁殖体压力和引进时间两个因素(Lockwood *et al.*, 2005; Thuiller *et al.*, 2006; Pyšek *et al.*, 2009)。在物种功能性状的比较研究中需要排除繁殖体压力和引进时间等因素的影响, 并结合植物的入侵阶段和

具体环境因子,才有可能找到决定外来植物入侵的关键性状。

虽然入侵植物功能性状的研究存在很多困难,但其研究结果对外来入侵种的早期预测、及时防治与潜在危害的风险评估具有重要作用。以下四个方面的深入研究有望最终揭示影响植物入侵性的功能性状: (1)外来入侵种的生物地理学研究; (2)外来入侵种与本地近缘种的比较研究; (3)外来入侵种与外来非入侵种的比较研究; (4)案例研究的整合分析(meta-analysis)。

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