



•综述•

入侵植物的繁殖策略以及对本土植物繁殖的影响

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摘要: 理解入侵生物的繁殖策略是阐明生物入侵机制的一个重要方面。入侵植物常表现出一些共同的繁殖特征, 如以两性花为主的性系统、自动自交为主的繁育系统或不依赖传粉媒介的无融合生殖和无性繁殖以及高生殖投资的资源配置策略等。成功入侵的外来植物通过影响本土的传粉者, 在种群和群落水平上影响本土植物的有性繁殖, 甚至促使某些本土植物在繁殖对策和表型性状上发生快速转变。目前, 入侵植物繁殖策略及其生态效应的研究多侧重于入侵种的快速演化, 而有关外来植物与本土植物间的相互影响及其可能存在的协同适应研究还较为缺乏。探讨本土植物在外来种入侵压力下的繁殖对策和响应机制, 将丰富人们对物种间竞争、共存及群落构建等机制的深入了解。从繁殖和适应的角度探求入侵植物与本土植物之间的复杂关系, 将有助于解析生物入侵的机制及人类干扰下的物种演化规律, 也为预测和防控入侵植物提供科学依据。

关键词: 生物入侵; 繁育系统; 繁殖对策; 入侵植物; 本土植物; 留存植物

On reproductive strategies of invasive plants and their impacts on native plants

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Abstract: Non-native plant invasion imposes great threats to global diversity and ecological safety, and now is a hot-spot of ecological studies. Understanding the reproductive strategies of invasive plants could provide insights into the invasion mechanisms and be helpful for proposing prevention and control strategies. Non-native invasive plants generally possess following reproductive traits: hermaphrodite-dominated sexual system, autonomous selfing-dominated breeding system, even asexual reproduction and apomixis, and high proportion of resources allocated to sexual reproduction, which may facilitate the success of some invasive plants. In turn, non-native plants could alter native plant–pollinator interactions, and in most cases decrease pollinator visitation and fitness of native plants. In addition, non-native plants may act as environmental stresses triggering rapid adaptation and evolution in reproductive strategies and phenotypes of resident native species in receipt communities. Studies in this field mostly have focused on rapid adaptation of invasive species to their new environments, while how native and non-native plants co-adapt and diverge remains largely unexplored, in particular from the perspective of plant reproduction. A better understanding of competition and cooperation between native and non-native plants will shed lights on rapid responses of native plants to non-native plant invasions. Such community studies of interspecific interactions with or without a competitor could provide evidence for displacement of reproductive traits and species coexistence, and improve our ability to predict and manage non-native invasive plants.

Key words: biological invasion; breeding system; reproductive strategy; invasive plant; native plant; remnant plant.

外来生物入侵是导致本土物种或种群消亡的一个重要原因, 严重威胁全球生物多样性、人类社

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会发展甚至人类健康,已成为当今生态学领域亟待解决的问题(Pimentel et al, 2000; Ludsins & Wolfe, 2001; Weber et al, 2008; Jeschke et al, 2014)。伴随经济和贸易全球化进程的不断加快,全球范围内越来越多的物种被人类有意或无意引入新的地域,其中一部分物种可能成为新的入侵生物(Weber & Li, 2008; 解焱, 2008; 牛红玉等, 2010; Webber & Scott, 2012; Jeschke et al, 2014)。同时,当今全球气候变化可能进一步加剧现有入侵种危害并提高新物种入侵的风险(Walther et al, 2002, 2009)。因此,明确外来物种入侵机制、提高人类预测和治理入侵生物的能力,是目前各国亟待解决的重大科学问题(Ren & Zhang, 2009)。

入侵植物较本土植物常表现出较高的生长速率、资源利用效率、表型可塑性和环境胁迫耐受能力等,可取得竞争优势(Sakai et al, 2001; DeWalt et al, 2004; Meyer et al, 2005; Sundaram & Hiremath, 2012);同时,一些入侵种在入侵过程中的资源分配策略和天敌防御等方面发生分化以应对环境的变化(Blossey & Nötzold, 1995)。如相对于原产地种群,在入侵地一些外来种的植株将更多资源分配于生长或光合作用、降低对专一性天敌的防御水平,从而提高其竞争力(Blossey & Nötzold, 1995; Feng et al, 2009)。繁殖策略作为植物生活史中的一个重要环节,在植物种群增长和扩散、群落结构和生态系统功能等生态过程中均具有重要作用(Brown & Eckert, 2005; Barrett et al, 2008)。已有研究表明,植物繁殖策略影响着外来植物入侵进程及其生态学效应,但目前有关研究相对较少(张大勇, 2004; Brown & Eckert, 2005; Barrett et al, 2008; Li et al, 2012)。明确外来植物的繁殖策略以及对本土植物繁殖的影响,将有利于进一步剖析外来植物的入侵机制,为预测和防控入侵生物提供指导。鉴于此,本文将从繁殖模式、生活型、性系统等方面,概述有关外来入侵植物繁殖策略及其生态学影响的研究,为未来的研究提供一个可参考的视角。

1 入侵植物的繁殖策略

1.1 入侵植物的自交与Baker定律

了解入侵植物的繁殖特性与入侵能力间的相关性有利于人们预测入侵植物的风险。自交亲和(self-compatibility),尤其是自动自花授粉(autono-

mous self-pollination),是植物应对交配限制(mate limitation)和传粉者不足等环境压力,实现短期内种群快速增长、扩散和传播的重要繁殖策略。Baker (1955)首次提出:能自交亲和的外来植物,特别是能进行自动自花授粉的物种,更可能定植而成为入侵种。因为植物被人类有意或无意地长距离移送到一个新环境之后,最初只有极少量的个体,存在着严重的交配限制和传粉者不足的情况;只有自交亲和的、能进行自动自花授粉的植物通过自我繁育,才能快速克服生殖的障碍。Stebbins (1957)把这一发现称为Baker定律(Baker's Law或Baker's Rule)。随着Baker定律的发现,大量的实验数据表明自交亲和的植物比自交不亲和的植物更容易成为入侵种。例如,菊科大部分种是自交不亲和的,但广泛分布于我国的12种入侵菊科植物中有8种自交亲和(2/3),而全球36.8%的菊科入侵植物自交亲和(Hao et al, 2011)。分布于南非的17种入侵植物中有13种木本植物均能自动自花授粉(Rambuda & Johnson, 2004);入侵阿根廷的两种蔷薇属(*Rosa*)植物可通过自动自花授粉、无融合生殖以及风媒传粉来结实,种子的产量和质量与虫媒传粉的结果并无差异(Mazzolari et al, 2017)。但是,也有不少入侵植物拥有自交不亲和的性系统,不完全支持Baker定律(例如, Jesse et al, 2006; Hong et al, 2007; Elam et al, 2007; Lafuma & Maurice, 2007)。

以上例证可能存在着因研究者选材偏好或选择物种较少造成的样本误差,对多地区多物种整合分析的结果能更好地检验Baker定律。基于美国142种外来入侵植物的整合分析, Sutherland (2004)发现自交亲和的入侵种比例显著低于非入侵种,不支持Baker定律。然而Pyšek和Richardson (2007)指出,在这项研究中自交亲和与自动自花授粉被看作二项变量,而不是连续变量,因此不能有效区分高度自动自花授粉的物种和轻微自动自花授粉的物种;其次,研究人员未能排除物种间系统发育关系对分析结果的潜在影响。van Kleunen和Johnson (2007)排除了上述两种可能的影响,对来源于欧洲的361个外来种的研究表明:能自交亲和的植物在美国有更大的入侵面积,支持Baker定律。van Kleunen等(2008)选取了来自鸢尾科9个属或亚属的10对物种(自然归化种vs.非自然归化种),通过隔绝传粉者的方式来检测繁殖策略,结果表明自然归化种比非归化种具

有更高的自交结实率。近年来Burns等(2011)、van Etten等(2017)和Razanajatovo等(2016)基于更大样本的整合分析也表明自交/自交亲和的繁育系统促进了外来植物的入侵。

1.2 入侵植物的无性(克隆)繁殖与无融合生殖

植物的无性(克隆)繁殖与无融合生殖方式可以说是Baker定律的极端情况,两种繁殖方式在理论上保证了植物仅有一个繁殖体便可在新生境中定植和建群。大量研究表明,无性繁殖和无融合生殖也是入侵植物的重要繁殖模式(Yu et al, 2009; 董鸣, 2011)。如在我国515种入侵植物中克隆植物有196种,占总数的38.1% (王宁等, 2016); 北美和欧洲入侵植物中的克隆植物也占46.9%和66.7% (Pyšek, 1997)。能无融合生殖的西洋蒲公英(*Taraxacum officinale*)原来分布于欧亚大陆,现在已是美洲、非洲南部、澳洲和新西兰等地的杂草(Kandori et al, 2009)。研究表明克隆繁殖和无融合生殖能提高植物在异质环境下获取资源的能力,而提高植物应对环境胁迫的能力是一些外来植物入侵的重要机制。如原产巴西已成为全球危害最为严重的物种之一凤眼莲(*Eichhornia crassipes*, 俗称水葫芦)为三型花柱植物,在入侵地北美和中国每个种群基本上只有一种交配型,几乎完全依赖无性繁殖来定植和扩散(任明迅等, 2004; Ren et al, 2005; Barrett et al, 2008)。在我国危害最为严重的喜旱莲子草(*Alternanthera philoxeroides*),在原产地南美为雌花两性花异株植物,能行有性繁殖,但在入侵地仅通过匍匐茎、根状茎和宿根等方式行无性繁殖(潘晓云等, 2006; Wang et al, 2009; Dong et al, 2012)。

仅进行克隆繁殖或自动自交繁殖的植物,遗传瓶颈(genetic bottleneck)和遗传漂变可制约其种群增长。然而,在入侵和扩散过程中,高度的表型可塑性可有效弥补此类植物因遗传多样性降低所带来的不足,减少对生态型分化的依赖,从而适应多样且复杂的生境(耿宇鹏等, 2004; 陆霞梅等, 2007)。对于那些遗传多样性比较低、同时又占据多样化生境的入侵种,表型可塑性和入侵能力的正相关可能是一条普遍法则(耿宇鹏等, 2004)。

1.3 入侵植物繁育系统的改变

外来植物的繁育系统在入侵后发生改变,主要是从异交(或有性繁殖)为主转变成自交(或无性)繁殖,即在入侵过程中由于遗传漂变和奠基者效应,

仅有一种交配型被保留下来从而被迫进行自交(无性)繁殖(Barrett, 1992; Philbrick & Les, 1996; Brown & Eckert, 2005; Barrett et al, 2008)。如Ward等(2012)发现入侵到澳大利亚的3种萝藦属(*Asclepias*)植物均具有自交亲和的繁育系统,这在普遍自交不亲和的萝藦属中非常罕见,虽然研究涉及的2种在原产地自交亲和,但其中1种在原产地为自交不亲和。入侵澳大利亚的一年生植物车前叶蓝蓟(*Echium plantagineum*, 原产欧洲南部和地中海地区)和黄矢车菊(*Centaurea solstitialis*, 原产地中海盆地)均为自交亲和,但在原产地均自交不亲和(Petanidou et al, 2012)。源自美洲大西洋沿岸和墨西哥湾的互花米草(*Spartina alterniflora*)种群在入侵滩涂的自交结实数量比原产地高出2倍(Davis, 2005)。显然,从异交到自交的繁殖系统改变促进了入侵植物在新生境的定植和建群,从侧面也支持了Baker定律。

生物入侵主要包括引入、建群、时滞期(也称适应期)和扩散四个阶段。繁育系统的改变不仅表现在建群阶段,也表现在时滞期(lag-phase)和扩散阶段。在时滞期可能伴随着大量的遗传重组和分化(Barrett, 2015),以便克服入侵过程中的遗传瓶颈效应和自交带来的近交衰退(inbreeding depression)(Ward et al, 2012)。对具有混合繁育系统(自交和异交)的入侵植物来说,从时滞期开始会涉及从自交为主到异交为主的繁育系统改变,从而为后续的自然选择提供更多的遗传变异(van Kleunen & Johnson, 2007; Barrett, 2015)。这种可塑的繁育系统可赋予入侵植物更强的适应和入侵能力:入侵早期从异交到自交的繁殖策略促进了入侵植物在新生境的快速定植和建群,入侵后从自交到异交的繁殖策略提高了外来植物对更广阔领地的拓殖能力。然而目前这方面的研究鲜有报道(Barrett, 2015)。Burns等(2011)基于141种植物的分析,发现入侵植物比本土植物拥有更高的自交结实比例,但入侵植物和外来非入侵植物间并没有区别。这一研究表明:自交可能有助于入侵物种的快速建群,但自交本身不能促进植物入侵,预示繁育系统的改变对入侵植物的重要性。

1.4 入侵植物的生活型与性系统

72%的有花植物具两性花,而雌雄同(异)株雌花两性花同(异)株和雄花两性花同(异)株等性系统共占28% (Huang & Guo, 2000)。两性花比其他性分

离的系统更容易实现自交,增加其在新生境中缺少交配对象时的自我繁殖机会,极有可能在入侵植物中广泛分布。统计结果支持了这一推测,如van Etten等(2017)系统分析了美国分布的1,077种植物的性系统,发现入侵植物具有更高比例的两性花系统,而本土植物则多为雌雄同株;同样地,美国的木本入侵植物中也具有高比例的两性花性系统(Reichard & Hamilton, 1997)。

入侵植物和本土植物在生活型和性系统上也存在差异。整合分析的结果支持了植物生活型与入侵性有内在的关系。如Razanajatovo等(2016)利用系统发育广义线性模型和路径分析的方法,分析了全球1,752种植物的繁育系统、生活史特征及其与原产地和入侵地分布范围的关系,认为自交繁育系统更多地出现在一年生和两年生草本植物中,这些植物具有更广的分布范围;而异交更多地出现在多年生木本植物中。入侵木本植物多为专性远交(obligate out-breeder),完全依赖传粉媒介来结实(Traveset & Richardson, 2014; Mazzolari et al, 2017)。这在理论上也能得到解释:木本植物较长的寿命保证了先期到达新生境的少量植株可通过较长期地等待后来者以减少交配限制的不利影响(Barrett, 2010)。

1.5 入侵植物的资源配置策略

天敌逃逸假说(Enemy Release Hypothesis)和竞争力进化增强假说(Evolutionary Increased Competitive Ability Hypothesis, EICA)推测:外来植物在入侵地由于逃脱了原产地天敌的束缚和制约,可将在原产地部分用于抵抗天敌的资源重新分配到营养和繁殖器官,从而提高入侵植物对新环境的适应和拓殖能力(Blossey & Nötzold, 1995; Barrett et al, 2008; Joshi et al, 2014)。

验证两个假说可采用同质园(common garden)种植实验,以比较不同来源(原产地与入侵地)种群的性状。目前比较多地采用营养性状或者生物量数据,相对缺乏繁殖性状(Chun et al, 2010; Felker-Quinn et al, 2013)。究其原因可能是繁殖性状需要耗费研究者更长时间,特别是那些花期较长和果实成熟较慢的拥有无限花序的物种;另外,植物的结实数量受到当地同质园天气和传粉环境的影响,特别是当不同来源种群植株的花期不同步时。少数对繁殖性状的比较研究支持了上述两个假说,如入侵植物在入侵地往往比在原产地产生更多的花朵和种子

(Blair & Wolfe, 2004; Brown & Eckert, 2005; Mason et al, 2008; Gonzalez-Teuber et al, 2017)。在原产地有天敌攻击繁殖器官的类群中这种效应更加明显。如雌雄异株的叉枝蝇子草(*Silene latifolia*)在欧洲原产地有较厚的果皮保护种子免遭啃食,但在缺乏天敌的美洲入侵地果皮变薄并产生较大较多的种子(Blair & Wolfe, 2004)。将来的比较研究若能考虑个体内营养生长与生殖生长间以及物理防御与化学防御间可能存在的权衡关系(trade-off),有望为天敌逃逸或竞争力进化增强假说提供有力的证据。

2 入侵植物对本土植物繁殖和演化的影响

对依赖传粉者受精结实的外来植物来讲,能否成功整合到本地的传粉网络中并借助本地的传粉者为其授粉,是决定外来植物能否成功入侵的关键(McKinney & Goodell, 2011; Powell et al, 2011)。由于在繁殖策略、繁殖系统和性系统等方面与本土植物存在差异,外来植物一旦整合到当地传粉系统中,将可能改变原有植物与传粉者互作的网络结构,影响本土植物的繁殖性状及其演化(Bjerknes et al, 2007; Mitchell et al, 2009; Yang et al, 2011; King & Sargent, 2012)。研究表明,入侵植物可从下述三个层次和水平影响本土植物。

2.1 入侵植物与本土植物间的传粉者竞争/促进作用

入侵植物可通过传粉者竞争(pollinator competition)或促进间接影响本土植物的繁殖能力。传粉者竞争被用来描述入侵植物与本土植物竞争有限的传粉者、降低本土植物的传粉者访问频率等,进而抑制本土植物的有性繁殖过程。在美国东部,千屈菜(*Lythrum salicaria*)的入侵导致36种同域分布的本土植物的传粉者访问频率平均降低20%以上(Goodell & Parker, 2017)。Flanagan等(2010)发现千屈菜入侵显著降低本土植物沟酸浆(*Mimulus ringens*)的结实率。原产喜马拉雅地区的具腺凤仙花(*Impatiens glandulifera*)入侵到欧洲(Chittka & Schurkens, 2001)以及千屈菜和西洋蒲公英在入侵地既降低了近缘本土植物的传粉者访问频率,也降低了其结实率(Brown et al, 2002; Kandori et al, 2009)。

传粉者促进(pollinator facilitation)是指入侵植物常通过较大的花和较多的开花数量来增强对传粉者的吸引力,导致其种群拥有更高的传粉者访问

频率和种子产量(Bjerknes et al, 2007)。如具腺凤仙花和金银忍冬(*Lonicera maackii*, 原产中国)被认为是磁石物种(magnet species), 两物种分别在入侵地英国布里斯托和美国俄亥俄州吸引了大量传粉者, 提高了本土植物的访花频率和结实率(Lopezaraiz-Mikel et al, 2007; McKinney & Goodell, 2011)。具腺凤仙花与不同地域的本土植物相遇时, 表现出传粉者竞争(Chittka & Schürkens, 2001)和促进(Lopezaraiz-Mikel et al, 2007)两种不同的效应。

原产北美洲的加拿大一枝黄花(*Solidago canadensis*)在入侵地中国的中东部虽然与同科的苦苣菜(*Sonchus oleraceus*)和山苦荬(*Ixeris chinensis*)具有相似的花部形态, 但它与苦苣菜之间有强烈的传粉者促进效应, 而与山苦荬存在显著的传粉者竞争关系(Sun et al, 2013)。这种一正一反的生态效应导致了不同的后果。传粉者竞争会加剧零星分布的本土植物种群消亡, 这对稀有、濒危物种来说尤为不利; 而传粉者促进却能促使某些本土植物繁盛。因此, 了解入侵物种和本土物种与共享传粉者间的相互作用, 对制定入侵种管理对策以及本土植物保护策略有借鉴意义。但入侵种对本土种的两种不同效应是如何发生的, 是否与物种间的亲缘关系、花部性状的相似性、生长环境以及同域共存物种有关系, 至今没有发现具有普遍意义的规律(Charlebois & Sargent, 2017)。其中, 物种间的空间距离或者物种的排列方式被认为有一定的影响(Charlebois & Sargent, 2017)。

2.2 入侵植物对本土传粉网络的影响

入侵植物可通过改变传粉网络的结构来影响本土植物的繁殖与种群动态。植物-传粉者互作网络结构的研究是近年来在国际上兴起的研究群落内物种关系的新方向(方强和黄双全, 2012)。对生态网络的监测和定量分析有助于我们深入理解生态过程和物种的种间关系(Tylianakis & Morris, 2017)。通过考察群落内所有开花植物与传粉者间的网状结构关系, 借助网络拓扑学的方法来定性或定量分析某类植物(动物)的变化(演替、迁移、灭亡和入侵等)对本土传粉系统结构的影响(Memmott & Waser, 2002; Lopezaraiza-Mikel et al, 2007; Kaiser-Bunbury et al, 2011, 2014)。已有研究表明, 群落中不同物种所处的角色和地位不同, 少数物种的连接伙伴(相互作用的物种)数目很多, 而大量物种的连接伙伴

很少, 于是在传粉网络上就表现出连接强度的不一致。那些吸引多个昆虫访问的物种以及能访问多个物种的超级传粉者对群落的稳定性和功能起着关键作用(Bascompte et al, 2006; Blüthgen et al, 2006; Vázquez et al, 2007)。

通过传粉网络来研究入侵植物对本土群落的影响目前还鲜有报道。如Lopezaraiza-Mikel等(2007)和Albrecht等(2014)观察到入侵植物可与本土的泛化传粉者构建稳定的连接, 融入当地的传粉网络结构当中, 进而主导传粉网络, 导致许多本土植物的繁殖受到强烈的花粉干扰。而Padrón等(2009)认为一些入侵植物虽然与泛化传粉者构建了稳定连接, 也融入了本土传粉网络, 但始终不能成为群落的核心物种, 这就不会显著影响传粉网络的结构和群落构成。Kaiser-Bunbury等(2017)分析了塞舌尔群岛8个岛(4个岛移除了外来植物并已恢复植被)上64个群落的植物-传粉者互作网络, 认为没有外来植物的干扰, 传粉者物种数量、访问次数和互作多样性显著提升, 具有更高的功能性生态冗余。Larson等(2016)在美国南部对丝路蓟(*Cirsium arvense*)入侵和未入侵的群落传粉者网络进行了分析, 发现入侵群落的模块化(modularity)程度较低, 而连接数较高, 从而提高了整个群落的稳定性。因此, 在群落水平上量化入侵植物在传粉网络结构上的功能和地位, 有助于了解生物入侵的机制, 并为本地植物群落恢复和生物多样性保护提供理论依据。

已有的植物与传粉者互作研究多关注传粉者访花的种类和频率, 却很少定量分析传粉的后果, 即花粉传递的数量和质量。近年来, 传粉网络的研究开始从基于访花观察的植物-传粉者互作网络, 逐渐深入到传粉者在不同物种间的混访和异种花粉传递网络, 即植物与植物之间的关系(Fang & Huang, 2016)。如Fang和Huang (2013, 2016)在中国西南山区高山草甸开展的传粉网络研究表明, 虽然传粉者在不同物种间有高的混访次数, 但混访传递的异种花粉数量却不多。这一结果揭示了在自然群落中, 避免种间花粉干扰是不同植物共存的机制之一; 仅观察传粉者的访花行为不能反映真实的花粉传递情况。Emer等(2015)调查了10个被凤仙花属植物*Impatiens glandulifera*入侵的群落和10个本土群落的异种花粉传递网络, 结果表明尽管传粉者携带了大量入侵植物的花粉, 但是其花粉只落置在少数

本土植物的柱头上,入侵植物并没有改变原有的异种花粉传递网络结构。Arceo-Gómez 和 Ashman (2016)分析表明入侵植物引起的异种花粉干扰结实的不利影响比本土植物引起的干扰更严重。未来的研究如果细化到传粉者混访行为和异种花粉传递,量化其对雄性和雌性适合度的影响,将能更精确地反映入侵物种对群落中本土植物由传粉者所介导的生殖成功的多样化作用。

2.3 入侵植物促进本土植物繁殖性状的分化

入侵生物的进化生物学研究已成为入侵生物学中一个活跃的分支(Hanfling & Kollmann, 2002; Blair & Wolfe, 2004; 李博等, 2010; Zenni et al, 2014)。植物入侵(即新竞争者的到来)可促进本土植物的形态分化,加快物种的演化过程。对很多本土植物来讲,外来植物的出现可看作是一个新的选择动力,促进它们快速表型分化和物种演化(Oduor, 2013)。这方面的研究在国际上已经起步,目前侧重于营养竞争的角度(Callaway et al, 2005; Strauss et al, 2006; Leger, 2008; Leger & Espeland, 2010)。如入侵北美的斑点矢车菊(*Centaurea maculosa*)能通过化感作用抑制本土植物的生长,与未经历(naïve)入侵的种群相比,受入侵“历练”(experienced) 20–30年后的本土植物留存种群(remnant population)拥有更强的挥发物耐受性,因而有更好的生长表现(Callaway et al, 2005)。在北美洲具腺凤仙花的入侵地,一种本土凤仙花(*Impatiens capensis*)则通过降低植株高度、增加侧向分枝数和提高花枝数的方法来提高资源竞争能力(Beans & Roach, 2015a)。

如果入侵植物和某种(些)本土植物为同属的近缘种或在花形或颜色上非常类似的物种,那么外来植物和本土植物则极有可能共享传粉者,导致物种间的花粉传递。异种花粉的传递往往会对本土植物的生殖成功造成干扰,这可能会驱使本土植物的花部特征包括花期物候等产生歧化,从而增强对入侵种的传粉竞争能力(类延宝等, 2010; Oduor, 2013; Beans & Roach, 2015b)。由于入侵植物的竞争,一些本土植物在一段时间内可能因传粉者服务减少而无法产生足以维持种群更新的种子数量,从而向自交的繁育系统演化(Fishman & Wyatt, 1999),或通过增加同时开花数(即花展示大小, floral display size)来提高对传粉者的吸引力(Wassink & Caruso, 2013),或通过改变花期以避免或减少与入侵植物

的花期重叠(Barrett et al, 2008),抑或通过花部特征的替代(character displacement)减小种间竞争来获取繁殖与生存的空间(Muchhala & Potts, 2007; Eaton et al, 2012)。迄今,植物入侵导致本土植物花部性状分化的实验研究只有一例(Beans & Roach, 2015b),即具腺凤仙花的入侵促使一种本土凤仙花的花冠变得更长。可见,比较有入侵种的种群和无入侵种的本土留存物种的种群,为性状演化和特征替代的研究提供了很好的实验系统。

3 研究展望

我国是全球生物多样性最为丰富的国家之一,但近几十年来,生境片段化、过度放牧和围垦等人为干扰造成了原有植被生境的丧失或破坏,也为生物入侵创造了生态条件。这些外来植物在入侵地的大面积暴发,显著降低了本土群落的生物多样性,对很多残存的本土植物造成了极大抑制,严重威胁着本已脆弱的生态系统。如具泛化传粉系统的恶性杂草加拿大一枝黄花在我国中东部的肆意扩散(董梅等, 2006),以及具有泛化传粉者的异型雄蕊植物刺萼龙葵(*Solanum rostratum*)在内蒙古、新疆以及华北地区的急速扩张(陈天翌等, 2013),对原有的生态系统构成了极大威胁。伴随着世界贸易的进一步扩大,预期未来将有更多的外来物种被传入世界各地,其中一些可能成为新的入侵种(Weber & Li, 2008; Jeschke et al, 2014)。因而分析入侵植物对本土植物繁殖和生态的影响、解析植物入侵机制、制定切实有效的防治策略以提高气候变化背景下应对外来生物入侵的能力,成为当前生态学领域亟待解决的一个科学命题。

在过去10年间,我国学者主要在入侵植物的扩散(Wang & Wang, 2006)、入侵机制(如植物克隆完整性和表型可塑性等)(Wang et al, 2017)、入侵植物的快速进化(Feng et al, 2009; Liu et al, 2016, 2017)、生态学效应(Liao et al, 2008; Li et al, 2014)及对气候变化的响应(Lu et al, 2013, 2015)等方面取得了诸多成果。但有关植物繁殖策略(尤其是繁育系统)如何影响植物入侵进程及其生态学原理、入侵过程中植物繁殖策略的变化、入侵植物对本土植物的生殖干扰(如何影响本土植物的传粉网络、异种花粉输出的损失到底对入侵植物或本土植物有多大危害,以及本土植物的繁殖策略如何响应或适应植物入侵等方

面尚缺乏深入研究。这些研究的开展, 无疑将进一步加深我们对种间竞争的认识, 了解外来植物的入侵机制, 为我国预测和防控植物入侵、保护本土植物多样性提供参考依据。

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