

入侵植物乌桕防御策略的适应性进化研究

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摘要 生长于不同昆虫群落胁迫下的植物地理种群可能进化出不同的防御策略。入侵植物在原产地同时受到专食性昆虫和广食性昆虫的取食危害, 而在入侵地“逃逸”了专食性昆虫的取食危害。入侵植物对不同昆虫防御策略的演化可能在其成功入侵的过程中起着至关重要的作用。该文主要以原产中国入侵北美的木本植物乌桕(*Triadica sebifera*)为例, 并结合其他入侵植物防御策略演化的研究, 从抗性和耐受性、直接抗性和间接抗性、组成抗性和诱导抗性三个方面系统分析不同昆虫选择压力下入侵植物防御策略的演化, 同时探讨入侵植物防御策略演化对生物防治效果的影响, 指出未来的重点研究方向。

关键词 生物防治, 防御策略, 植物和昆虫互作关系, 入侵机制

A review of adaptive evolution of defense strategies in an invasive plant species, Chinese tallow (*Triadica sebifera*)

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Abstract

Selection on defense strategies of plant species may be different in direction and magnitude among sites, because of differences in the herbivore communities in which plant populations are embedded. This may be the case for some invasive species, which are often introduced without coevolved specialists, but suffer generalist damage comparable to their native ones. We review recent advances in the adaptive evolution of defense strategies in Chinese tallow (*Triadica sebifera*) and other invasive plant species. We focus particularly on resistance and tolerance, direct and indirect resistance, and constitutive and induced resistance to understanding the effects of herbivores on invasive plant success. Furthermore, we evaluate the effects of changes in defense strategies on the efficiency of biological control. We also propose future research on defense strategies of invasive plant species.

Key words biological control, defense strategies, interactions between plant and insect, invasive mechanism

基于植物和天敌昆虫之间的相互作用关系, 外来植物能够成功地建立种群、形成扩散, 往往归因于在新的环境中缺少天敌。天敌逃逸假说(enemy release hypothesis, ERH)认为: 外来植物在被引入到一个新的区域后, 逃逸了专食性昆虫的取食危害, 从而在与其他植物的竞争中获得优势, 最终导致其数量上的增长和空间分布上的扩大(Maron & Vilà, 2001; Keane & Crawley, 2002)。在此基础上, 增强竞争力进化假说(evolution of increased competitive ability hypothesis, EICA)认为: 外来植物摆脱了原产地的专食性天敌, 在引入地没有或有少量广食性天敌的情况下, 新的选择压力会驱动植物的防御策略发生进化, 把更多的资源从防御转移到生长繁

殖, 进而提高植物的竞争力(Blossey & Nötzold, 1995)。因此, 入侵植物防御策略的演化在其成功入侵的过程中可能起至关重要的作用(Müller-Schärer *et al.*, 2004; Chun *et al.*, 2010; Orians & Ward, 2010)。

植物抵御天敌昆虫取食危害的防御策略包括抗性和耐受性。根据对昆虫的不同作用方式, 抗性可分为直接抗性和间接抗性, 根据不同的表达方式又可分为组成抗性和诱导抗性(Agrawal, 2007, 2011; Turley *et al.*, 2013)。研究表明, 植物的不同防御策略会随环境的变化做出相应的改变(Agrawal *et al.*, 2004; Leimu & Koricheva, 2006; Núñez-Farfán *et al.*, 2007)。然而, 以往大部分研究主要关注昆虫群落变化对入侵植物直接抗性的影响, 而忽略了间接

抗性和耐受性以及不同防御策略的诱导能力 (Bossdorf *et al.*, 2005; Orians & Ward, 2010), 导致人们对天敌昆虫如何影响入侵植物防御策略的演化以及如何促进外来植物的成功入侵缺乏全面的认识 (Colautti *et al.*, 2004; Chun *et al.*, 2010)。

目前, 对原产中国入侵北美的大戟科植物乌柏 (*Triadica sebifera*) 防御策略演化的研究较为系统和深入, 涉及抗性、耐受性、组成抗性、诱导抗性、直接抗性和间接抗性等多个方面。为此, 本文以乌柏为主要研究对象, 并结合其他入侵植物防御策略的研究, 从抗性和耐受性、直接抗性和间接抗性、组成抗性和诱导抗性三个方面展开, 系统分析入侵植物防御策略对天敌昆虫群落变化的响应, 并探讨入侵植物防御策略改变对生物防治效果的影响。最后, 对未来入侵植物防御策略的研究提出展望。

1 抗性和耐受性

抗性 (resistance) 是植物减少昆虫取食偏好性以及延缓和降低昆虫生长发育的特性 (Strauss *et al.*, 2002)。野外调查和同质园实验证实乌柏入侵地种群被天敌昆虫取食危害率显著高于原产地种群 (Siemann & Rogers, 2001; Zou *et al.*, 2008b), 化学物质测定结果表明乌柏入侵地种群主要抗性物质单宁含量显著低于原产地种群 (Siemann & Rogers, 2001, 2003c; Huang *et al.*, 2010; Wang *et al.*, 2012)。这些研究结果支持EICA假说关于入侵植物降低对防御投入的预测。然而, 在其他研究体系中所得结果不尽相同。Herrera等(2011)研究发现, *Genista monspessulana* 入侵地种群的抗性与原产地种群无显著差异。Ridenour等(2008)对 *Centaurea maculosa* 的研究结果与EICA假说关于防御的预测完全相反, 入侵地种群的抗性显著高于原产地种群。Oduor等(2011)在对 *Brassica nigra* 的研究中也发现入侵地种群的抗性显著升高。

相互矛盾的研究结果可能是由于以往研究未能区分专食性昆虫和广食性昆虫。在入侵地, 入侵植物只是逃逸了专食性昆虫的取食危害, 而没有完全逃逸广食性昆虫, 甚至有些入侵植物上会聚集更多的广食性昆虫 (Agrawal & Kotanen, 2003)。因此, 入侵植物可能会降低对专食性昆虫的防御, 维持或增强对广食性昆虫的防御 (Müller-Schärer *et al.*, 2004; Orians & Ward, 2010)。Huang等(2010)研究了

专食性昆虫癩皮夜蛾 (*Gadirtha inexacta*) 和广食性昆虫黄刺蛾 (*Cnidocampa flavescens*) 在乌柏入侵地种群和原产地种群上的生长发育, 结果发现专食性昆虫在入侵地种群的生长发育较好, 而广食性昆虫的生长发育在入侵地种群和原产地种群无显著差异。Wang等(2012)发现乌柏入侵地种群防御专食性昆虫的抗性物质(单宁)含量显著低于原产地种群, 而入侵地种群和原产地种群防御广食性昆虫的抗性物质(类黄酮)含量无显著差异。以上研究结果证实: 乌柏入侵地种群对专食性昆虫的抗性降低, 而对广食性昆虫的抗性不变。对入侵植物 *Senecio jacobaea* 的研究发现专食性昆虫 *Tyria jacobaeae* 在入侵地种群存活率较高, 表明入侵地种群降低了对专食性昆虫的抗性; 而广食性昆虫 *Mamestra brassicae* 在入侵地种群存活率较低, 表明入侵地种群提高了对广食性昆虫的抗性 (Joshi & Vrieling, 2005)。

耐受性 (tolerance) 是指植物在被昆虫取食危害后的恢复再生能力 (McNaughton, 1983; Strauss & Agrawal, 1999)。在资源有限的情况下, 植物减少对抗性的投入, 可能会增加对耐受性的投入, 反之亦然。目前, 这种权衡关系已在一些研究体系中得到证实 (Fineblum & Rausher, 1995; Leimu & Koricheva, 2006)。人工模拟和昆虫取食等研究均证实乌柏入侵地种群的耐受性显著高于原产地种群, 这表明耐受性和抗性之间存在权衡关系 (Rogers & Siemann, 2005; Zou *et al.*, 2008b; Wang *et al.*, 2011)。乌柏原产地种群具有较高的抗性和较低的耐受性; 入侵地种群具有较低的抗性和较高的耐受性。高耐受性可能与乌柏入侵地种群具有较低的根冠比、较高的叶面积指数、光合能力和CO₂同化速率有关 (Zou *et al.*, 2007)。此外, 在比较乌柏入侵地种群和原产地种群对不同食性昆虫取食耐受性的进一步研究中发现, 入侵地种群对广食性昆虫的耐受性显著高于对专食性昆虫的耐受性 (Huang *et al.*, 2010, 2012a)。这种对广食性昆虫的高耐受性, 可能有利于提高乌柏在入侵地对主要昆虫类群(广食性昆虫)的防御能力, 但其内在的机制还不清楚。入侵植物具有较高的耐受性, 在其他研究体系中也得到了证实 (Stastny *et al.*, 2005; Li *et al.*, 2012)。Ashton和Lerdau (2008)比较了入侵植物、外来植物和本地植物耐受性的差异, 结果发现入侵植物具有较高的耐受性, 并且这种较高的耐受性有利于外来植物的成

功入侵。

地下植食性昆虫在生态系统中同样起着重要的作用(van Dam, 2009; van Dam & Heil, 2011), 但是由于观察和操作手段的落后(Brown & Gange, 1990; Bardgett *et al.*, 2005), 人们往往对地下昆虫取食危害所造成的影响缺乏足够的认识(Blossey & Hunt-Joshi, 2003)。目前, 研究多集中于入侵植物与地上昆虫之间的相互作用, 而忽略了地下昆虫对入侵植物成功入侵的影响(Bardgett & Wardle, 2003; Wardle *et al.*, 2004; Bezemer & van Dam, 2005; van Dam, 2009)。因此, 了解地上昆虫与地下昆虫的相互作用, 特别是地上昆虫与地下昆虫同时对入侵植物的影响, 有助于深入地了解外来植物的潜在入侵机制。Rogers和Siemann (2004)采用人工剪除模拟地下昆虫取食, 结果同样发现乌桕入侵地种群对地下昆虫的耐受性强于原产地种群。由于人工模拟不能真实地反映昆虫取食对植物的影响(Howe & Jander, 2008), Huang等(2012b)采用专食性昆虫红胸律点跳甲(*Bikasha collaris*)研究乌桕入侵地种群和原产地种群对地上成虫和地下幼虫昆虫的抗性和耐受性。与以往研究结果相同, 入侵地种群降低了对地上昆虫的抗性, 增加了耐受性; 同时研究发现入侵地种群对地下昆虫的抗性也降低, 但耐受性没有发生改变。抗性和耐受性在地上和地下的变化可能说明入侵植物乌桕主要逃逸了地下植食性昆虫的取食危害。

从原产地到入侵地昆虫群落的变化可能导致入侵植物的防御策略发生演化, 进而促进外来植物的成功入侵。这主要是因为植物的防御是有成本的(Strauss & Agrawal, 1999; Strauss *et al.*, 2002), 并且防御体系中抗性和耐受性的成本在不同种群中也不相同(Pilson, 2000; Fornoni *et al.*, 2004)。乌桕在入侵地没有专食性昆虫, 特别是在没有地下专食性昆虫取食危害的情况下, 将资源从抗性转移至地上耐受性。研究表明, 耐受性的成本往往低于抗性的成本(Hakes & Cronin, 2011), 节余的资源将会转向植物的生长繁殖, 进而增强植物的竞争力。以上研究结果也是对EICA假说的深化, 入侵植物乌桕只是降低了对抗性的投入, 而增加了对耐受性的投入。

2 直接抗性和间接抗性

直接抗性(direct resistance)是指通过直接影响

取食植物的昆虫来减少危害, 主要包括各种直接驱避、毒杀和影响植食性昆虫消化的次生代谢物质(Beck, 1965; Stamp, 2003)。间接抗性(indirect resistance)是通过吸引取食昆虫的天敌, 降低取食昆虫对植物的不利影响, 主要包括各种挥发性物质和花外蜜(extrafloral nectarines) (Arimura *et al.*, 2005; Heil, 2008)。目前对入侵植物的研究主要集中于直接抗性(Wolfe *et al.*, 2004; Oduor *et al.*, 2011; Franks *et al.*, 2012; Kumschick *et al.*, 2013), 忽略了不同昆虫选择压力下间接抗性的演化。由于直接抗性只涉及两级营养级关系(植物—取食昆虫), 而间接抗性涉及三级营养关系的互相作用(植物—取食昆虫—昆虫天敌) (Karban, 2011), 这将导致植物间接抗性所受到的选择压力往往大于直接抗性(Rudgers, 2004)。例如, Abdala-Roberts和Mooney (2013)对草本植物*Ruellia nudiflora*的研究发现: 不同基因型植株之间有害昆虫发生量的变异系数为7%, 而昆虫天敌发生量的变异系数则高达13%, 施肥处理产生同样的结果。对于入侵植物而言, 入侵地和原产地的生物和非生物环境往往存在巨大差异, 间接抗性相对于直接抗性可能更容易发生演化。

花外蜜是一种重要的植物间接防御方式, 主要通过吸引蚂蚁等捕食性和寄生性天敌昆虫来降低植食性昆虫对植物的危害, 提高植物的适合度(Oliveira & Freitas, 2004; Brent *et al.*, 2010)。研究表明超过100个科1 000种植物能够产生间接防御物质花外蜜(Heil, 2011)。Carrillo等(2012a)通过比较乌桕入侵地种群和原产地种群的花外蜜含量, 分析入侵植物间接抗性的演化模式, 结果发现入侵地种群分泌花外蜜的叶片数量、花外蜜总量和花外蜜含糖量均显著低于原产地种群, 首次证实入侵植物乌桕的间接抗性降低。研究结果支持EICA假说关于入侵植物降低对防御投入的预测, 入侵植物乌桕逃逸了天敌昆虫的取食危害, 显著降低了对直接抗性和间接抗性的投入。目前在其他入侵植物上还没有关于间接抗性演化的报道。

3 组成抗性和诱导抗性

组成抗性(constitutive resistance)是指无论植物是否受到植食性昆虫取食危害都一直存在和表达的抗性(Stamp, 2003), 而诱导抗性(induced resistance)是植物在遭受到植食性昆虫取食后所诱导产

生的一种抗虫特性(Karban, 2011)。在入侵地长期缺乏专食性昆虫的取食为害可能会使入侵植物对不同食性昆虫的诱导防御能力不同(Cipollini *et al.*, 2003)。此外,大量研究证实组成抗性和诱导抗性可能存在权衡关系(van Zandt, 2007; Kempel *et al.*, 2011)。因此,综合研究入侵植物应对不同食性昆虫抗性物质的变化对于揭示外来入侵植物化学防御的演化具有重要意义。

Wang等(2012)比较了乌柏入侵地种群和原产地种群在不同食性昆虫取食危害后抗性物质的变化,结果发现入侵地种群和原产地种群单宁和类黄酮含量均显著增加。结合组成抗性的研究,入侵植物乌柏的组成抗性和诱导抗性无权衡关系。Eigenbrode等(2008)通过化学分析发现入侵植物 *Cynoglossum officinale* 主要抗性物质生物碱含量在入侵地种群和原产地种群无显著差异,人工模拟昆虫取食后二者之间仍无显著差异。Cipollini等(2005)在入侵植物 *Alliaria petiolata* 的研究体系中同样没有发现组成抗性和诱导抗性存在权衡关系。然而,Beaton等(2011)通过昆虫生物测定发现入侵植物 *Lespedeza cuneata* 对广食性昆虫的组成抗性和诱导抗性存在权衡关系,与原产地种群相比,入侵地种群对广食性昆虫的组成抗性下降,诱导抗性升高。

Rogers等(2003)第一次报道了人工模拟取食能显著地增加乌柏原产地种群和入侵地种群花外蜜的分泌,但未发现入侵地种群和原产地种群之间存在差异。然而,人工模拟取食不能真实地反映昆虫取食对植物的影响(Howe & Jander, 2008), Carrillo等(2012b)选用两种广食性昆虫——草地贪夜蛾 (*Spodoptera frugiperda*) 和米兰褐软蚧 (*Coccus hesperidum*), 分析昆虫取食对乌柏入侵地种群和原产地种群花外蜜的诱导能力,结果发现草地贪夜蛾取食显著增加叶片花外蜜的分泌,但是诱导能力与乌柏来源地无关。研究结果进一步证实入侵地种群和原产地种群被昆虫诱导的间接抗性水平无显著差异。然而,米兰褐软蚧取食对乌柏入侵地种群和原产地种群花外蜜的分泌无影响。这可能是由于两种昆虫的取食方式不同所致。鳞翅目昆虫草地贪夜蛾采用咀嚼方式取食植物,导致茉莉酸途径的代谢表达,茉莉酸会显著增加花外蜜的分泌(Heil, 2004)。同翅目昆虫采用刺吸方式取食植物,诱导水杨酸途径的代谢表达,水杨酸不增加花外蜜的分泌

(Walling, 2008; Soler *et al.*, 2012)。Wang (2012)综合分析不同食性昆虫对乌柏入侵地种群和原产地种群的间接抗性的诱导能力,结果发现专食性昆虫诱导原产地种群产生更多的花外蜜,而广食性昆虫取食和人工模拟昆虫取食后入侵地种群和原产地种群的花外蜜无显著差异。在入侵地,乌柏只是逃逸了专食性昆虫,而没有完全逃逸广食性昆虫,因而降低了对专食性昆虫间接抗性的诱导能力,维持了对广食性昆虫间接抗性的诱导能力。

4 防御策略与生物防治

入侵植物会改变入侵地的生态系统结构和功能,造成巨大的经济损失。为此,人们已经采用一系列防治方法以减少其所带来的危害(Wittenberg & Cock, 2005)。生物防治以天敌逃逸假说为理论依据,通过在入侵植物原产地引入专食性天敌控制入侵植物的扩散。目前,有些生防天敌虽然能够在入侵植物上成功建立种群,但是无法有效地控制入侵植物的生长和扩散(McFadyen, 1998),这可能和入侵植物防御策略的演化有关。

为了分析入侵植物防御策略的演化对生物防治效果的影响,Wang等(2011)研究了两种专食性昆虫 癩皮夜蛾 (*Gadirtha inexacta*) 和 乌柏卷象 (*Heterapoderopsis bicallosicollis*) 对乌柏入侵地种群和原产地种群的控制效果。结果发现癩皮夜蛾在入侵地种群生长发育较好,乌柏卷象在入侵地种群的种群数量更大,从昆虫的个体发育和种群数量上看,入侵地种群对专食性昆虫的抗性下降。植物被昆虫危害的程度与植物的生长发育之间并不一定存在负相关,因为植物还可以通过再生长能力得以恢复(McNaughton, 1983; Strauss & Agrawal, 1999)。由于入侵地种群具有较强的耐受性,乌柏入侵地种群的生长仍显著高于原产地种群(生物量和株高)。入侵地种群较低的抗性会使专食性昆虫很容易建立种群,然而入侵地种群较强的耐受性会减弱专食性昆虫的防治效果。这一观点将有助于解释在很多生物防治项目中,生物防治昆虫都建立了较大的种群,有的甚至相比其在原产地的种群大很多倍,但是对入侵植物仍然没有很好地控制的原因(Müller-Schärer *et al.*, 2004)。将来所选的生物防治天敌必须克服入侵地种群较高的耐受性。

大量研究表明,竞争胁迫(Tilman, 1982, 1994;

Goldberg & Novoplansky, 1997)和昆虫取食(Maron & Crone, 2006)会对植物产生不利的影响, 并且两者的交互作用会加剧这种不利影响(Hambäck & Beckerman, 2003; Haag *et al.*, 2004; Schädler *et al.*, 2007)。竞争胁迫和昆虫取食如何影响外来植物, 对此还研究较少(Zou *et al.*, 2008a; Blank, 2010; Suwa

et al., 2010)。Huang等(2012a)比较了不同竞争强度胁迫下乌桕入侵地种群和原产地种群对不同食性昆虫耐受性的差异。大田盆栽试验发现, 在竞争强度较高的情况下, 专食性昆虫对入侵地种群的影响显著地高于广食性昆虫。然而, 在竞争强度较低的情况下, 专食性昆虫和广食性昆虫对入侵地种群的

表1 乌桕入侵地种群和原产地种群昆虫生长发育、植物耐受性和次生代谢物质的差异

Table 1 Differences in insect performance, plant tolerance and secondary metabolites of *Triadica sebifera* between invasive and native populations

昆虫取食类型 Insect feeding type	昆虫种类 Insect species	测定指标 Measured index	变化 Variation	参考文献 Reference
专食性昆虫取食 Specialist insects feeding	癩皮夜蛾 <i>Gadirtha inexacta</i>	幼虫生长速率 Larval growth rate (mg·d ⁻¹)	↑	Huang <i>et al.</i> , 2010
		幼虫体重 Larval weight (g)	↑	Huang <i>et al.</i> , 2010; Wang <i>et al.</i> , 2012
		蛹重 Pupal weight (g)	↑	Wang <i>et al.</i> , 2011
		取食叶片量 Leaf mass consumed (mg·d ⁻¹)	↑	Huang <i>et al.</i> , 2010
		花外蜜分泌量 Volume of extrafloral nectarines production	↓	Wang, 2012
	耐受性 Tolerance	↑	Huang <i>et al.</i> , 2010; Wang <i>et al.</i> , 2011; Huang <i>et al.</i> , 2012a	
	乌桕卷象 <i>Heterapoderopsis bicallosicollis</i>	卷象数量 Number of weevils	↑	Wang <i>et al.</i> , 2011
		耐受性 Tolerance	↑	Wang <i>et al.</i> , 2011
	红胸律点跳甲 <i>Bikasha collaris</i>	地上昆虫取食率 Aboveground insect feeding rate (%)	↑	Zou <i>et al.</i> , 2008b; Huang <i>et al.</i> , 2012b
		地上耐受性 Aboveground tolerance	↑	Zou <i>et al.</i> , 2008b; Huang <i>et al.</i> , 2012b
地下昆虫存活率 Belowground insect survival rate (%)		↑	Huang <i>et al.</i> , 2012b	
地下耐受性 Belowground tolerance		-	Huang <i>et al.</i> , 2012b	
广食性昆虫取食 Generalist insects feeding	黄刺蛾 <i>Cnidocampa flavescens</i>	幼虫体重 Larval weight (g)	-	Huang <i>et al.</i> , 2010; Wang <i>et al.</i> , 2012
		幼虫生长速率 Larval growth rate (mg·d ⁻¹)	-	Huang <i>et al.</i> , 2010
		取食叶片量 Leaf mass consumed (mg·d ⁻¹)	-	Huang <i>et al.</i> , 2010
	耐受性 Tolerance	↑	Huang <i>et al.</i> , 2010, 2012a	
	蝗虫 <i>Melanoplus angustipennis</i>	危害率 Damage rate (%)	↑	Lankau <i>et al.</i> , 2004
		耐受性 Tolerance	↑	Rogers & Siemann, 2005
	米兰褐软蚧 <i>Coccus hesperidum</i>	花外蜜分泌量 Volume of extrafloral nectarines production	-	Carrillo <i>et al.</i> , 2012b
草地贪夜蛾 <i>Spodoptera frugiperda</i>	花外蜜分泌量 Volume of extrafloral nectarines production	-	Carrillo <i>et al.</i> , 2012b	
模拟昆虫取食 Simulated insects feeding	花外蜜分泌量 Volume of extrafloral nectarines production	-	Rogers <i>et al.</i> , 2003; Carrillo <i>et al.</i> , 2012a	
	耐受性 Tolerance	↑	Rogers & Siemann, 2004, 2005	
自然昆虫取食 Natural insects feeding	危害率 Damage rate (%)	↑	Siemann & Rogers, 2003c, 2003d; Zou <i>et al.</i> , 2008a	
无昆虫取食 No insect feeding	叶片单宁含量 Foliar tannin content	↓	Siemann & Rogers, 2001, 2003c; Huang <i>et al.</i> , 2010; Wang <i>et al.</i> , 2012	
	叶片黄酮含量 Foliar flavonoid content	↑	Wang <i>et al.</i> , 2012	

↑, 与原产地乌桕种群相比, 入侵地种群昆虫发育较好, 耐受性较强或次生代谢物质含量增加; ↓, 与原产地乌桕种群相比, 入侵地种群昆虫发育较差, 耐受性较弱或次生代谢物质含量减少; -, 与原产地乌桕种群相比, 入侵地种群昆虫发育、耐受性和次生代谢物质含量无显著变化。

↑, relative to native populations of *Triadica sebifera*, insect performed better, tolerance greater or content of secondary metabolites increased for invasive populations of *T. sebifera*; ↓, relative to native populations of *T. sebifera*, insect performed worse, tolerance lesser or content of secondary metabolites decreased for invasive populations of *T. sebifera*; -, relative to native populations of *T. sebifera*, insect performance, tolerance and content of secondary metabolites were not significantly changed for invasive populations of *T. sebifera*.

表2 入侵植物乌柏和入侵地乡土植物昆虫生长发育和植物耐受性的差异

Table 2 Differences in insect performance and plant tolerance between invasive plant *Triadica sebifera* and native plant species in invaded range

植物种 Plant species	昆虫取食类型 Insect feeding type	测定指标 Measured index	变化 Variation	参考文献 Reference
糖朴 <i>Celtis laevigata</i>	自然昆虫取食 Natural insects feeding	危害率 Damage rate (%)	↑	Siemann & Rogers, 2003b, 2006
	模拟地上昆虫取食 Simulated aboveground insects feeding	耐受性 Tolerance	↑	Rogers & Siemann, 2002
北美枫香 <i>Liquidambar styraciflua</i>	蝗虫 <i>Melanoplus angustipennis</i> <i>Orphullela pelidna</i>	危害率 Damage rate (%)	↓	Lankau <i>et al.</i> , 2004
	蝗虫 <i>Melanoplus angustipennis</i> <i>Orphullela pelidna</i>	危害率 Damage rate (%)	↓	Lankau <i>et al.</i> , 2004

↑, 与入侵地乡土植物相比, 乌柏上昆虫发育较好或耐受性增加; ↓, 与入侵地乡土植物相比, 乌柏上昆虫发育较差或耐受性降低。
 ↑, relative to native plant species in the invaded range, insect performed better or tolerance increased for *Triadica sebifera*; ↓, relative to native plant species in the invaded range, insect performed worse or tolerance decreased for *T. sebifera*.

表3 乌柏入侵地种群和原产地种群生理特性、繁殖和生长的差异

Table 3 Differences in physiological property, reproduction and growth of *Triadica sebifera* between invasive and native populations

性状 Trait	测定指标 Measured index	变化 Variation	参考文献 Reference
生理性状 Physiological traits	叶面积 Leaf area (cm ²)	↑	Zou <i>et al.</i> , 2007, 2009
	光合组织分配 Photosynthetic tissue allocation (m ² ·g ⁻¹)	↑	Zou <i>et al.</i> , 2007
	非光合组织分配 Non-photosynthetic tissue allocation (m ² ·g ⁻¹)	↑	Zou <i>et al.</i> , 2007
	净CO ₂ 同化速率 Net CO ₂ assimilation rate (μmol·m ⁻² ·s ⁻¹)	↑	Zou <i>et al.</i> , 2007
	暗呼吸速率 Dark respiration rate (μmol·m ⁻² ·s ⁻¹)	–	Zou <i>et al.</i> , 2007
	叶片碳氮比 Foliar C:N	↑	Siemann & Rogers, 2001
	叶片碳水化合物蛋白质比 Foliar carbohydrate : protein	↑	Huang <i>et al.</i> , 2010
	繁殖性状 Reproductive trait	植株结实率 Percentage of the trees produced seed (%)	↑
生长性状 Growth traits	地径 Stem diameter (cm)	↑	Siemann & Rogers, 2001, 2003c
	株高 Plant height (cm)	↑	Siemann & Rogers, 2003d; Zou <i>et al.</i> , 2009; Huang <i>et al.</i> , 2010
	相对株高生长速率 Relative plant height growth rate (mm·cm ⁻¹ ·d ⁻¹)	–	Rogers & Siemann, 2004, 2005; Zou <i>et al.</i> , 2007
	叶片数 Total number of leaves	–	Zou <i>et al.</i> , 2008a
	地上生物量 Aboveground biomass (g)	↑	Rogers & Siemann, 2004, 2005; Zou <i>et al.</i> , 2006, 2008a, 2009; Huang <i>et al.</i> , 2010, 2012b
	地下生物量 Belowground biomass (g)	–	Rogers & Siemann, 2004; Huang <i>et al.</i> , 2010, 2012b
	总生物量 Total biomass (g)	↑	Zou <i>et al.</i> , 2006, 2008a, 2009; Huang <i>et al.</i> , 2010, 2012b
	根冠比 Ratio of root to shoot	↓	Zou <i>et al.</i> , 2006, 2007; Huang <i>et al.</i> , 2010, 2012a, 2012b
	相对生长速率 Relative growth rates (mg·g ⁻¹ ·d ⁻¹)	↑	Zou <i>et al.</i> , 2007
	幼苗存活率 Seedlings survival (%)	↑	Siemann <i>et al.</i> , 2006

↑, 与原产地乌柏种群相比, 入侵地种群生理特性、繁殖或生长增强; ↓, 与原产地乌柏种群相比, 入侵地种群生理特性、繁殖或生长减弱; –, 与原产地乌柏种群相比, 入侵地种群生理特性、繁殖和生长无显著变化。

↑, relative to native populations of *Triadica sebifera*, physiology, reproduction or growth increased for invasive populations of *T. sebifera*; ↓, relative to native populations of *T. sebifera*, physiology, reproduction or growth decreased for invasive populations of *T. sebifera*; –, relative to native populations of *T. sebifera*, physiology, reproduction or growth was not significant changed for invasive populations of *T. sebifera*.

影响无显著差异。这表明强竞争胁迫和专食性昆虫取食可有效地降低入侵地种群的耐受性。在生物防

治天敌对入侵植物不能取得理想的控制效果时, 人为地栽种竞争力强的植物, 增加其竞争强度, 可有

表4 入侵植物乌桕和入侵地乡土植物生长和繁殖的差异

Table 4 Differences in growth and reproduction between invasive plant *Triadica sebifera* and native plant species in invaded range

植物种 Plant species	测定指标 Measured index	变化 Variation	参考文献 Reference
小须芒草 <i>Schizachyrium scoparium</i>	地上生物量 Aboveground biomass (g)	↑	Zou <i>et al.</i> , 2009
	地下生物量 Belowground biomass (g)	↑	
	总生物量 Total biomass (g)	↑	
	相对株高生长速率 Relative plant height growth rate (mm·cm ⁻¹ ·d ⁻¹)	↑	
北美枫香 <i>Liquidambar styraciflua</i>	存活时间 Survival time (d)	↑	Siemann <i>et al.</i> , 2006; Nijjer <i>et al.</i> , 2008
	地下生物量 Belowground biomass (g)	↑	
	总生物量 Total biomass (g)	↑	
	相对株高生长速率 Relative plant height growth rate (mm·cm ⁻¹ ·d ⁻¹)	↑	
黑橡胶树 <i>Nyssa sylvatica</i>	地下生物量 Belowground biomass (g)	↑	Nijjer <i>et al.</i> , 2008
	相对株高生长速率 Relative plant height growth rate (mm·cm ⁻¹ ·d ⁻¹)	↑	
黑栎 <i>Quercus nigra</i>	地下生物量 Belowground biomass (g)	-	Siemann & Rogers, 2006; Nijjer <i>et al.</i> , 2008
	存活时间 Survival time (d)	↑	
	种子数 Number of seeds	↑	
糖朴 <i>Celtis laevigata</i>	株高 Plant height (cm)	↑	Rogers & Siemann, 2002; Siemann & Rogers, 2003a, 2003b, 2006; Siemann <i>et al.</i> , 2006
	地上生物量 Aboveground biomass (g)	↑	
	总生物量 Total biomass (g)	↑	
	种子数 Number of seeds	↑	
美国榆 <i>Ulmus americana</i>	种子数 Number of seeds	↑	Siemann & Rogers, 2006

↑, 与入侵地乡土植物相比, 乌桕生长或繁殖增强; ↓, 与入侵地乡土植物相比, 乌桕生长或繁殖减弱; -, 与入侵地乡土植物相比, 乌桕生长和繁殖无显著变化。

↑, relative to native plant species in the invaded range, growth or reproduction increased for *Triadica sebifera*; ↓, relative to native plant species in the invaded range, growth or reproduction decreased for *T. sebifera*; -, relative to native plant species in the invaded range, growth or reproduction was not significant changed for *T. sebifera*.

效地控制入侵植物的生长, 降低入侵植物的耐受性。

此外, 由于乌桕入侵地种群对地下昆虫取食危害的防御水平下降, 地下生物防治天敌的投放可能会取得理想效果。例如, 地下生防昆虫跳甲 (*Aphthona nigriscutis*和*A. lacertosa*)已成功控制了乳浆大戟(*Euphorbia esula*)在美国北卡罗来纳州的入侵(Setter & Lym, 2013)。Huang等(2012b)同时研究入侵植物对不同部位昆虫取食危害的响应, 发现当被地上昆虫取食危害时, 入侵地种群的总生物量显著高于原产地种群; 当被地下昆虫取食危害时, 两者总生物量无显著差异。这表明地下生防天敌可有效地控制入侵植物的生长。将来筛选生物防治的天敌时, 应对地下昆虫给予更多的重视。

5 总结

综上所述, 昆虫群落的改变驱动入侵植物防御

策略适应性演化, 进而导致了外来植物的成功入侵。在入侵地, 由于逃逸了专食性昆虫, 而没有完全逃逸广食性昆虫, 乌桕降低了对专食性昆虫的直接抗性及其诱导能力, 提高了对广食性昆虫诱导的直接抗性和耐受性(表1, 表2)。由于耐受性的成本往往低于抗性, 诱导抗性的成本往往低于组成抗性, 节约的资源可能分配给植物的生长繁殖, 进而提高其入侵能力(表3, 表4)。

6 展望

6.1 组学结合

植物的化学防御并不只是某一类次生代谢产物在起作用, 一些未知的化学物质可能在植物抵御昆虫胁迫中发挥着更大的作用(Bennett & Wallsgrove, 1994)。由于受分析手段的限制, 以上研究都只是针对一小类已知的次生代谢产物, 未能全面地反映植物的化学防御策略。代谢组学

(metabonomics)的创立为系统研究植物化学防御策略提供了理想的手段(Jansen *et al.*, 2009)。代谢组学应用的高灵敏度、高通量检测技术,可同时对大量代谢产物进行定性定量分析,较为全面地研究植物不同时期或者不同部位代谢产物种类和含量的变化,以及植物对外界刺激的代谢应答(Bundy *et al.*, 2009)。例如,Franks等(2012)采用气相色谱质谱联用的方法综合分析了*Melaleuca quinquenervia*入侵地种群和原产地种群萜类化合物的变化,发现入侵地种群和原产地种群有20种萜类物质的含量存在显著差异,证实在新的选择压力下*M. quinquenervia*的化学防御发生演化。入侵植物防御策略演化分子机制的研究目前还处于起步阶段,这可能是由于入侵植物没有可供参考的基因组信息所致(Stewart *et al.*, 2009)。转录组学(transcriptomics)可以对任意物种的全基因组进行分析,无需预先设计特异性探针。这对非模式植物,特别是入侵植物的研究尤为重要(Whiteman & Jander, 2010; Dlugosch *et al.*, 2013)。例如, Hodgins等(2013)采用定制Nimblegen芯片比较*Ambrosia artemisiifolia*入侵地种群和原产地种群基因表达的差异,发现180个基因的表达量存在差异,并证实部分基因可能参与次生代谢物质的调控。综上所述,各种组学的结合应用可以在探索入侵生物的快速进化、对环境改变的代谢应答及生物入侵的分子遗传学机制等方面发挥更大的作用。

6.2 气候变化

气候变化会改变生物多样性,引起物种分布区的变化以及改变物种间的相互作用关系(Gellesch *et al.*, 2013)。温室气体增多、气温升高、降水不平衡和极端气候事件增多等可能会使部分地区生态系统抵御外来生物入侵的能力降低,而外来生物的入侵能力增强(Chuine *et al.*, 2012; Barbet-Massin *et al.*, 2013; Perry *et al.*, 2013; Seabloom *et al.*, 2013)。大量研究已将生物入侵与气候变化相结合(Fennell *et al.*, 2013; Sorte *et al.*, 2013)。然而,目前对气候变化如何影响入侵植物的天敌昆虫群落,如何影响入侵植物的防御策略,如何影响入侵植物和天敌昆虫的相互作用关系等研究还处于起步阶段。因此,与全球气候变化相结合,可有效地预测入侵植物在生物(昆虫群落的改变)和非生物(如:氮沉降、增温、干旱)胁迫下防御策略的进化方向和趋势。

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