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飞机草入侵种群与原产地种群生长性状的差异

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摘要:飞机草(*Chromolaena odorata*) 是我国热带地区危害严重的外来入侵植物,为揭示适应进化对其成功入侵的贡献,在同质种植园中,比较研究了飞机草 10 个入侵地种群与 12 个原产地种群生长性状的差异,为排除奠基者效应的可能影响,进一步比较了飞机草 10 个入侵地种群与其原产地可能的祖先种群间的差异。结果表明,飞机草 10 个入侵地种群的基茎、株高、分枝数、生物量和比叶面积均显著高于 12 个原产地种群; 与可能的祖先种群相比,飞机草 10 个入侵种群的生物量、分枝数和比叶面积仍更高。这些结果表明,在长期的入侵过程中飞机草通过进化提高了资源向生长的分配,支持增强竞争能力的进化假说。

关键词:飞机草; 同质种植园; 增强竞争能力的进化; 生长; 入侵

Differences in growth traits between *Chromolaena odorata* plants from invasive and native populations

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Abstract: Biological invasions are serious socio-economic and environmental problems. Invasion ecology has become one of the hotspots in recent years. However, the mechanisms underlying exotic plant invasions are still not well elucidated, although many related studies have been conducted worldwide. The Evolution of Increased Competitive Ability (EICA) Hypothesis predicts that invasive plant species may decrease resource allocation to defense and therefore increase allocation to growth in response to enemy release in their new ranges. To test this hypothesis, many studies have been carried out in both invasive and native ranges of many introduced plants. Some of these studies do not provide any evidence for the EICA hypothesis, although more studies support this hypothesis. One of the reasons for the inconsistent results is that almost all related studies compared the differences in performance between plants from invasive and native populations in general, without considering the potential influence of founder effect. To exclude the influence of confounding founder effect, we should compare the difference between the plants from invasive populations and the plants from their source native populations. However, the source populations of invasive species are rarely known with certainty. To investigate the role of post-introduction evolution in successful invasion of *Chromolaena odorata* (L.) King & Robinson (Asteraceae), we compared the overall differences in growth traits between the plants originating from seeds collected in 10 populations in its invasive range in Asia and the plants originating from seeds collected in 12 populations in its native range in America in a

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common garden. In order to decrease or even exclude the influence of founder effect, we specifically compared the plants from the 10 invasive populations with the plants from their six putative source populations. *Chromolaena odorata* is native to North, Central, and South America, but a noxious perennial invasive forb or subshrub throughout the tropics in Africa, Asia, and Oceania. It was introduced into Calcutta, India in the middle of the nineteen century. It was first found in Yunnan, southwest China in 1934. Now it occurs in Yunnan, Guangxi, Guizhou, Hainan, Guangdong, Taiwan, Hongkong, and Macao, becoming one of the most noxious invasive plants in China. *Chromolaena odorata* harbours more than 240 enemies in its native range and 25% of them are specialists to the invader. However, only few generalists were found for the invader in its native range in China. *Chromolaena odorata* plants invading in Asia may originate from Florida and Trinidad according to the results of studies with molecular markers. In the common garden, *C. odorata* plants from the 10 invasive populations were significantly higher in stem diameter, plant height, branch number, total biomass, and specific leaf area than the plants from the 12 native populations. Compared with the plants from the six putative source populations, the plants from the 10 invasive populations were also higher in total biomass, branch number, and specific leaf area. Our results indicate that *C. odorata* appears to have increased resource allocation to growth through post-introduction evolution, providing more convincing evidence for the EICA hypothesis than general comparisons between invasive plants and their native conspecifics without considering their ancestors.

Key Words: *Chromolaena odorata*; common garden; evolution of increased competitive ability; growth; invasion

为揭示外来植物成功入侵的机制，各国科学家开展了大量研究，提出很多理论或假说，如增强竞争能力的进化（Evolution of Increased Competitive Ability，EICA）假说[1-2]、氮分配的进化假说[3-4]、天敌逃逸假说[5-6]、新武器假说[2,7-8]。EICA 假说认为，脱离原产地的天敌后，进化使外来物种失去对天敌的抗性，并把原来用于维持抗性的资源用于生长、生殖等过程，从而提高入侵能力[1]，有很多研究支持该假说[9-12]。例如，Barney 等[13]发现，与原产地种群相比，北艾（*Artemisia vulgaris*）入侵种群具有更多的分枝，更大的根系和更高的生物量，从而具有更强的竞争力。但不支持 EICA 假说的证据也时有报道。例如，在同质种植园中，葱芥（*Alliaria petiolata*）原产地种群的株高和果实产量高于入侵种群[14]，豚草（*Ambrosia artemisiifolia*）入侵种群的防御力并未降低，植株也小于原产地种群[15]。入侵地种群可能只源自原产地的少数个体或种群，在同质种植园中笼统地比较入侵地种群与原产地种群生物量、分枝数、株高、繁殖能力等数量性状的差异不能排除奠基者效应（由原产地少数个体建立并发展起来的入侵种遗传多样性降低，且与其少数祖先相近）的影响，难以得出入侵植物是否发生引入后进化的确切结论[2]。为排除奠基者效应的可能影响，我们应该比较研究入侵种群与其祖先种群的差异。

飞机草（*Chromolaena odorata*（L.）King & Robinson; Asteraceae）原产于中、南美洲，现已扩散至非洲、亚洲、大洋洲、西太平洋群岛的大部分热带及亚热带地区[16-17]，是世界上危害最严重的 100 种有害外来入侵物种之一[18]。1934 年在我国云南南部首次发现飞机草，目前已扩散到台湾、广东、香港、澳门、海南、广西、云南和贵州，是我国首批公布的恶性入侵杂草之一。在原产地飞机草有 240 种节肢动物天敌，其中很多对飞机草具有寄主专一性[19]。而在入侵地，据我们的野外调查仅有蜗牛、蚜虫等少数天敌取食飞机草，且危害程度非常低。Ye 等[20]利用简单序列重复区间扩增多态性（*ISSR*，Inter-Simple Sequence Repeat）分子标记研究发现，入侵中国的飞机草的居群内遗传多样性很低，居群间遗传分化程度也很低，总的遗传多样性（H_T）仅为 0.0406，Shannon 信息指数 也仅为 0.0623，推测飞机草在入侵过程中存在着严重的奠基者效应。余香琴等[21]通过对叶绿体 DNA 片段和核基因内转录间隔区序列（*ITS*，internal transcribed spacers）测序以及微卫星 DNA 分析发现，来自亚洲 10 个国家的 29 个飞机草居群均为一种单倍型，遗传多样性很低，可能均来自原产地的特立尼达和佛罗里达。Paterson 等[22]也发现，入侵非洲西部和亚洲的飞机草属同一种生态型，认为这一生态型的原始种源很可能来自特立尼

达和佛罗里达。为揭示引入后进化对飞机草成功入侵的贡献，本研究在同质种植园中，比较研究了飞机草10个入侵种群和12个原产地种群及其原产地可能的祖先种群的生长差异，以期更好地验证EICA假说。

1 材料和方法

1.1 实验地概况

同质种植园设在云南省勐腊县勐仑镇中国科学院西双版纳热带植物园内，该园位于21°56′N，101°15′E，海拔约580 m，属北热带西南季风气候，一年中有明显的干季（11—4月）和雨季（5—10月）之分，平均气温21.7℃，平均相对湿度86%，平均降雨量1500—1600 mm（其中雨季占83%—87%，干季占13%—17%）[23]。

1.2 实验材料

2009年3—6月，在飞机草原产地（中美洲）和入侵地（亚洲）采集各种群的种子（表1），在每个地点（种群）随机选10株采种子，任意两株之间至少间隔20 m，每株的种子（家系）分别保存。2010年6月，将各种群的种子在苗床上育苗，8月将大小一致（约10 cm）的幼苗移栽到同质种植园中生长，作为种质圃。

表1 各种群飞机草基本信息

Table 1 Information on sample populations of *Chromolaena odorata*

国家/区域 Country / Region	纬度 Latitude	经度 Longitude	海拔 Elevation / m
入侵地种群 Invasive populations			
泰国中部 Central Thailand	14°25′N	101°23′E	739
云南景东 Yunnan JingDong	24 °17′N	100 °50′E	1263
云南勐仑 Yunnan MengLun	21°56′N	101°15′E	544
马来西亚 Malaysia	2°22′N	102°21′E	50
菲律宾 Philippines	8 ° 10′N	124 °10′E	107
斯里兰卡 Sri Lanka	7°11′N	80°25′E	451
云南思茅 Yunnan SiMao	22°46′N	100°56′E	1380
海南三亚 Hainan SanYa	18 °19′N	109 °12′E	23
老挝万象 Lao Vientiane	17°58′N	102°37′E	170
越南南部 Southern Vietnam	11°20′N	107°24′E	125
原产地种群 Native populations			
佛罗里达 Florida	26°08′N	80°06′W	1—5
墨西哥 Mexico	23°40′N	99°11′W	600
墨西哥 Mexico	16°44′N	93°09′W	640
古巴 Cuba	22°45′N	82°50′W	565
佛罗里达 Florida	25°52′N	80°29′W	1—5
佛罗里达 Florida	27°06′N	80°15′W	1—5
佛罗里达 Florida	25°38′N	80°20′W	1—5
墨西哥 Mexico	18°51′N	103°37′W	950
波多黎各 Puerto Rico	18°12′N	67°06′W	103
波多黎各 Puerto Rico	18°12′N	67°06′W	103
特立尼达 Felicity，Trinidad & Tobago	10°31′N	61°25′W	10
特立尼达 Mamoral，Trinidad & Tobago	10°27′N	61°17′W	63

1.3 育苗及移栽

2012年12月中旬，在地表10 cm处割掉同质种植园中生长的飞机草（10个入侵地种群和12个原产地种群，每个种群10个家系，共220株）地上部全

部枝叶,使其萌生幼芽。2013 年 3 月 21 日,当飞机草茎桩上幼芽约 5 cm 高时,在每株上挑选 10 个大小一致、长势良好的芽,扦插到沙床(沙:土=1:1),每天浇水。1 个月后,幼芽上长出根,选大小一致的幼苗移栽到 10 L 的花盆中,每盆 1 株,每个家系 1 盆,每个种群 10 盆,共 220 盆。每 22 株(盆)为一列,每列包括来自原产地和入侵地的各种群飞机草各 1 株,盆与盆之间的距离是 50 cm,列与列之间的距离是 70 cm。根据需要进行浇水(滴灌)、除草、喷药(排除天敌取食压力)、定时转盆(尽量减小位置效应的影响)。幼苗栽种后在透光率 50%的遮阴网下生长 1 个月,之后移去遮阴网,使其在全光下生长。

栽培基质由林内去表面枯落物后的 25 cm 以上表土(砖红壤)和河砂按 6:4(体积比)混匀而成,每盆装土 10 kg。施肥前基质养分含量为:pH 值为 4.91,有机质为 8.72 g/kg,全 N 为 0.80 g/kg,总 P 为 0.21 g/kg,总 K 为 22.39 g/kg,水解 N 为 43.42 mg/kg,有效 P 为 1.17 mg/kg,有效 K 为 43.33 mg/kg(中国科学院西双版纳热带植物园生物地球化学实验室测定)。按土壤肥力的评价标准[24-25],此基质的有机质和总 N、P、K 含量较高,有效 N、P、K 含量严重不足。

1.4　测定

幼苗成活后,用刻度尺测量初始株高。为观测飞机草幼苗生长动态在产地间的差异,于 2013 年 6、8 和 9 月再测定 3 次株高(每月 1 日)。移栽 130d 后,每株选 10 片成熟叶片,用 LI-3000C 叶面积仪(Li-Cor, Lincoln, NE, USA)测定叶面积,烘干称重,计算比叶面积;用数显游标卡尺测定植株的基径(两个垂直方向测定值的均数),统计各株 5 cm 以上长的分枝数。最后收获全部植株,带回实验室,在 60℃ 烘干 48 h,用电子天平(精确度 0.01 g)称重。

1.5　统计分析

用一元嵌套方差分析(线性混合模型)检验飞机草 10 个入侵种群与全部 12 个原产地种群的差异;产地为固定因子,种群嵌套在产地中做随机因子。为排除奠基者效应的影响,进一步用一元嵌套方差分析比较飞机草 10 个入侵种群与 6 个原产地可能的祖先种群(特立尼达和佛罗里达)各参数的差异。用 Pearson 相关(one-tailed)分别分析了生物量、株高、分枝数和基茎与比叶面积的相关关系。所有数据分析均用 SPSS 21.0(SPSS Inc. Chicago, IL, USA)。

2　结果

与 12 个原产地种群相比,飞机草 10 个入侵地种群株高(产地: $F_{1,20}=4.695$, $P=0.043$; 种群: $F_{20,216}=9.422$, $P<0.001$)、基茎(产地: $F_{1,20}=5.454$, $P=0.030$; 种群: $F_{20,216}=9.056$, $P<0.001$)、分枝数(产地: $F_{1,20}=15.848$, $P=0.001$; 种群: $F_{20,216}=2.251$, $P<0.01$)、总生物量(产地: $F_{1,20}=11.355$, $P=0.003$; 种群: $F_{20,216}=7.991$, $P<0.001$)和比叶面积(产地: $F_{1,20}=6.501$, $P=0.019$; 种群: $F_{20,216}=5.039$, $P<0.001$)分别升高了 12.0%、8.6%、12.9%、25.3%和 6.8%,差异均达显著水平(图 1,图 2)。株高连续测定结果也表明,飞机草入侵种群生长速率高于原产地种群(图 3)。与可能的 6 个祖先种群相比,飞机草 10 个入侵种群分枝数(产地: $F_{1,14}=16.546$, $P=0.001$; 种群: $F_{14,158}=2.095$, $P<0.05$)、总生物量(产地: $F_{1,14}=6.606$, $P=0.022$; 种群: $F_{14,158}=5.832$, $P<0.001$)和比叶面积(产地: $F_{1,14}=11.145$, $P=0.019$; 种群: $F_{14,158}=5.039$, $P<0.001$)分别升高了 15.9%、18.3%和 8.3%,差异均达显著水平(图 4,图 5)。

飞机草 22 个种群的比叶面积与其生物量($r=0.186$, $P=0.003$)和分枝数($r=0.272$, $P<0.001$)显著正相关,但与基茎($r=-0.022$, $P=0.379$)和株高($r=0.003$, $P=0.484$)相关不显著(表 2)。

表 2　飞机草 22 个种群的比叶面积与生长性状间的相关性

Table 2　Correlations between specific leaf area and four growth traits in 22 populations of *Chromolaena odorata* according to Pearson correlation (one-tailed)

参数 Parameter		比叶面积 Special leaf area	生物量 Biomass	分枝数 Branch Number	基茎 Stem diameter	株高 Plant height
比叶面积 Special leaf area	Pearson 相关系数 (r) Pearson Coefficients (r)	1	0.186	0.272	−0.022	0.003
	显著性(单尾) Significance (one-tailed)		0.003	0.000	0.379	0.484
	样本数 sample size (N)	218	218	218	218	218

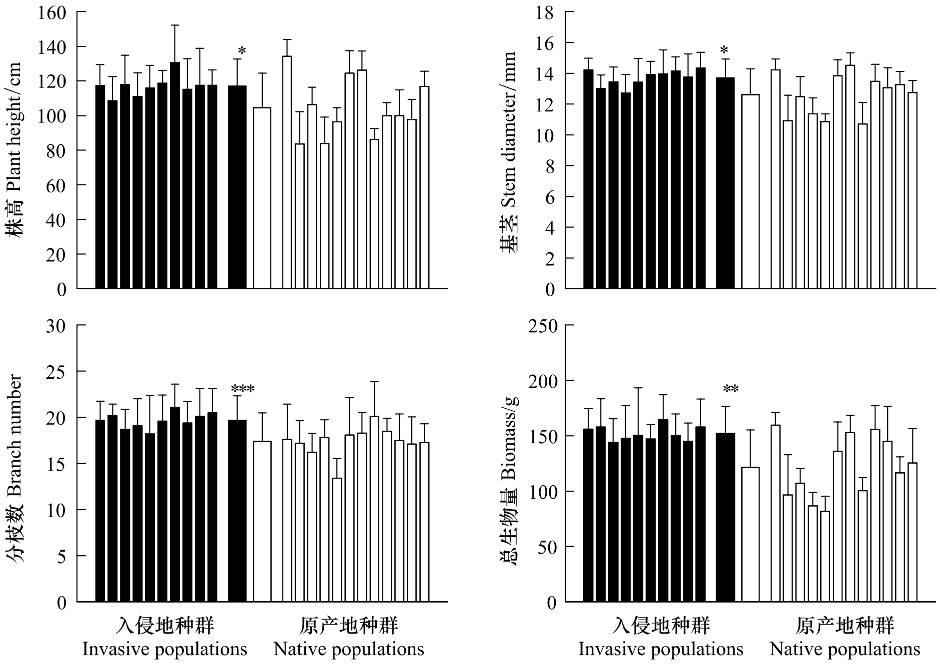

图 1　不同产地间飞机草株高、基茎、分枝数和生物量的差异

Fig.1　Differences in plant height, stem diameter, branch number, and total biomass between *Chromolaena odorata* plants from invasive and native populations

窄柱表示每个种群的平均值+标准误($n=10$);中间的两个粗柱表示入侵地和原产地种群的平均值+标准误(入侵地 $n=10$; 原产地 $n=12$);*、**和***分别表示产地间在 $P<0.05$、$P<0.01$ 和 $P<0.001$ 水平上差异显著(一元嵌套方差分析)

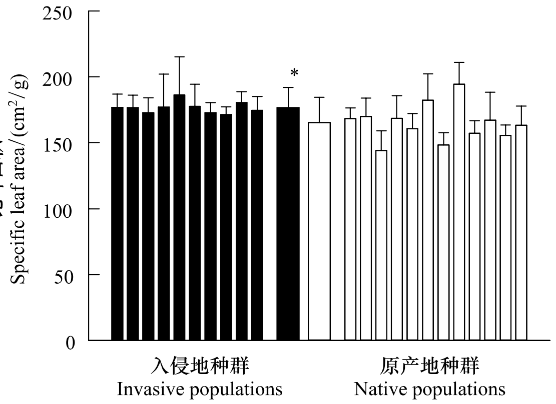

图 2　不同产地间飞机草比叶面积的差异

Fig.2　Difference in specific leaf area between *Chromolaena odorata* plants from invasive and native populations

窄柱表示每个种群的平均值+标准误($n=10$);中间的两个粗柱表示入侵地和原产地种群的平均值+标准误(入侵地 $n=10$; 原产地 $n=12$)。* 表示产地间在 $P<0.05$ 水平上差异显著(一元嵌套方差分析)

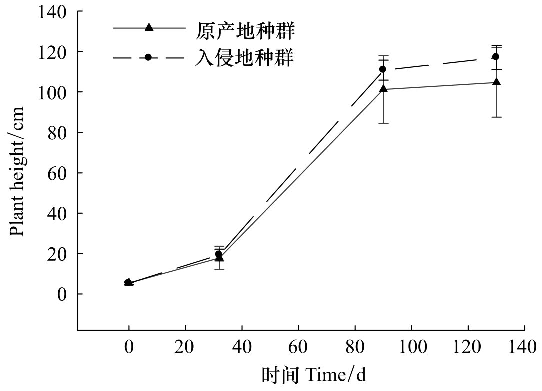

图 3　不同产地间飞机草种群株高生长速率的差异

Fig.3　Difference in growth rate between *Chromolaena odorata* plants from invasive and native populations

3　讨论

和 12 个原产地种群相比,飞机草入侵种群具有更高的生物量、株高、基茎、分枝数,高的生长活力有利于飞机草成功入侵,这与 EICA 假说一致[1]。株高和分枝数增加有利于飞机草在与本地植物竞争中获取更多的光照和空间,促进光合碳积累,并可通过荫蔽作用排挤本地植物,有利于其成功入侵[27-28]。高的比叶面积可能是飞机草入侵种群具有高生长活力的原因之一,比叶面积与生长速率密切相关[28],本文也发现,飞机草的比叶面积与生物量和分枝数呈正相关。Feng 等[29]发现,与外来非入侵植物相比,两种外来入侵植物较高的比叶面积导致其较低的叶

片构建成本、较多的叶氮分配到光合系统、较高的光合氮利用效率，促进其成功入侵。

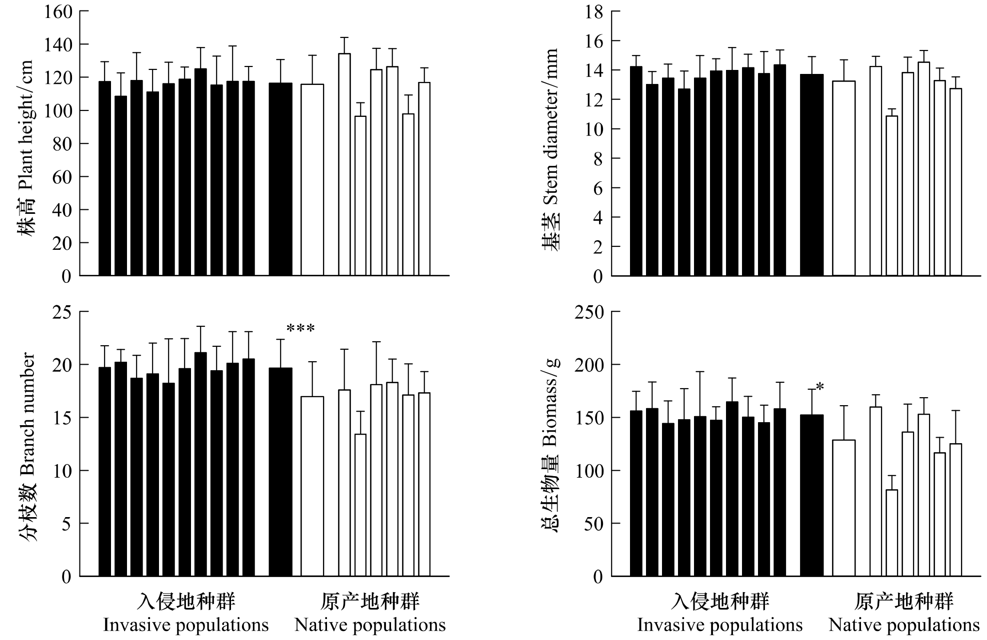

图 4　飞机草入侵地种群与原产地可能的祖先种群株高、基茎、分枝数和生物量的差异

Fig.4　Differences in plant height, stem diameter, branch number, and total biomass between *Chromolaena odorata* plants from 10 invasive populations and their six putative ancestral populations

窄柱表示每个种群的平均值+标准误($n = 10$) ; 中间的两个粗柱表示入侵地和原产地种群的平均值+标准误(入侵地 $n = 10$; 可能的祖先种群 $n = 6$) ; * 和＊＊＊分别表示产地间在 $P < 0.05$ 和 $P < 0.001$ 水平上差异显著(一元嵌套方差分析)

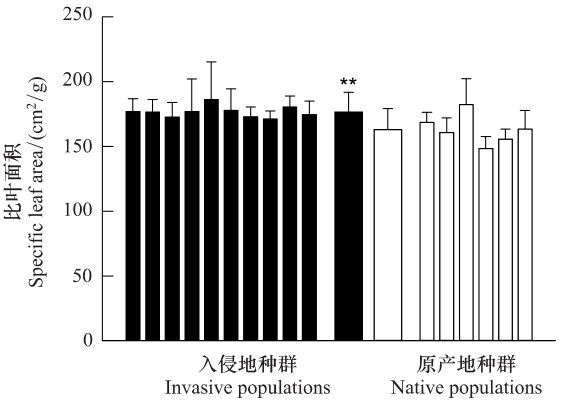

图 5　飞机草入侵地种群与原产地可能的祖先种群比叶面积的差异

Fig.5　Difference in specific leaf area between *Chromolaena odorata* plants from 10 invasive populations and their six putative ancestral populations

窄柱表示每个种群的平均值+标准误($n = 10$) ; 中间的两个粗柱表示入侵地和原产地种群的平均值+标准误(入侵地 $n = 10$; 可能的祖先 $n = 6$) ; ＊＊表示产地间在 $P < 0.01$ 水平上差异显著(一元嵌套方差分析)

飞机草高的生长活力可能是其在入侵地对逃离专性天敌取食压力做出的进化响应，把在原产地用于天敌防御的资源投入到生长的结果。张茹等[30]发现，在两种不同的养分条件下，飞机草入侵地种群茎和叶片半纤维素含量均低于原产地种群，这可能是其对入侵地专性天敌缺乏做出的进化响应; 但飞机草入侵种群总酚含量高于原产地种群，有利于飞机草防御入侵地的广谱天敌。

大量研究发现，外来植物入侵种群生长好于原产地种群[3-4,9,31]，但很少有研究比较入侵种群与其原产地可能的祖先种群间的差异[32-33]，不能排除奠基者效应的影响[2-3]。假如入侵种群只来源于原产地的一个或少数种群，而这个(些) 种群恰好竞争能力较强，通过比较多个入侵种群和多个原产地种群的差异，可能会发现支持 EICA 假说的证据; 反之，这个(些) 祖先种群竞争能力较弱，通过笼统比较入侵种群和原产地种群的差异，可能会发现不利于 EICA 假说的证据。这很有可能就是种由奠基者效应引起的入侵植物产地间的差异，而不是与引入后的适应进化的结果无关。Qin 等[2]认为，同质园种植实验排除了表型可塑性对入侵植物产地间比较结果的影响，但并不能排除奠基者效应的影响，为确定飞机草入侵种群与原产地种群间生物地学上的差异是否是引入后进化的结果，需比较飞机草入侵种群与其原

产地祖先种群间的差异。本研究表明，与来自佛罗里达和特立尼达的 6 个可能的祖先种群相比，飞机草入侵种群的总生物量等仍然高于原产地种群，即排除奠基者效应的可能影响后，飞机草入侵种群生长仍好于原产地种群，进一步证明入侵地飞机草高的生长速率很可能是引入后适应进化的结果。

本研究仅在一种养分条件下比较了飞机草原产地和入侵地种群间生长性状的差异，结论有一定的局限性，需要在更多的（养分）条件下比较飞机草入侵种群与其原产地祖先种群的差异。Liao 等[34]发现，实验条件影响同质种植环境下入侵植物产地间差异的比较结果，并认为这与入侵植物对入侵地非生物环境适应进化导致的生物量分配变化有关。

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