

人工群落中苗期紫茎泽兰的化感作用和对光环境的适应

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摘要:在有、无活性炭的条件下分别构建紫茎泽兰 (*Ageratina adenophora*) 与 4 种受体植物——飞机草 (*Chromolaena odorata*)、鬼针草 (*Bidens pilosa*)、胜红蓟 (*Ageratum conyzoides*) 和兰花菊三七 (*Gynura* sp.) 混种的人工群落, 研究了群落中紫茎泽兰的化感作用和对群落光环境的适应, 探讨了化感作用和光适应特性与其入侵性的关系。结果表明, 活性炭处理对 4 种受体植物的生长、生理特性影响不显著, 说明苗期紫茎泽兰化感作用不明显, 推测入侵初期化感作用不是紫茎泽兰排挤本地种的主要原因。4 种受体植物可以通过化感作用对紫茎泽兰产生某些影响, 但群落的光环境对其影响更大。紫茎泽兰能很好地适应群落中不同的光环境。苗期紫茎泽兰处于群落下层, 叶片受光指数低, 此时它能长期忍耐并缓慢生长; 随着叶片受光指数的升高, 其最大净光合速率、超氧化物歧化酶活性、叶绿素 a/b 比、总生物量、总叶面积、地茎、叶片数和分支数升高, 比叶面积和比茎长降低, 这有利于它维持叶片能量平衡并导致对邻近植物的严重遮荫。紫茎泽兰强的光适应能力、强光下对其它物种的遮荫效应与其入侵性密切相关。

关键词:紫茎泽兰; 化感作用; 光适应; 入侵性; 人工群落

文章编号:1000-0933(2006)06-1809-09 **中图分类号:**Q948 **文献标识码:**A

Allelopathy and light acclimation characteristic for *Ageratina adenophora* seedlings grown in man-made communities

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Abstract: As one of the most noxious plant invaders in China, *Ageratina adenophora* (Sprengel) R. M. King & H. Robinson not only severely threatens the biodiversity security and but also leads to huge economic costs to the country. To simulate the natural environments, *A. adenophora* was grown together with 4 receiver plants, *Chromolaena odorata* (L.) R. M. King & H. Robinson, *Bidens pilosa* L., *Ageratum conyzoides* L. and *Gynura* sp. respectively, to set-up four types of man-made communities. In half of the communities activated carbon was used to absorb allelochemicals, and in turn to eliminate allelopathy between plants. In this way allelopathy and irradiance acclimation characteristics of *A. adenophora* were studied separately, and their relationships with invasiveness were discussed.

After growing with *A. adenophora* for more than three months, *C. odorata*, *A. conyzoides*, *B. pilosa* and *Gynura* sp. in communities with activated carbon did not show any significant difference with the plants of the same species in communities without activated carbon in all of the morphological and physiological parameters measured in this study. These results indicated that in the early phase of invasion *A. adenophora* did not affect its neighbors by allelopathy. In contrast, *A. adenophora* were affected in few traits by the receiver's allelochemicals. *C. odorata* reduced its basal diameter; *B. pilosa* reduced its leaf

基金项目:中国科学院知识创新工程重大资助项目 (KSCX1-SW-13-0X-0X)

收稿日期:2005-02-06; **修订日期:**2005-09-25

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Foundation item: The project was supported by Key Project of Knowledge Innovation Engineering of Chinese Academy of Sciences (No. KSCX1-SW-13-0X-0X)

Received date:2005-02-06; **Accepted date:**2005-09-25

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numbers but increased its height; *Gynura* sp. reduced its ascorbate peroxidase activity. At early invasion stage, *A. adenophora* seedlings were located in the lower layer in all of the four types of microcosms constructed in this study, so irradiance around them was weak. *A. adenophora* could adequately acclimate to the light environments in the communities. Twelve parameters measured in this study were significantly associated ($p < 0.05$) with the light intensities that *A. adenophora* encountered in the communities. *A. adenophora* could tolerate weak light environments. With the increase of light intensity *A. adenophora*'s maximum net photosynthetic rate, activity of superoxide dismutase, the ratio of chlorophyll a to b, total plant biomass, total leaf area, basal diameter, numbers of leaves and branches increased, while its specific leaf area and specific stem length decreased. These morphological and physiological changes made it possible for *A. adenophora* to keep leaves energy balance and to shade-out its neighbors in high light environment. We attributed *A. adenophora*'s invasiveness to its remarkable light acclimation ability, especially to its shading-out effect on native plant species in high light environment.

Key words: *Ageratina adenophora*; allelopathy; light acclimation; invasiveness; man-made community

化感作用(Allelopathy)是自然界普遍存在的现象。从广义上讲,植物之间,植物与微生物间,植物与动物间都存在化感作用^[1]。研究发现在入侵群落中入侵种化感物质的合成和释放比在原群落中多^[2],入侵植物的化感物质能减少本地种的生物量^[3]、杀灭病菌、防御草食动物取食、降低枯落物的分解速率^[4]。Bais等^[5]认为化感作用在外来植物入侵过程中具有重要作用。紫茎泽兰(*Ageratina adenophora* (Sprengel) R. M. King & H. Robinson)是我国首批公布的危害最严重的入侵种之一,植株不同部位的浸溶物均有抑菌、抗虫作用,并能抑制一些植物的种子萌发和幼苗生长^[6-8],但到目前为止还没有直接的证据表明群落中紫茎泽兰能通过化感物质抑制本地种生理过程和生长,从而入侵成功。

研究植物间化感作用通常是将不同种的单个植株相互接触,观察某些生长指标的变化^[3,9],但自然状况下植株通常处于群落中,与简单的异种单株栽培方式显然不同。通过比较植物在同、异种植物组成的群落中的差别也可以研究化感作用,但是单种群落和混种群落内部环境(尤其是光环境)不同,这对植物也有影响,较难确定处理间差异的真正原因。活性炭是常用的吸附剂^[10],具有很大的活性表面积和吸附能力^[11]。化感物质多为有机酸、生物碱、酚和醌等物质,其主要通过雨水淋溶、残体分解、根系分泌等进入土壤而起作用。活性炭可以吸附水提取物和土壤中化感物质,在培养基质中加入活性炭可以排除实验室内和田间试验中化感作用的影响^[3,9,11-14]。在有、无活性炭的条件下,紫茎泽兰分别与其它4种植物混种组成人工群落,在相同群落条件下研究了紫茎泽兰的化感作用,主要关注:(1)入侵初期紫茎泽兰是否通过化感作用影响其它物种?(2)紫茎泽兰对群落内部光环境的适应;(3)化感作用和光适应特性与紫茎泽兰入侵性的关系。

1 材料和方法

1.1 试验地点和材料

试验在中国科学院西双版纳热带植物园进行。该园自然环境概况见冯玉龙等^[15]。

试验以紫茎泽兰(*Ageratina adenophora*)为供体植物,以飞机草(*Chromolaena odorata* (L.) R. M. King & H. Robinson)、鬼针草(*Bidens pilosa* L.)、胜红蓟(*Ageratum conyzoides* L.)和兰花菊三七(*Gynura* sp.)为受体植物,这5种植物都属菊科,亲缘关系较近,且都有化感物质^[16]。在云南省澜沧县和西双版纳州鬼针草、胜红蓟和兰花菊三七都是常见物种,但紫茎泽兰入侵后它们很快消失;飞机草是两地低海拔地区的入侵物种,在有些地区可与紫茎泽兰共存。

1.2 材料处理

在相对光强为50%的荫棚中挖长、宽各为2 m,深为0.4 m的坑24个(小区),坑内装满由河沙与林内10 cm以上表土(砖红壤)(2:1)混合而成的培养基质,并且在其中的12个小区中按体积均匀混入2%粉状活性炭^[9]。2003年9月从野外采集5种植物约10 cm的当年实生幼苗,把飞机草、鬼针草、胜红蓟和兰花菊三七分别与紫茎泽兰混种。每种混种处理3个加活性炭和3个未加活性炭的小区。每个小区株、行距均20 cm,共10行100株。每个混种处理的6个小区相互靠近,之间相隔50 cm,构成一个大区,不同大区相隔2 m以上。试

验期间,每天傍晚对植株地上部喷水以淋溶化感物质和补充土壤水分,每月施复合肥一次,随时清除杂草、防治病虫害。2003年12月测定了各物种最大净光合速率(P_{max})、叶绿素含量、抗氧化酶活性、植株生长和生物量分配等参数,测定各参数时每小区各选2个植株,计为6个重复。

1.3 光合参数的测定

按王俊峰等^[17]的方法用 Li-6400 便携式光合作用系统(LI-COR, Lincoln, Nebraska, USA)测定上数第三片离体成熟叶片光合作用光响应曲线,计算最大净光合速率 P_{max} 。在测定日黎明剪下植株,置于荫处备用。为避免导管中形成气泡影响水分运输,剪切操作在水中进行,且第一次剪切后从截面以上 10 cm 处再次剪切,全部操作过程中植株不离开水面。预备试验表明,紫茎泽兰连体和离体叶片光合作用差异不显著。

1.4 生化参数的测定

酶提取按照冯玉龙等^[18]的方法,超氧化物歧化酶(SOD)是清除活性氧的第一道防线,其活性参照 Giannopolitis 和 Ries^[19]的方法测定,酶活单位(unit)定义为单位时间内 1 ml 反应液中抑制 NBT 光还原 50% 的酶量;过氧化氢酶(CAT)能直接清除 H_2O_2 ,其活性参照 Jablonski 和 Anderson^[20]的方法测定,以每分钟 A_{240} 变化 0.01 为一个酶活单位;抗坏血酸过氧化物酶(APX)的活性按照 Zhang 和 Kirkham^[21]的方法测定,抗坏血酸(AsA)在 290 nm 的消光系数按 $2.8 \text{ mmol}/(\text{L}\cdot\text{cm})$ 计算,以 1 min 催化 $1\mu\text{mol}$ ASA 变化为一个酶活单位。

按 Lichtenthaler 和 Wellburn^[22]的方法测定叶绿素含量。丙二醛(MDA)是常用的衡量膜脂过氧化程度的指标,其含量的测定参照王以柔等^[23]的方法。可溶性蛋白质含量的测定采用考马斯亮蓝染色法^[24]。

1.5 生长参数的测定

用直尺(精确度 1mm)测定株高和冠宽,其中冠宽取两个垂直方向测定值的平均数;用游标卡尺测地茎(Basal diameter);用 Li-3000 型面积仪(LI-COR, Lincoln, Nebraska, USA)测叶面积;称重部分在 80°C 烘 48 h,电子天平(精确度 0.0001g)称量。求出如下参数^[25]:根生物量分数(root mass fraction, RMF, 根重/植株总重),支持结构生物量比(support biomass fraction, SBF, 支持结构生物量/植株总重),叶生物量分数(leaf mass fraction, LMF, 叶重/植株总重),根冠比(root mass/crown mass, R/C, 根生物量/地上部分生物量),平均单叶面积(mean leaf area, MLA, 总叶面积/叶片数),比叶面积(specific leaf area, SLA, 总叶面积/总叶重),叶面积比(leaf area ratio, LAR, 总叶面积/植株总重),叶根比(leaf area root mass ratio, LARMR, 总叶面积/总根重),比茎长(specific stem length, SSL, 茎长/茎重),冠面积(Crown area, $0.25\pi \times \text{冠宽}^2$),叶面积指数(leaf area index, LAI, 总叶面积/冠面积)。

1.6 叶片受光指数的测定

由于不同种植物生长速率不同,与不同种受体植物混种时紫茎泽兰所处的光环境不同。在测定紫茎泽兰叶片生理、生化参数之前,用 Li-1400(LI-COR, Lincoln, Nebraska, USA)测量了待测叶片(上数第二或三片)着生处和群落上方水平位置全天接受的光量子数,两者相比得出的数值再乘以荫棚透光率 50%,得到待测叶片相对太阳光强的受光指数(Index of light received by leaf)。生长和生物量分配指标对应的受光指数是目的植株顶部的值,测量方法同上。

1.7 统计分析

活性炭对各参数的影响采用 student's *t*-test 分析;不同混种处理对紫茎泽兰某参数的影响采用一维方差分析(One-way ANOVA)。比较多种因素对某一变量的影响采用协方差分析(ANCOVA),独立因素间的交互作用由软件自动取舍。所有统计分析用 SPSS 10.0(SPSS Inc. Chicago, Illinois, USA)完成,所有图形用 Sigma Plot 8.0(SPSS Inc. Chicago, Illinois, USA)绘制。

2 结果

2.1 活性炭处理对混种时受体植物和紫茎泽兰的影响

有、无活性炭处理组间 4 种受体植物的所有参数差异均不显著(表 1)。与飞机草混种时,活性炭处理使紫茎泽兰地茎显著升高;与胜红蓟混种时,活性炭处理使紫茎泽兰叶片显著增多,株高显著降低;与兰花菊三七混种时,活性炭处理使紫茎泽兰 APX 活性显著升高。各混种组合下活性炭处理对紫茎泽兰其它参数影响

表 1 活性炭对受体植物和紫茎泽兰各参数的影响
Table 1 The influence of activated carbon on the parameters of the receiver plants and *Ageratina adenophora* under each treatments

参数 Parameters	处理 I Treatment I		处理 II Treatment II		处理 III Treatment III		处理 IV Treatment IV	
	飞机草 <i>Chromolaena odorata</i>	紫茎泽兰 <i>Ageratina adenophora</i>	鬼针草 <i>Bidens pilosa</i>	紫茎泽兰 <i>Ageratina adenophora</i>	胜红蓟 <i>Ageratum conyzoides</i>	紫茎泽兰 <i>Ageratina adenophora</i>	兰花菊三七 <i>Gynura sp.</i>	紫茎泽兰 <i>Ageratina adenophora</i>
最大净光合速率	19.55 ± 2.06	12.58 ± 1.38	17.89 ± 1.66	9.20 ± 1.16	15.97 ± 1.18	13.43 ± 1.46	18.05 ± 2.09	9.91 ± 1.40
P_{max} ($\mu\text{mol}/(\text{m}^2 \cdot \text{s})$)	15.32 ± 1.36	12.36 ± 1.29	13.81 ± 0.70	6.47 ± 0.47	16.04 ± 1.54	11.69 ± 1.07	13.94 ± 0.43	10.20 ± 1.20
蛋白含量	18.33 ± 3.17	13.31 ± 1.51	12.33 ± 0.66	13.97 ± 2.33	21.65 ± 3.38	10.59 ± 0.92	11.38 ± 0.75	11.45 ± 2.92
Protein content (mg/g FW)	20.73 ± 1.66	13.28 ± 1.66	13.59 ± 1.11	15.73 ± 4.16	22.58 ± 3.42	13.94 ± 1.54	9.02 ± 1.54	10.61 ± 1.27
丙二醛含量	32.45 ± 4.3	20.95 ± 3.37	20.17 ± 4.76	19.33 ± 1.44	21.52 ± 2.25	15.77 ± 1.18	8.81 ± 1.57	21.39 ± 1.42
MDA content (nmol/g FW)	33.95 ± 1.89	15.85 ± 1.04	16.87 ± 1.49	15.65 ± 1.41	22.00 ± 2.63	21.10 ± 3.35	12.02 ± 2.06	24.16 ± 6.38
APX 活性	4.32 ± 0.45	4.21 ± 0.69	7.76 ± 1.65	4.16 ± 0.56	4.24 ± 0.44	3.73 ± 0.73	1.46 ± 0.26	2.80 ± 0.31
(unit/mg Protein)	3.94 ± 0.74	3.93 ± 0.45	7.88 ± 1.30	3.12 ± 0.28	3.34 ± 0.57	3.41 ± 0.51	1.69 ± 0.35	3.99 ± 0.21*
CAT 活性	3.18 ± 0.46	2.96 ± 0.46	7.02 ± 0.79	3.30 ± 0.50	5.39 ± 0.65	3.24 ± 0.55	10.27 ± 2.25	2.67 ± 0.31
(unit/mg Protein)	3.20 ± 0.47	4.08 ± 0.67	6.14 ± 0.77	3.53 ± 0.42	4.24 ± 0.64	3.02 ± 0.43	5.26 ± 1.29	2.37 ± 0.26
SOD 活性	6.20 ± 1.09	7.73 ± 0.33	7.76 ± 0.63	8.54 ± 1.29	5.69 ± 0.26	10.16 ± 0.50	4.90 ± 1.10	5.40 ± 1.33
(unit/mg Protein)	5.65 ± 1.17	8.76 ± 0.9	8.17 ± 1.12	4.99 ± 1.26	4.48 ± 0.80	9.18 ± 0.47	7.90 ± 0.84	5.90 ± 1.51
叶绿素含量	0.0277 ± 0.002	0.0357 ± 0.005	0.0373 ± 0.006	0.0292 ± 0.003	0.0372 ± 0.003	0.032 ± 0.006	0.0329 ± 0.002	0.0308 ± 0.002
Chlorophyll content (mg/cm ²)	0.0236 ± 0.002	0.0327 ± 0.006	0.031 ± 0.006	0.0258 ± 0.002	0.0365 ± 0.004	0.0316 ± 0.003	0.0278 ± 0.004	0.0294 ± 0.003
叶绿素 a/b 比	3.00 ± 0.21	3.01 ± 0.09	3.26 ± 0.06	2.79 ± 0.17	3.15 ± 0.15	3.23 ± 0.05	3.42 ± 0.10	3.07 ± 0.15
Chl a/b	3.38 ± 0.14	3.10 ± 0.11	3.27 ± 0.09	2.82 ± 0.05	3.24 ± 0.10	3.36 ± 0.05	3.16 ± 0.15	2.92 ± 0.04
株高	134.35 ± 6.65	84.18 ± 3.45	81.17 ± 5.70	86.22 ± 7.20	182.73 ± 5.62	71.33 ± 2.40	152.90 ± 3.28	73.48 ± 7.85
Plant height (cm)	117.77 ± 3.96	75.45 ± 5.97	87.40 ± 3.55	73.00 ± 5.58	186.2 ± 8.21	61.42 ± 1.13**	143.50 ± 6.08	82.07 ± 1.78
总重 Total	22.70 ± 2.39	7.54 ± 1.20	11.05 ± 2.45	6.60 ± 0.75	34.89 ± 9.24	8.03 ± 1.02	34.00 ± 3.46	5.48 ± 1.70
plant weight (g)	17.91 ± 2.17	8.81 ± 2.24	10.70 ± 0.12	5.88 ± 0.61	45.24 ± 14.4	10.46 ± 0.98	36.07 ± 5.12	4.00 ± 0.65
根生物量分数	0.132 ± 0.015	0.134 ± 0.004	0.063 ± 0.009	0.112 ± 0.014	0.057 ± 0.007	0.120 ± 0.006	0.068 ± 0.013	0.115 ± 0.012
RMF	0.145 ± 0.007	0.128 ± 0.007	0.093 ± 0.015	0.110 ± 0.018	0.056 ± 0.004	0.116 ± 0.014	0.069 ± 0.014	0.119 ± 0.009
支持结构生物量	0.598 ± 0.017	0.562 ± 0.013	0.682 ± 0.003	0.548 ± 0.018	0.842 ± 0.019	0.531 ± 0.008	0.731 ± 0.025	0.547 ± 0.022
分数 SBF	0.584 ± 0.009	0.554 ± 0.012	0.661 ± 0.008	0.552 ± 0.014	0.836 ± 0.010	0.514 ± 0.016	0.753 ± 0.032	0.546 ± 0.013
叶生物量分数	0.269 ± 0.013	0.304 ± 0.014	0.255 ± 0.012	0.339 ± 0.006	0.101 ± 0.018	0.349 ± 0.010	0.201 ± 0.022	0.338 ± 0.022
LMF	0.271 ± 0.007	0.318 ± 0.007	0.246 ± 0.014	0.339 ± 0.008	0.107 ± 0.011	0.369 ± 0.010	0.178 ± 0.032	0.335 ± 0.013
叶重分数	0.310 ± 0.015	0.351 ± 0.015	0.272 ± 0.010	0.383 ± 0.012	0.107 ± 0.019	0.397 ± 0.01	0.216 ± 0.024	0.382 ± 0.023
LMF	0.317 ± 0.008	0.365 ± 0.009	0.271 ± 0.012	0.38 ± 0.007	0.114 ± 0.011	0.418 ± 0.013	0.191 ± 0.033	0.380 ± 0.014
根冠比	0.154 ± 0.020	0.155 ± 0.005	0.068 ± 0.011	0.128 ± 0.018	0.061 ± 0.008	0.137 ± 0.007	0.074 ± 0.015	0.132 ± 0.016
RC (g/g)	0.169 ± 0.010	0.147 ± 0.010	0.103 ± 0.018	0.126 ± 0.024	0.060 ± 0.004	0.133 ± 0.018	0.075 ± 0.016	0.136 ± 0.012

续表 1

参数 Parameters	处理 I Treatment I		处理 II Treatment II		处理 III Treatment III		处理 IV Treatment IV	
	飞机草 <i>Chromolaena odorata</i>	紫茎泽兰 <i>Ageratina adenophora</i>	鬼针草 <i>Bidens pilosa</i>	紫茎泽兰 <i>Ageratina adenophora</i>	胜红刺 <i>Ageratum conyzoides</i>	紫茎泽兰 <i>Ageratina adenophora</i>	兰花菊三七 <i>Gynura sp.</i>	紫茎泽兰 <i>Ageratina adenophora</i>
总面积	1893.7 ± 174.5	1130.67 ± 179.2	969.0 ± 314.1	649.6 ± 112.9	1572.6 ± 652.2	984.2 ± 162.4	2573.2 ± 519.3	766.8 ± 197.8
Total leaf area (cm ²)	1440.0 ± 106.8	1240.2 ± 268.4	1007.7 ± 137.4	893.1 ± 96.4	1933.7 ± 732.3	1406.5 ± 114.3	2473.3 ± 597.2	673.3 ± 116.8
平均叶面	17.49 ± 1.21	19.16 ± 6.81	6.90 ± 0.22	12.28 ± 2.72	5.60 ± 1.01	13.21 ± 1.68	15.97 ± 1.02	14.09 ± 2.52
Mean leaf area (cm ²)	14.82 ± 0.66	18.31 ± 0.87	7.76 ± 1.46	14.03 ± 1.91	8.32 ± 1.02	10.93 ± 0.31	12.45 ± 1.76	15.77 ± 2.16
比叶面积	314.62 ± 8.40	496.52 ± 40.75	330.69 ± 32.11	318.98 ± 59.90	362.85 ± 32.00	342.67 ± 8.18	356.91 ± 9.78	437.92 ± 24.94
SLA (cm ² /g)	305.75 ± 17.76	459.48 ± 34.94	380.54 ± 37.63	450.85 ± 21.24	390.72 ± 45.63	366.55 ± 9.22	385.87 ± 18.7	502.20 ± 27.29
叶面积比 LAR (cm ² /g)	84.23 ± 2.60	149.91 ± 11.50	84.15 ± 8.14	108.18 ± 20.27	37.50 ± 8.45	119.89 ± 5.79	72.70 ± 9.87	150.57 ± 18.46
叶根比	83.19 ± 5.95	146.48 ± 12.41	93.93 ± 11.7	152.99 ± 9.49	40.17 ± 2.54	135.19 ± 3.94	71.35 ± 15.04	169.61 ± 15.38
LARMR (cm ² /g)	679.4 ± 89.0	1122.3 ± 88.4	1395.0 ± 245.5	1005.1 ± 249.2	694.3 ± 158.8	1017.4 ± 86.1	1293.3 ± 242.7	1393.4 ± 236.0
地茎	588.5 ± 66.1	1150.7 ± 78.7	1062.4 ± 189.8	1597.6 ± 298.1	729.1 ± 69.4	1262.2 ± 179.9	1249.2 ± 325.2	1480.1 ± 198.1
Basal diameter (mm)	7.99 ± 0.57	4.95 ± 0.43	6.23 ± 0.67	5.89 ± 0.37	8.14 ± 0.77	6.38 ± 0.38	8.38 ± 1.65	5.02 ± 0.58
叶片数	9.33 ± 0.81	6.53 ± 0.50*	7.59 ± 0.71	5.32 ± 0.36	8.69 ± 0.36	6.60 ± 0.13	11.54 ± 0.61	4.26 ± 0.18
Number of leaves	108.67 ± 6.66	74.67 ± 10.42	138.67 ± 41.07	62.00 ± 11.36	242.67 ± 84.7	80.50 ± 15.81	154.4 ± 25.22	59.33 ± 12.25
分枝数	98.17 ± 8.34	67.50 ± 13.04	132.33 ± 7.22	65.50 ± 6.47	228.50 ± 70.16	128.17 ± 8.34*	194.83 ± 38.26	45.67 ± 8.11
Number of branches	29.00 ± 2.37	9.00 ± 2.44	32.33 ± 10.17	5.50 ± 1.43	54.33 ± 13.21	13.17 ± 2.95	40.20 ± 5.08	6.50 ± 2.08
比茎长	24.83 ± 4.33	6.67 ± 1.91	28.00 ± 5.51	5.33 ± 1.59	71.83 ± 12.93	18.50 ± 1.18	45.00 ± 8.34	5.33 ± 1.50
SSL (cm/g)	14.30 ± 0.89	43.75 ± 8.57	23.29 ± 5.3	30.95 ± 2.5	18.15 ± 3.35	24.84 ± 2.57	11.65 ± 1.13	51.38 ± 8.01
冠面积	15.61 ± 1.06	33.79 ± 6.64	25.00 ± 0.73	41.20 ± 3.63	13.27 ± 0.91	21.79 ± 1.58	10.78 ± 1.07	53.36 ± 5.73
Crown area (cm ²)	1536.3 ± 131.5	1111.2 ± 210.5	2063.7 ± 355.5	649.3 ± 86.6	3687.4 ± 857.1	726.1 ± 101.4	6149.6 ± 1336.4	593.1 ± 198.9
叶面积指数	1.25 ± 0.09	1.37 ± 0.5	0.47 ± 0.11	1.11 ± 0.24	0.45 ± 0.17	1.38 ± 0.17	0.61 ± 0.15	1.41 ± 0.13
LAI	1.48 ± 0.26	1.21 ± 0.08	0.37 ± 0.09	1.14 ± 0.07	0.24 ± 0.02	1.57 ± 0.14	0.48 ± 0.1	1.22 ± 0.16

表中数值为 6 次重复的平均值 ± 标准误; 对于每一个参数, 上面一行表示不加活性炭的结果, 下面一行表示加活性炭的结果; * 和 ** 分别表示活性炭处理与对照在 $p < 0.05$ 和 $p < 0.01$ 水平差异显著; 处理 I、II、III 和 IV 分别表示紫茎泽兰与飞机草、鬼针草、胜红刺和兰花菊三七混种。The data in the table were mean ± S.E. of 6 replicates; For each parameter, the data in the upper line were for the plants without activated carbon treatment, those in the low line for the plants with carbon treatment; * and ** means significant difference between treatments with and without activated carbon at $p < 0.05$ and $p < 0.01$ levels (student's t-test), respectively; Treatment I, II, III and IV represent *Ageratina adenophora* mixed with *Chromolaena odorata*, *Bidens pilosa*, *Ageratum conyzoides* and *Gynura sp.*, respectively; MDA: Malondialdehyde; APX: Ascorbate peroxidase; CAT: Catalase; SOD: Superoxide dismutase; Chl.: Chlorophyll; RMF: Root mass fraction; SBF: Support biomass fraction; LMF: Leaf mass fraction; R/C: root mass/crown mass; MLA: Mean leaf area; LAR: Leaf area ratio; LARMR: Leaf area root mass ratio; SSL: Specific stem length; LAI: Leaf area index

不显著(表 1)。

2.2 受光指数、化感作用对混种处理中显著受活性炭影响的紫茎泽兰 4 个参数的影响

紫茎泽兰在不同混种处理中所处的光环境不同(图 1),这可能会影响其某些参数。通过协方差分析可以将活性炭和光的影响区分开, F 值大的因素对参数的变化起决定作用。表 1 中显著受活性炭影响的 4 个参数的变化都是由活性炭处理(即受体植物化感作用)决定的(表 2),尽管受光指数对与飞机草混种的紫茎泽兰的地茎和与胜红蓟混种的紫茎泽兰的叶片数也有显著影响。

2.3 受体植物对紫茎泽兰叶片受光指数的影响

测定生化和生长参数用的材料不同,所以紫茎泽兰受光指数有两个。苗期紫茎泽兰生长缓慢,处于群落下层,所处环境光强较低。与胜红蓟混种时紫茎泽兰叶片和植株的受光指数最高,与鬼针草混种时紫茎泽兰叶片和植株的受光指数最低(图 1)。同种组合有、无活性炭处理时,紫茎泽兰叶片和植株受光指数差异不显著(与兰花菊三七混种,用于生长指标测定的材料除外)。

表 2 受光指数和化感作用对混种处理时显著受活性炭影响的紫茎泽兰 4 个参数的影响

Table 2 The influence of index of light received by leaf and allelopathy on the 4 parameters that affected significantly by activated carbon in *Ageratina adenophora*

	受光指数		有、无活性炭	
	Index of light received by leaf		With or without activated carbon	
	F	P	F	P
处理 I 地茎 Basal diameter in treatment I	8.041	*	9.557	*
处理 III 株高 Plant height in treatment III	0.008	N	12.577	**
处理 III 叶片数 Number of leaves in treatment III	7.876	*	11.655	**
处理 IV 抗坏血酸过氧化物酶活性 APX activity in treatment IV	0.000	N	7.398	*

以有无活性炭处理为固定变量,受光指数为协变量,对表 1 中显著受活性炭影响的 4 个参数进行一维协方差分析。N 表示处理与对照间无差异,* 和 ** 分别表示处理与对照间在 $p < 0.05$ 和 $p < 0.01$ 水平差异显著。处理 I、III 和 IV 的含义见表 1。One-way ANCOVA was carried out for the 4 parameters significantly influenced by activated carbon in table 1. During the analyses, the activated carbon treatment was used as fixed factors and index of light received by leaf as co-variance. N indicates non-significant difference between treatment and control, while, * and ** means significant difference at $p < 0.05$ and $p < 0.01$ levels respectively. See table 1 for treatment I, III and IV

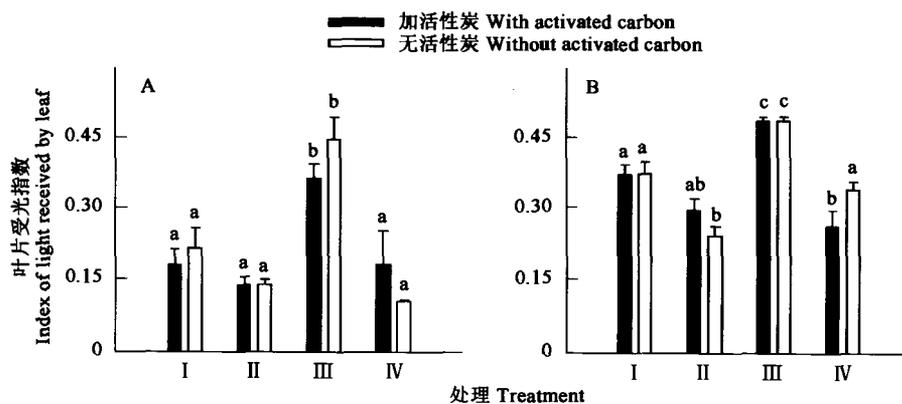


图 1 与不同受体植物混种时紫茎泽兰叶片受光指数

Fig. 1 Index of light received by leaf in *Ageratina adenophora* mixed with different species

A 是测定生理生化参数所用植株的叶片受光指数;B 是测定生长指标所用植株的受光指数;数据为平均值 + 标准误 ($n = 6$);不同字母表示处理间差异显著 ($p < 0.05$, LSD 检验);处理 I、II、III 和 IV 的含义见表 1 A represents the index of light received by leaf of *A. adenophora* involved in physiological and biochemical parameters determination; B represents the index of light received by plant, in *A. adenophora* involved in growth related parameters determination; The data were mean + S.E. of 6 replicates; Different letters indicate significant difference ($p < 0.05$, LSD test) among treatments; See table 1 for treatment I, II, III and IV

2.4 4 种混种处理对紫茎泽兰各参数的影响

可从两个方面分析紫茎泽兰所处的环境:混种物种和有无活性炭处理。混种物种间除化感相互影响外,

还有水、肥和光的竞争,由于本试验条件下不缺水 and 肥,可以只考虑物种间化感作用和光的竞争。表 1 表明有活性炭处理对紫茎泽兰的大部分参数影响不显著,表 2 中受化感决定的参数,在有活性炭的小区中其值也与化感无关。把受化感控制的数据舍去后,可以只从光竞争角度分析紫茎泽兰。一维方差分析(One-way ANOVA,以 4 种混种处理为固定因子, $n = 47$)表明,与不同受体植物混种时紫茎泽兰的 12 个参数差异显著,分别为:最大净光合速率($F = 6.929, p < 0.001$)、超氧化物歧化酶活性($F = 5.227, p < 0.01$)、叶绿素 a/b 比($F = 8.129, p < 0.001$)、株高($F = 3.064, p < 0.05$)、总生物量($F = 5.176, p < 0.01$)、叶生物量分数($F = 5.584, p < 0.01$)、总叶面积($F = 4.783, p < 0.01$)、比叶面积($F = 6.180, p < 0.001$)、地茎($F = 9.251, p < 0.001$)、叶片数($F = 6.530, p < 0.001$)、分枝数($F = 11.997, p < 0.001$)、比茎长($F = 9.434, p < 0.001$)。并且,这些参数都与受光指数有显著的回归关系(图 2)。其中株高和叶生物量分数与受光指数呈显著的二次方程关系,在受光指数 0.35 左右时分别达到最大(图 2D)和最小值(图 2L)。其它参数与受光指数呈显著的线性关系,其中比叶面积(图 2H)和比茎长(图 2L)随受光指数的升高显著降低,其它参数增大。

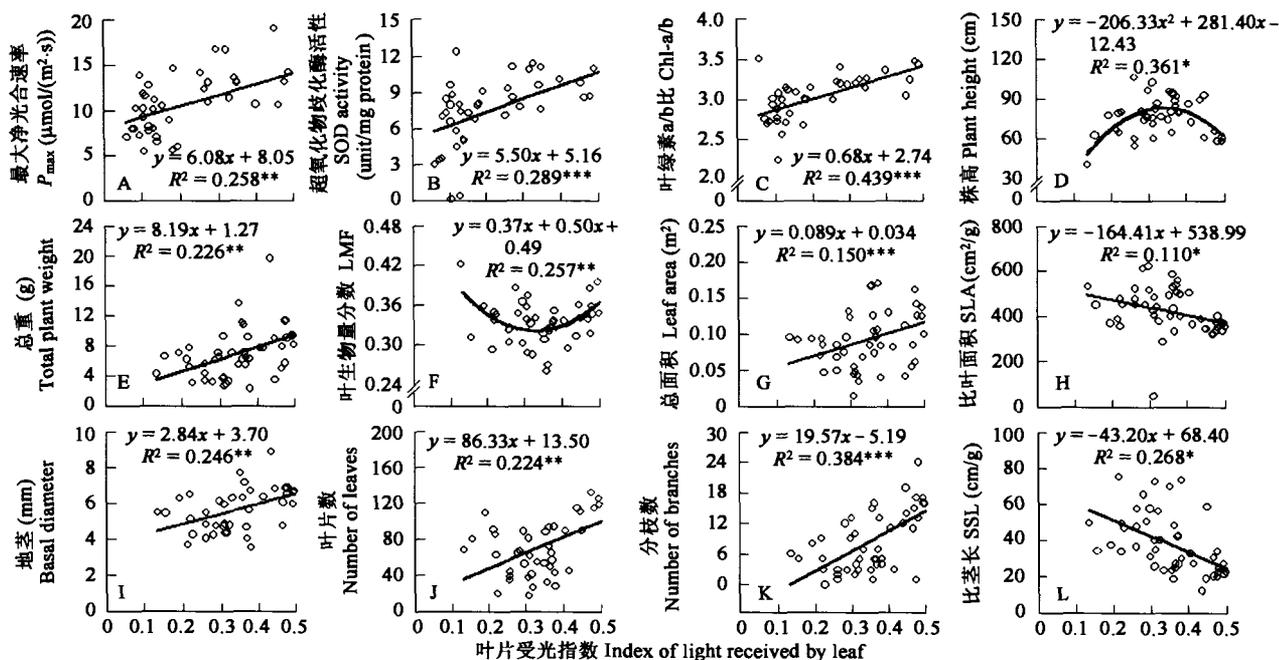


图 2 显著受光影响的紫茎泽兰各参数与叶片受光指标的回归关系

Fig.2 The relationships between index of light received by leaf and other parameters influenced significantly by irradiance in *Ageratina adenophora* 化感效应已被排除,图中列出了回归方程、决定系数(R^2)和方差分析结果,其中*、**、***分别表示在 $p < 0.05, p < 0.01, p < 0.001$ 水平自变量和因变量显著关联;缩写的含义见表 1 Allelopathic effects were excluded. Regression equation, coefficient of determination (r^2) and ANOVA results were shown; *, ** and *** means significant association between the dependent and independent variables at $p < 0.05, p < 0.01, p < 0.001$ levels, respectively; See table 1 for all abbreviations

3 讨论

紫茎泽兰扩散最快、最有可能的方式是通过种子的远距离传播。在其入侵的最初阶段,它容易在资源充足且竞争压力小的空旷环境中(如路边、河岸、撂荒地等)定植下来。本试验模拟了这种情况。在这样的环境中,紫茎泽兰的幼苗必定会与其它植物幼苗发生相互作用,其关系大体可分为两个方面:一是对环境因子——诸如对光、肥、水等的竞争;另一方面通过向环境释放化学物质,以此影响周围植物,即化感作用。

有些入侵种在幼苗期(入侵初期)就通过释放化感物质来抑制其它植物幼苗的生长,例如原产欧亚大陆的 *Centaurea diffusa* 与某些北美本地种混种后,本地种的生物量减少了 85.7%^[3]。但紫茎泽兰不是这样,试验期间它对混种在一起的其它植物影响不显著(表 1),说明在入侵初期紫茎泽兰不能直接通过化感作用抑制这些植物。已知紫茎泽兰成熟植株能产生化感物质,并能抑制包括兰花菊三七在内的多种植物的种子萌发和幼苗

生长^[6],表明不能用化感作用的种间特异性解释上述现象。这可能是由于苗期紫茎泽兰不产生化感物质,或化感物质少,不足以影响其它植物,当然此时紫茎泽兰生物量低也是原因之一。在入侵初期,不合成或少合成化感物质对紫茎泽兰未必是坏事。在种子发芽后相当一段时间内,紫茎泽兰植株极微小且生长很慢,可以设想,即使这期间它能够旺盛地分泌化感物质,也很难达到能影响临近植物生长的剂量。而且化感物质主要来自次生代谢途径,次生代谢的活跃进行会影响原生代谢,进而影响植物的生长^[26]。

幼苗期是紫茎泽兰生活史中最脆弱的时期,植株处于光线较弱的群落下层,在与本地种的竞争中处于劣势,需要化感物质抑制与之竞争的本地物种生长,但此时却未检测到紫茎泽兰的化感作用(表1)。入侵中、后期,紫茎泽兰成熟植株处于群落的中上层,已具有较强的抗逆性,在竞争中已处于优势地位,即使没有化感作用紫茎泽兰仅凭其生理、生长上的优势已可以排挤掉本地物种^[17,25],为什么偏偏在并不需要的时候紫茎泽兰才耗费能量牺牲生长^[26]合成化感物质?推测此时紫茎泽兰合成化感物质并不是为了抑制本地物种,而是为了防止病虫害的发生。在入侵中后期紫茎泽兰个体增大,处于群落中上层,数量增多,群落生物多样性降低,群落中的单优种很容易受到病虫害的攻击,所以有必要合成化感物质来对抗这种威胁,这与自然状态下紫茎泽兰很少有病虫害的现象是一致的。这种化学防御策略可能是紫茎泽兰具有入侵性的重要原因之一^[28]。对病菌、害虫有害的物质同样会影响植物^[27],所以此时能观测到紫茎泽兰对植物的化感作用。

虽然混种植物的化感物质会对紫茎泽兰幼苗产生某些影响(表1),但最主要的影响却体现在对生存资源之一——光的竞争上(图2)。本试验中,紫茎泽兰叶片受光指数最低只有10%左右(图1),在如此弱的光下很多本地阳性物种无法生存,但紫茎泽兰能长期存活并缓慢生长(图2)。随着叶片受光指数的增大,紫茎泽兰 P_{max} 、叶片数、总面积和分枝数显著升高(图2),这都利于其在强光下保持叶片能量平衡,快速生长,形成对邻近植物的遮荫。荫棚中的盆栽试验表明,紫茎泽兰可以在4%~100%光下生长^[17,25]。弱光下的长期忍耐和强光下对邻近植物的遮荫是紫茎泽兰表现入侵性的重要原因。荫棚中红光/远红光比(R/FR)不变,自然群落中植物间相互遮荫形成的弱光环境 R/FR 明显降低^[29]。紫茎泽兰幼苗的许多生理、生长特性对这两种光环境中的光强的响应相似^[17,25](图2),表明光强是决定紫茎泽兰光适应的主导因素。紫茎泽兰的光适应能力强,适应光强范围大,具体适应机制见文献^[17,25]。

以往对于紫茎泽兰化感作用的研究都是在实验室条件下,以生物测定法(bioassays)完成的,所得到的结果只能说明紫茎泽兰是否有化感物质、化感物质的具体成分及作用^[6-8],而不能直接说明在自然条件下化感物质与其入侵性的真实关系。本文通过构建模拟群落的方法,在一定程度上揭示了这种关系。但本试验的受体植物较少,时间较短,也未考虑紫茎泽兰入侵对养分循环、土壤动物和微生物等的影响。在更真实的自然条件下研究化感作用与紫茎泽兰入侵性的关系是必要的。

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