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# 生态学报

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# 生态学报

(SHENGTAI XUEBAO)

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**封面图说:** 白鹭展翅为梳妆, 玉树临风巧打扮——这是大白鹭繁殖期时的美丽体态。大白鹭体羽全白, 身长 94—104cm, 寿命 20 多年。是白鹭中体型最大的。繁殖期的大白鹭常常在湿地附近的大树上筑巢, 翩翩飞舞吸引异性, 其繁殖期背部披有蓑羽, 脸颊皮肤从黄色变成兰绿色, 嘴由黄色变成绿黑色。大白鹭是一个全世界都有它踪迹的广布种, 一般单独或成小群, 在湿地觅食, 以小鱼、虾、软体动物、甲壳动物、水生昆虫为主, 也食蛙、蝌蚪等。

**彩图提供:** 陈建伟教授 国家林业局 E-mail: cites.chenjw@163.com

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郭伟, 李钧敏, 胡正华. 酸雨和采食模拟胁迫下克隆整合对空心莲子草生长的影响. 生态学报, 2012, 32(1): 0151-0158.

Guo W, Li J M, Hu Z H. Effects of clonal integration on growth of *Alternanthera philoxeroides* under simulated acid rain and herbivory. Acta Ecologica Sinica, 2012, 32(1): 0151-0158.

## 酸雨和采食模拟胁迫下克隆整合对 空心莲子草生长的影响

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**摘要:** 研究表明克隆整合可以显著提升异质环境中克隆植物的生长, 然而当克隆植物遭受均质环境压力时, 整合对植物生长影响的研究相对较少。以典型入侵克隆植物空心莲子草 (*Alternanthera philoxeroides*) 为例, 研究均质环境压力酸雨和采食模拟胁迫对空心莲子草生长的影响, 以及克隆整合在空心莲子草适应不利环境过程中所起的作用。酸雨设 3 种浓度梯度: pH 值 3.5、pH 值 4.5 和 pH 值 6.5 (对照); 采食设 3 种水平: 不去叶、去叶 50% 和去叶 90%; 整合水平: 匍匐茎切断和连接。结果表明: 无论保持或切断匍匐茎的连接, 酸雨处理都不影响空心莲子草生物量。当保持匍匐茎连接时, pH 值 4.5 酸雨处理增加了空心莲子草匍匐茎长度和分株数目, 因此, 低度酸雨可能对空心莲子草生长有一定的促进作用。同样, 无论匍匐茎是否被切断, 采食处理都显著降低了空心莲子草克隆片段生物量, 而显著增加了叶片数目。当切断匍匐茎连接时, 采食处理使空心莲子草分株数目显著增加。结论: 空心莲子草能较好地适应酸雨和采食的环境压力, 当空心莲子草全部克隆分株遭受均质环境胁迫时, 克隆整合并不能显著改善它的生长。

**关键词:** 克隆整合; 模拟酸雨; 模拟采食; 均质环境压力; 空心莲子草

### Effects of clonal integration on growth of *Alternanthera philoxeroides* under simulated acid rain and herbivory

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**Abstract:** Effects of clonal integration on growth and reproduction of plants in heterogeneous environments have been extensively studied, but relatively little is known about the roles of clonal integration in homogeneous, stressful environments. We conducted a greenhouse experiment to investigate the effects of clonal integration on the stoloniferous invasive plant *Alternanthera philoxeroides* (alligator weed) under homogeneous, stressful environments, i. e., under simulated acid rain and herbivory. There were three levels of acid rain treatments [pH = 6.5 (control), 4.5 (mild acid rain) and 3.5 (severe acid rain)], three levels of herbivory [0 (control), 50% (moderate herbivory) and 90% leaf removal (heavy herbivory)] and two levels of clonal integration (no integration-stolon connection was severed; with integration-stolon connection was intact). In the control (i. e., no acid rain and no herbivory), severing stolon did not affect biomass or biomass allocation of alligator weed, but increased total stolon length, number of ramets and number of

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leaves. The simulated acid rain treatments did not affect biomass of alligator weed, no matter whether the stolons were intact or severed. When the stolons were left intact, the mild acid rain treatment (pH=4.5) markedly increased total stolons length and number of ramets, suggesting that mild acid rain may improve plant growth. Meanwhile, the acid rain treatments significantly affected biomass allocation to roots and stolons. Under mild acid rain treatment (pH=4.5) biomass allocation to stolons increased significantly, whereas that to roots decreased; however, severe acid rain (pH=3.5) did not affect biomass allocation of alligator weed. When the stolons were severed, the acid rain treatments did not affect growth or biomass allocation of alligator weed. The results suggest that alligator weed can well adapt to acid rain stress and clonal integration play a limited role under acid rain stress. When the stolons were left intact, the simulated herbivory treatments markedly affected biomass and number of leaves of alligator weed, but did not affect total stolon length or number of ramets. With increasing herbivory levels, biomass of alligator weed significantly decreased, but number of leaves increased. When the stolons were severed, effects of the herbivory treatments on biomass, total stolon length and number of leaves were the same as those in the intact clonal fragments. Therefore, despite the status of the stolons, the simulated herbivory treatments markedly decreased growth of alligator weed. The herbivory treatments also modified biomass allocation of alligator weed. With increasing herbivory levels, biomass allocation to leaves significantly increased and that to stolons and roots significantly decreased. The results suggest that alligator weed can also well adapt to herbivory stress and clonal integration also plays a limited role under herbivory stress. These features of alligator weed may be helpful for it to invade into new habitats, and clonal integration plays a limited role under homogeneous stressful, environments.

**Key Words:** clonal integration; simulate acid rain; simulate herbivory; homogeneous environmental stress; *Alternanthera philoxeroides*

植物入侵已成为全球生态系统的巨大威胁<sup>[1-3]</sup>。入侵植物具有很强的环境适应性,且生长快速<sup>[4-5]</sup>。一些入侵植物如空心莲子草、薇甘菊和五爪金龙等,能通过匍匐茎的生长产生大量分株,入侵当地群落并取代本地植物种,形成单优物种群落<sup>[6-7]</sup>,这种克隆生长习性对于植物入侵可能具有重要意义<sup>[8]</sup>。这类植物的分株在一定时间内都相互连接,分株间可以交换水分、养分、光合产物和次生产物等,即发生克隆整合现象<sup>[9-10]</sup>。当相互连接的克隆分株处于不同条件的斑块时,斑块间的生境条件梯度可能改变克隆整合格局<sup>[10-11]</sup>。不同斑块异质性的对比会影响克隆整合的强度和方向,而斑块对比度可通过克隆整合格局来改变克隆植物表型可塑性<sup>[12-13]</sup>。

研究表明,克隆整合可以显著提高植物幼苗的建立和成株的生长<sup>[14-17]</sup>,以及植物在逆境下的生存和生长,改变植物群落物种组成和生物量<sup>[15,18]</sup>。这些逆境包括低光<sup>[19-20]</sup>、低养<sup>[10]</sup>、水淹胁迫<sup>[21]</sup>、干旱胁迫<sup>[22]</sup>、盐胁迫<sup>[23]</sup>、沙埋<sup>[24-26]</sup>、风蚀<sup>[17]</sup>和重度采食<sup>[27]</sup>。尽管对克隆整合作用的研究已经广泛进行,但这些研究多数是讨论克隆整合在异质性环境中的作用,有关均质环境条件下时(如酸雨侵蚀和昆虫啃食等)克隆整合作用研究却比较缺乏。

在我国,受酸雨影响地区面积已占国土面积的40%<sup>[28]</sup>。研究表明,酸雨对陆地生态系统有明显影响,一方面酸雨淋溶对植物地上部分直接造成伤害,另一方面酸雨导致土壤酸化,因而对植物产生间接影响<sup>[29-31]</sup>。同样,采食在自然界也普遍存在,对植物群落结构和多样性都会产生显著影响<sup>[32-35]</sup>。植物经常遭受不同程度的采食作用,如昆虫蚕食和大型食草动物啃食等。植物通常具有忍耐动物采食的能力,遭受采食后会进行自我补偿作用<sup>[36-37]</sup>。

本文通过温室实验,研究酸雨和采食模拟影响下克隆整合对入侵克隆植物空心莲子草生长的影响。空心莲子草(*Alternanthera philoxeroides*(Mart.) Griseb.)是苋科莲子草属多年生草本植物,通常生长于河岸、湿地等水陆过渡地带<sup>[38]</sup>,入侵能力强,已经成为世界公认的恶性杂草之一<sup>[38-39]</sup>。自然状态下空心莲子草通常会遭受酸雨侵蚀、小型昆虫啃食以及大型动物的践踏。因此,本文研究在酸雨和采食模拟胁迫下克隆整合对空心莲



子草生长的影响,拟验证以下假说:(1)酸雨和采食会降低空心莲子草克隆分株的生长;(2)酸雨和采食会改变空心莲子草生物量分配格局;(3)克隆整合会提高空心莲子草在采食和酸雨胁迫下的克隆生长。

## 1 材料和方法

### 1.1 材料培养和实验设计

采用 378 个大小近似的空心莲子草克隆片段作为实验材料,这些克隆片段均繁殖于一个在江西省采集的空心莲子草片段。将空心莲子草克隆片段移栽到大小相同的营养钵中(10 cm×10 cm,直径×高),每个片段包括一个母株、多个子株和一个生长点。然后将第 2 个分株的节点用牙签固定到一个同样的营养钵中,让其生根,其中装满由沙子和草炭 1:1 混合成的基质。378 个空心莲子草片段随机分为 3 个区组,培养 1 星期开始实验。

模拟酸雨(Acid rain: A)对空心莲子草的影响:自然界酸雨为 pH 值小于 5.6 的降水,我国降水年均 pH 值范围在 4.3—7.47,且酸雨类型为典型的硫酸性酸雨<sup>[40]</sup>,因此,准备超纯水(pH 值 = 6.5, CK)以及 pH 值为 4.5 和 3.5 的硫酸溶液。用喷壶对每区组持续喷洒 15min,喷洒频率为每 5d 一次,时间选择在傍晚太阳落山之后。

模拟采食(Herbivory: H)对空心莲子草的影响:每一区组中,同时对空心莲子草的两部分进行去叶处理。先前的研究显示:通过摘除叶片来模拟采食和由莲草直胸跳甲的直接采食对空心莲子草生物量的影响是相似的<sup>[34]</sup>。因此,采用摘除叶片的方法来模拟昆虫对空心莲子草的采食。随机将每一区组分 3 个小组,对每小组克隆片段进行 3 种处理:不去叶(CK)、去叶 50%(50% H)和去叶 90%(90% H)<sup>[37]</sup>,将摘取的叶片收集,记录数目,然后烘 48 h,称量。去叶是随机摘除已成熟的叶片,不影响新叶和新芽的生长,第一次去叶在喷洒酸雨之后第 2 天进行,每隔 15d 去叶 1 次。每小组中,随机将上述 21 个空心莲子草的匍匐茎切断(Severed: S),而另外 21 个的匍匐茎保持连接(图 1)。

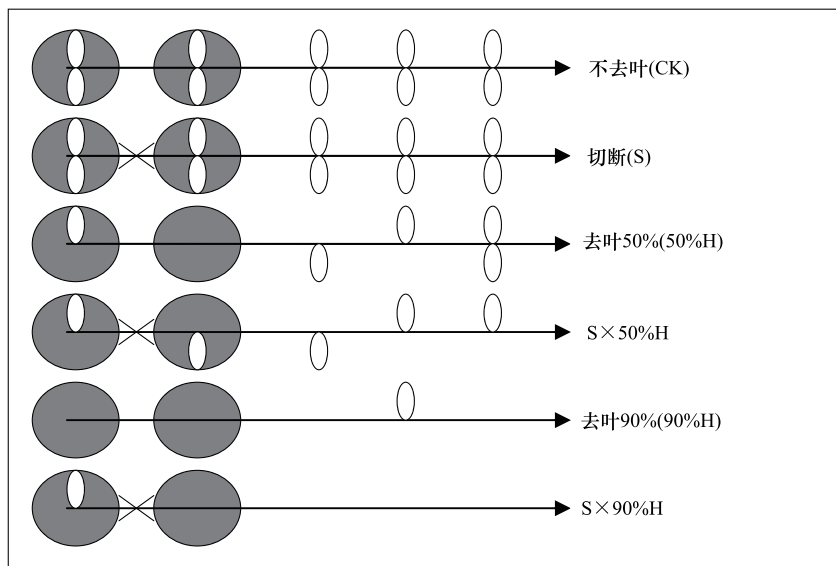


图 1 实验设计图示

Fig. 1 Schematic representation of the experimental design

每个空心莲子草片段包括一个母株(第 1 个营养钵中的片段)、多个子株和一个生长点(黑箭头);对母株和子株各个分株上的叶片在 3 个水平上(0, 50% 和 90%)随机摘除;母株和子株之间的匍匐茎要么保持连接,要么切断(叉号)

本实验在温室进行,排除了土壤养分、水分利用、光照强度、外界干扰和竞争等对实验的影响。实验时间为 2009 年 8 月 12 日至 2009 年 10 月 15 日。在收获时,分别统计了每个空心莲子草克隆片段的分株数目、叶片数目(包括摘掉的叶片数)、匍匐茎总长度等指标。然后将其分为根、茎、叶,在 70 °C 下烘 48 h,分别称重。

## 1.2 数据分析

采用 3 因素方差分析方法分析了切断匍匐茎、3 种酸雨水平和 3 种去叶水平以及三者之间交互作用对空心莲子草克隆生长和生物量分配格局的影响,并且用 Duncan 多重比较对显著性差异的结果进行了分析,以上过程均在 SPSS 16.0 统计分析软件中完成。

表 1 匍匐茎切断,采食程度,酸雨水平和三者交互对空心莲子草克隆片段的生长和生物量分配格局的影响

Table 1 Effects of stolon severance, herbivory, acid rain and the interaction on growth and biomass allocation of *Alternanthera philoxeroides* in whole clonal fragments

空心莲子草克隆片段 Clonal fragments	切断(S) $F_{1,378}$	采食(H) $F_{2,378}$	酸雨(A) $F_{2,378}$	S×H $F_{2,378}$	S×A $F_{2,378}$	A×H $F_{4,378}$	S×H×A $F_{4,378}$
生物量 Biomass	0.21 <sup>ns</sup>	84.96 <sup>***</sup>	0.30 <sup>ns</sup>	2.17 <sup>ns</sup>	1.10 <sup>ns</sup>	1.40 <sup>ns</sup>	0.05 <sup>ns</sup>
匍匐茎长度 Total stolon length	6.32 *	0.43 <sup>ns</sup>	6.35 **	2.90 <sup>ns</sup>	2.32 <sup>ns</sup>	1.12 <sup>ns</sup>	0.07 <sup>ns</sup>
叶片数目 Number of leaves	11.47 **	877.75 <sup>***</sup>	3.20 <sup>ns</sup>	1.79 <sup>ns</sup>	0.86 <sup>ns</sup>	3.76 **	0.87 <sup>ns</sup>
分株数目 Number of ramets	5.81 *	1.43 <sup>ns</sup>	6.67 **	3.09 *	2.78 <sup>ns</sup>	0.20 <sup>ns</sup>	0.47 <sup>ns</sup>
叶片生物量分配 Leaves biomass allocation	3.10 <sup>ns</sup>	952.16 <sup>***</sup>	2.32 <sup>ns</sup>	0.18 <sup>ns</sup>	0.54 <sup>ns</sup>	1.16 <sup>ns</sup>	0.39 <sup>ns</sup>
匍匐茎生物量分配 Stolon biomass allocation	0.22 <sup>ns</sup>	22.84 <sup>***</sup>	11.61 <sup>***</sup>	0.67 *	0.97 <sup>ns</sup>	0.73 <sup>ns</sup>	1.34 <sup>ns</sup>
根系生物量分配 Root biomass allocation	0.06 <sup>ns</sup>	65.84 <sup>***</sup>	16.32 <sup>***</sup>	0.63 <sup>ns</sup>	1.34 <sup>ns</sup>	0.57 <sup>ns</sup>	1.22 <sup>ns</sup>

显著性水平 ns  $P>0.05$ , \*  $P<0.05$ , \*\*  $P<0.01$ , \*\*\*  $P<0.001$

## 2 结果

### 2.1 模拟酸雨、采食和切断匍匐茎连接对空心莲子草生长的影响

切断匍匐茎连接显著增加了整个空心莲子草克隆片段匍匐茎长度、分株数目和叶片数目,但是并不影响空心莲子草生物量(表 1,图 2)。保持匍匐茎连接时,酸雨处理不影响空心莲子草克隆片段的生物量和叶片数目,显著影响匍匐茎长度和分株数目(表 1,图 2),pH 值 4.5 酸雨下,空心莲子草匍匐茎长度和分株数目都显著增加(图 2);切断匍匐茎连接时,酸雨处理不影响空心莲子草生长(表 1)。保持匍匐茎连接的情况下,采食处理显著影响空心莲子草克隆片段的生物量和叶片数目,而不影响匍匐茎长度和分株数目(表 1,图 2);随着采食程度增加,空心莲子草生物量显著减少,而叶片数目显著增加(图 2)。保持匍匐茎连接时,采食处理不影响空心莲子草分株数目;当切断匍匐茎连接时,采食处理显著增加了空心莲子草分株数目,呈显著交互效应(表 1,图 2)。

### 2.2 模拟酸雨、采食和切断匍匐茎连接对空心莲子草生物量分配的影响

切断匍匐茎连接不影响空心莲子草生物量分配格局(表 1,图 3)。保持匍匐茎连接时,酸雨处理显著影响匍匐茎和根系生物量分配(表 1),pH 值 4.5 酸雨下,空心莲子草对匍匐茎生物量分配显著增加而对根系生物量分配显著减少(图 3);切断匍匐茎连接时,酸雨处理不影响空心莲子草生物量分配格局(表 1)。保持匍匐茎连接情况下,采食处理显著影响空心莲子草生物量分配(表 1),随着采食程度的增加,空心莲子草对叶片生物量分配显著增加(图 3);90% 采食处理显著降低了对匍匐茎和根系生物量分配(图 3)。

## 3 讨论

克隆整合能显著提升植物在异质环境中的表现。Noble 和 Marshall 发现,生长在高营养条件下的沙生苔草母株能向生长在低营养条件下的子株输出营养<sup>[41]</sup>;Roiloa 和 Retuerto 对野草莓的研究发现,当子株生长在重金属污染的土壤中时,与其相连生长在正常土壤中的母株光化学效率也会增强<sup>[42]</sup>。然而,在自然栖息地中,克隆植物也会遭受均质环境压力,即整个克隆体都遭受胁迫。研究在这种压力环境下克隆整合的作用能进一步揭示克隆植物的生态适应策略。

自然生境中,酸雨侵蚀和动物采食都是空心莲子草所面临的经常性事件。酸雨和采食对空心莲子草的影响具有一定的普遍性,即胁迫处理(环境压力)通常是针对空心莲子草整个克隆体的。结果显示(图 2),空心

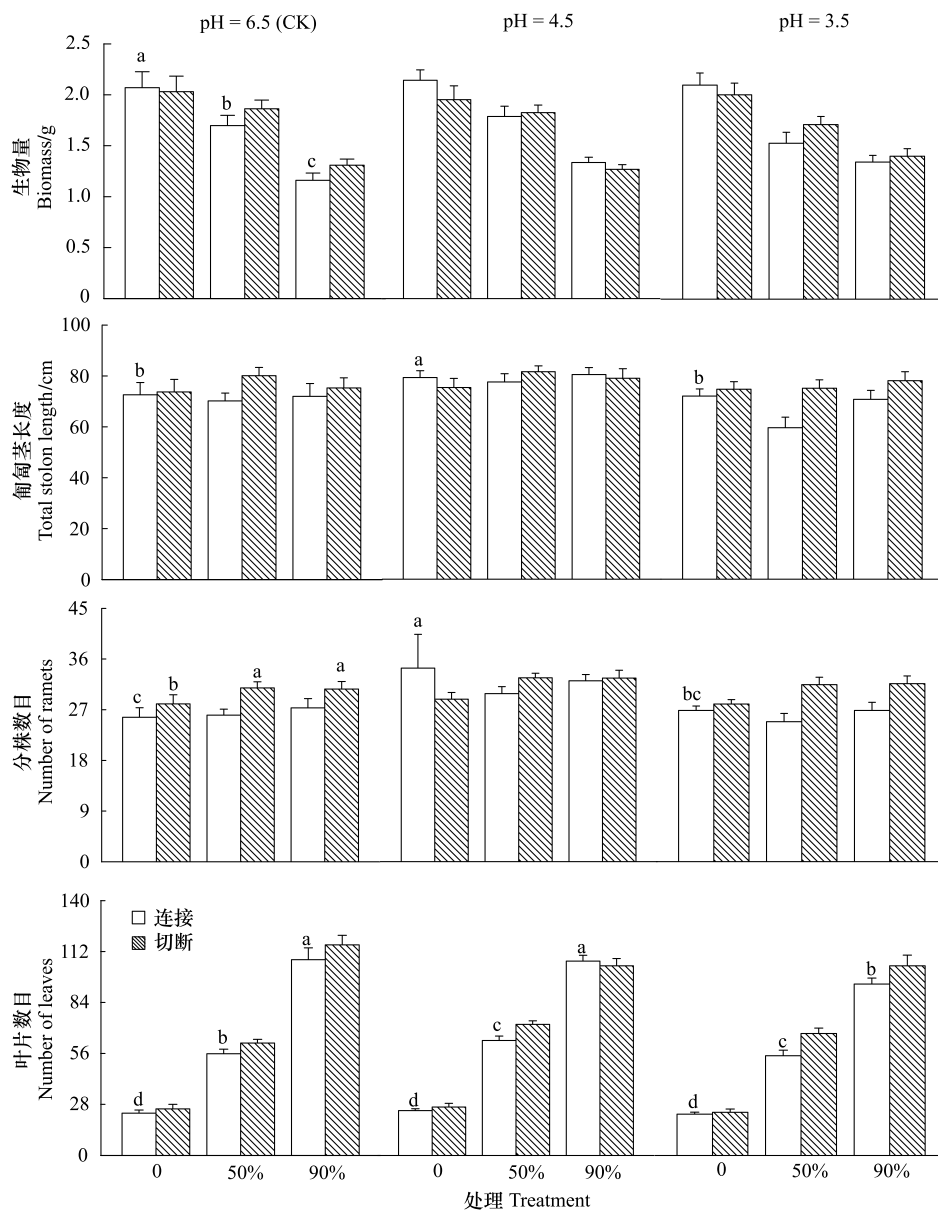


图2 切断或保持分株间匍匐茎连接的空心莲子草克隆片段在不同 pH 酸雨和不同程度采食下的生物量、匍匐茎长度、分株数目和叶片数目

Fig. 2 Biomass, total stolon length, number of ramets and number of leaves in the clonal fragments of *Alternanthera philoxeroides* suffered from acid rain and herbivory connected or disconnected stolon between the ramets

相同小写字母表示处理间在  $P < 0.05$  水平上没有显著差异,不同小写字母表示处理间在  $P < 0.05$  水平上显著差异;处理代码同表 1

莲子草对酸雨胁迫有较好的适应性。两种酸雨处理均没有显著降低空心莲子草的生长,反而轻度酸雨胁迫 (pH 值 4.5) 对空心莲子草生长有一定的促进作用。一方面,由于实验材料都是选取长势较好的克隆分株,且外来入侵植物可能对酸雨胁迫存在较强的抗性<sup>[43]</sup>。另一方面,轻度酸雨胁迫可诱导植物的自我保护,植物会投入更多的资源给可能受损的器官和组织<sup>[29]</sup>。当遭受酸雨侵蚀时,空心莲子草的母株和子株对营养物质都有积极的需求,同时,由于所受影响较弱,因此,克隆整合作用(空心莲子草内部的资源传输)对空心莲子草的帮助不显著。当对空心莲子草喷洒重度酸雨时(例如,pH 值 2.5),可能会对空心莲子草的生长产生严重影响,并且克隆整合的作用也会有所体现。

昆虫对植物的采食在湿地上频繁发生,而分布在这些地方的克隆植物可能通过克隆整合方式很好地适应

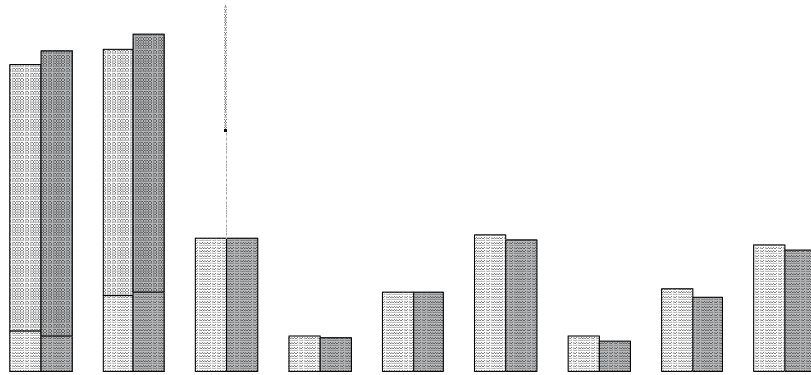


图3 切断或保持分株间匍匐茎连接的空心莲子草克隆片段在不同 pH 酸雨和不同程度采食下对根系、匍匐茎和叶片的生物量投资分配  
**Fig. 3 Proportional biomass allocation to roots, stolons and leaves in the clonal fragments of *Alternanthera philoxeroides* suffered from acid rain and herbivory connected or disconnected stolon between the ramets**

相同小写字母表示处理间在  $P < 0.05$  水平上没有显著差异,不同小写字母表示处理间在  $P < 0.05$  水平上显著差异;处理代码同表 1

这种干扰,从而比那些共生的非克隆植物更具生长优势<sup>[27]</sup>。然而,本实验中,当切断匍匐茎连接时,采食处理下的空心莲子草分株数目显著增加了(图 2),并且空心莲子草生物量也倾向于增加(图 2)。一种解释是:克隆植物的各个分株既是一个整体,又是一个独立个体,当克隆体所有分株都处于严重环境压力下时,克隆片段只有在满足自身生长的情况下,才可能援助压力端的分株;同时,克隆体内产生和维持分株间连接的物质(匍匐茎),也会损耗克隆植物本身的能量,并且分株间进行物质传输也会花费能量<sup>[44]</sup>。另一种解释是,匍匐茎的断裂阻止了匍匐茎顶端优势的信号传导,空心莲子草所拥有的强烈顶端优势被释放,空心莲子草克隆分株上的腋芽受刺激快速形成并生长<sup>[45-46]</sup>。因此,当空心莲子草遭受采食时,保持连接的空心莲子草片段生物量比切断的空心莲子草片段生物量有所降低。

采食显著降低了空心莲子草的生长(图 2),并显著改变了生物量分配格局(图 3)。对叶片的采食,使空心莲子草对叶片做出积极的补偿作用(图 2)。然而对于整个克隆片段而言,被采食后表现为不足补偿(图 2),且随着采食程度增加,对叶片的超补偿和对整体的不足补偿效应更加显著。对照组中,会有个别空心莲子草分株的老叶出现黄化脱落现象,但在去叶处理的空心莲子草片段中,未出现老叶黄化脱落现象。因此,适当摘除叶片会使空心莲子草内部资源得到充分利用。当植物器官受到损伤时,能通过对不同组织重新分配营养和利用存储器官的存储资源来修复受损组织<sup>[35]</sup>。这与本文实验结果一致,采食处理显著增加了对叶片的生物量分配,而显著减少了对根系和匍匐茎的生物量分配。因此,植物组织的破坏或去除会导致健康组织器官资源的转移,并且消耗整个系统的资源。

综上所述,空心莲子草能较好地适应酸雨和采食的环境压力。克隆整合没有显著提升均质压力环境下空心莲子草的克隆生长,即切断匍匐茎后空心莲子草长势依然良好。因此,在对空心莲子草的治理上,单纯的生物防治或机械去除可能效果不会十分显著。

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