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# 水淹对克隆植物空心莲子草种内关系的影响

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**摘 要** 为检验“水淹程度可以改变植物种内关系的类型和强度”的假说, 将克隆植物空心莲子草(*Alternanthera philoxeroides*)的3种不同密度的植株(每盆种植1、4或16株)置于4种不同的水淹处理下(水位分别为–20 (不水淹)、0、20或40 cm), 研究不同水淹程度对空心莲子草种内关系的影响。随着植株密度和水淹程度的增加, 空心莲子草的生长显著减慢, 但密度效应在不同的水淹处理下显著不同。在不发生水淹的情况下, 植株密度对生长的负面(竞争)效应最强; 在水位为0和20 cm的情况下, 植株密度对生长的效应仍为负面的, 但影响强度相对减小; 而在水位为40 cm的情况下, 空心莲子草植株的生物量随着植株密度的增大而倾向于增加。进一步分析相对邻体效应时发现, 随着水淹程度的增加, 相对邻体效应显著增加, 并且数值从负值(不水淹)逐渐变为正值(40 cm水位下)。这些结果支持胁迫梯度假说, 表明水淹可以影响植物的种内关系, 即随着水淹程度的增加, 植物种内竞争作用减弱, 而易化作用增强。

**关键词** 竞争, 易化, 植物作用关系, 胁迫, 胁迫梯度假说, 水位

## Effects of waterlogging on intraspecific interactions of the clonal herb *Alternanthera philoxeroides*

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**Abstract**

***Aims*** Plant-plant interaction is fundamental in plant ecology. Many studies have examined the effects of environmental factors such as light, nutrients and water on plant-plant interactions, but few have tested the effects of waterlogging. Our objective is to investigate the effects of waterlogging on intraspecific interactions and test the hypothesis that waterlogging can modify the type and intensity of intraspecific interactions.

***Methods*** We grew plants of *Alternanthera philoxeroides* outdoors at three densities (1, 4 or 16 plants in one pot) and four levels of waterlogging severity (water levels of –20 (no waterlogging), 0, 20 or 40 cm). After three months, plants were harvested and data were collected.

***Important findings*** With increasing plant density or waterlogging severity, growth of *A. philoxeroides* decreased significantly. However, the effect of density differed greatly under different levels of waterlogging severity. With no waterlogging, the effect of density on growth was negative and the competition intensity was high. With water levels of 0 and 20 cm, the density effect was still negative, but the intensity decreased. With a water level of 40 cm, however, the density effect was positive. Moreover, waterlogging severity significantly affected the relative neighbor effect and its values increased gradually from negative (under no waterlogging) to positive (in 40 cm). The results support a stress-gradient hypothesis and suggest that waterlogging can affect intraspecific interactions. With increasing waterlogging severity, intensity of competition decreases while that of facilitation increases.

**Key words** competition, facilitation, plant-plant interactions, stress, stress gradient hypothesis, water level

植物之间的相互作用是植物生态学的核心内容之一, 主要包括竞争和易化(或促进facilitation)两个方面(Bruno *et al.*, 2003; Callaway, 2007)。竞争是植物之间的负作用关系(negative interactions)中最常见的一种类型, 而易化作用是指植物之间的正作用关系(positive interactions; Callaway, 1997, 2007)。竞争和易化直接影响着植物个体的生长、形态、发育和生活史, 进而影响植物的分布、群落中物种的

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共存和多样性，以及生态系统的结构和功能(Brooker, 2006; Brooker *et al.*, 2007; Callaway, 2007; Vellend, 2008; Yu *et al.*, 2010; Li *et al.*, 2011a, 2011b)。

植物间的互作类型(竞争和易化)及互作强度可能随着环境条件的变化而改变(Bertness & Callway, 1994; Callaway, 2007; Crain, 2008)。Bertness和Callway于1994首次提出“胁迫梯度假说” (stress-gradient hypothesis)，认为随着环境中胁迫的增加，易化作用的重要性或强度将增加，而竞争作用将减弱。一些研究结果支持该假说(Walker & Chapin, 1987; Bertness & Shumway, 1993; Bertness & Hacker, 1994; Greenlee & Callaway, 1996; Kitzberger *et al*., 2000)。例如，频繁的植食活动会阻碍或防止劣势植物种被竞争排斥(Silvertown & Lovett-Doust, 1993)；营养水平对竞争有显著的影响(Wilson & Keddy, 1986)；延长光照时间和改变光照强度也能改变植物的种间关系(Hershenson, 1962; Anersson & Lundegårdh, 1999)。但也有一些研究发现，易化作用在中度胁迫环境下最强，而在非胁迫环境下和极端胁迫环境下均表现为竞争(Maestre & Cortina, 2004; Maestre *et al.*, 2005)。

水淹是许多植物常常面临的环境胁迫(李茂松等, 2004；胡田田和康绍忠, 2005)。国内外有关水淹对植物影响的研究主要集中在形态和生理方面(Holmes & Klein, 1987; Drew, 1997; Jackson & Ram, 2003；罗芳丽等, 2007; Hashiguchi *et al.*, 2009; Luo *et al.*, 2011)。例如，完全水淹可以减少光照强度和气体含量进而影响植物的气体交换(Drew, 1997; Jackson & Armstrong, 1999; Jackson & Ram, 2003)，而植物对水淹则表现出各种形态和生理响应，包括节间和叶柄的伸长、叶面积的增加(Setter & Laureles, 1996; Dinka & Szeglet, 1999; Voesenek *et al.*, 2004; Mommer *et al.*, 2005)，以及代谢途径的转换等(Perata & Alpi, 1993)。然而，有关水淹对植物之间作用关系，尤其是种内关系的研究尚不多见。

在一个室外实验中，作者将入侵克隆植物空心莲子草(*Alternanthera philoxeroides*)的3种不同密度的植株置于4种不同的水淹处理下，研究不同水淹程度对空心莲子草种内关系的影响。基于胁迫梯度假说(Bertness & Callway, 1994)，作者预测：在不发生水淹的情况下，空心莲子草的种内关系以竞争为主，而在完全水淹的情况下，种内关系可能以易化为主。

## 1 材料和方法

### 1.1 研究物种

空心莲子草，又名喜旱莲子草，为苋科莲子草属多年生宿根草本，原产于南美洲，被包括中国在内的许多国家列为恶性入侵植物(潘晓云等, 2007; Dong *et al.*, 2010)。空心莲子草根状茎单轴分枝，其幼苗生长到一定时期时，从其横生茎节点处产生侧向生长的匍匐茎，匍匐茎生长一段时间后可以继续产生次级茎。空心莲子草在陆地和水域均可生长，具有繁殖快、抗逆性强等特点，很容易大规模爆发，难以消除(Longstreth *et al*., 1984; Sainty *et al*., 1998; 潘晓云等, 2007; Dong *et al*., 2010)。空心莲子草具有较高的形态可塑性(Bazzaz, 1996; Geng *et al.*, 2007; 潘晓云等，2007)和生理可塑性(Yan *et al.*, 1990; Sainty *et al.*, 1998)。

### 1.2 材料采集和培养

本实验所用空心莲子草于2009年4月中旬采于浙江台州，属于陆生型，种植于中国科学院植物研究所实验网室内的水池(7 m × 1.2 m × 1 m)内进行培养(Dong *et al*., 2010)。2009年7月，剪取两端各含少许间隔子的空心莲子草茎节，种在装有沙子的塑料盒中培养。4周后，挑选出具有4个节间且节的粗细相近的植株，用于本实验的研究；其中的20株用于测量初始匍匐茎长度((13.7 ± 0.39) cm，平均值±标准误差)和初始生物量((0.201 3 ± 0.019 5) g，平均值±标准误差)。

### 1.3 实验设计

实验容器为直径21 cm、高20 cm的黑色塑料盆，盆的底部和侧面各有几个出水孔，盆内基质为泥炭土和沙子的均匀混合物(体积比1:1)。实验采用密度和水淹两个因素的因子实验设计(factorial design)。密度处理包括3个水平：(1)低密度(low density)，即每盆中央位置种植空心莲子草1株，不存在种内关系；(2)中密度(medium density)，即每盆种植空心莲子草4株，分为两排两列，同一排/列的植株之间的距离为4.0 cm；(3)高密度(high density)，即每盆种植空心莲子草16株，分为四排四列，同一排/列的相邻植株之间的距离为2.5 cm。低、中、高3种密度的重复分别为16、12和8个。水淹处理包括4个水位：(1)

–20 cm (不水淹)——种植有空心莲子草的塑料盆放置于水池中, 盆的底部与水池内的水平面平齐, 土壤平面高于水面20 cm; (2) 0 cm —— 塑料盆内的土壤平面与水平面平齐; (3) 20 cm —— 塑料盆内的土壤平面位于水平面下20 cm; (4) 40 cm —— 塑料盆内的土壤平面位于水平面下40 cm。4个水位对于陆生型空心莲子草的影响分别为: 适宜、轻微胁迫、轻微胁迫、重度胁迫。每个水淹处理内, 所有密度重复均分为4份, 按照低密度处理4个重复、中密度处理3个重复、高密度处理2个重复的顺序间隔摆放。摆放时靠近北侧水池壁, 以免水池壁遮阴。

实验于2009年8月6日开始, 10月12日结束。实验期间调整水龙头流量, 保持池子水位高度相对一致。

### 1.4　数据收集和分析

实验结束时, 清数空心莲子草每个存活植株的分枝数、节数和叶片数, 测量植株的主(匍匐)茎长、总茎长和总叶面积。总叶面积的测定用WinFOLIA多用途叶面积仪(WinFOLIA Pro 2004a, Regent Instruments Inc., Canada)。对低密度处理, 测量每个植株主茎自顶端起第4到第7节的节间长度, 计算平均节间长; 对中密度和高密度处理, 在每个塑料盆内选择两个植株, 测量其主茎第4到第7节的节间长度, 计算平均节间长。然后将每个盆内的植株分成根、茎和叶, 在70 ℃烘箱内烘干48 h后称重。对中密度和高密度处理, 用盆内植株的总生物量(根生物量、茎生物量和叶生物量)、总叶面积、总节数、总茎长、总叶片数和总节数除以盆内存活的植株数, 分别得到平均植株生物量、叶面积、茎长、节数、叶片数和分枝数。比节间长(specific internode length)由总茎长除以茎生物量得到。

采用相对邻体效应(relative neighbor effect, *RNE*)来度量在每种水淹处理下中密度和高密度空心莲子草的种内竞争强度(Kikvidze *et al.*, 2006)。计算公式如下:

$$RNE = (M - C)/\max(M, C)$$

其中, *M*是有相邻个体(即分别在中密度和高密度处理下)的植株的平均生物量, *C*是没有相邻个体(即在低密度处理下)的植株的平均生物量。*RNE*的数值在–1和1之间; 负值表示负的作用关系, 即竞争作用, 正值表示正的作用关系, 即易化作用(Kikvidze *et al.*, 2006)。在竞争(*RNE*为负值)的情况下, *RNE*数值越大(或绝对值越小)竞争强度越小; 在易化(*RNE*为正值)的情况下, *RNE*数值越大, 易化强度越高。

采用两因素方差分析(two-way ANOVA)考察密度(低、中和高)和水淹处理对空心莲子草平均植株生长指标(生物量、叶面积、茎长、节数和叶片数)和形态指标(节间长、比节间长、主茎长和分枝数)的影响。采用两因素方差分析检验密度(中和高密度)和水淹处理对*RNE*的影响。采用SPSS (13.0)统计学软件进行数据分析。

## 2　结果

### 2.1　水淹和密度对生长的影响

水淹处理显著影响空心莲子草的总生物量、根、茎和叶各部分生物量(表1); 随着水淹程度(水位)的增加, 其总生物量、根、茎和叶生物量逐渐下降(图1)。密度处理显著影响总生物量、根和叶生物量(表1); 随着密度的增加, 总生物量、根和叶生物量显著下降(图1), 但密度的这种效应在不同的水淹处理下显著不同(表1, 密度和水淹的交互效应均极显著)。在水位为–20 cm和不水淹的情况下, 密度的负面效应极为显著; 在水位为0和20 cm的情况下, 密度的负面效应相对减少; 而在水位为40 cm的情况下, 总生物量和茎生物量随着密度的增大而倾向于增加(图1)。

水淹和密度处理均显著影响空心莲子草平均植株总节数、总叶面积、总茎长和总叶数(表1)。随着密度或水淹程度的增加, 总叶面积、总叶数和总节数显著减少(图2)。水淹和密度的交互作用对这4个生长性状具有极显著的效应(表1)。密度的负效应在水位为–20 cm的情况下最为显著; 在水位为0和20 cm情况下, 密度的效应仍为负的, 但其效应相对小于–20 cm的情况; 而在40 cm情况下, 在中密度下总节数、总茎长和总叶数倾向于最大(图2)。

### 2.2　水淹和密度对相对邻体效应的影响

水淹处理对*RNE*的影响极为显著($F_{3,72}$ = 23.65, $p < 0.001$)。随着水淹程度的增加, *RNE*显著增加, 并且数值从负值(–20 cm水位下)逐渐变为正值(40 cm水位下), 并且这种效应在中密度和高密度处理下是一致的(图3)。密度处理($F_{1,72} < 0.01$, $p = 0.977$)以及密度与水淹处理间的交互作用($F_{3,72}$ = 2.27, $p$ =

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**表1** 水淹和植株密度对空心莲子草植株生长的影响
**Table 1** Effects of waterlogging and plant density on growth of *Alternanthera philoxeroides* plant

| 性状 Trait | 水淹 Waterlogging | | 植株密度 Plant density | | 交互作用 Interaction | |
|---|---|---|---|---|---|---|
| | *F* | *p* | *F* | *p* | *F* | *p* |
| 总生物量 Total biomass | 44.7 | <0.001 | 9.9 | <0.001 | 5.0 | 0.001 |
| 根生物量 Root biomass | 83.5 | <0.001 | 15.4 | <0.001 | 14.2 | <0.001 |
| 茎生物量 Stem biomass | 30.0 | <0.001 | 2.8 | 0.075 | 1.3 | 0.297 |
| 叶生物量 Leaf biomass | 45.5 | <0.001 | 52.6 | <0.001 | 14.7 | <0.001 |
| 总叶面积 Total leaf area | 28.4 | <0.001 | 40.4 | <0.001 | 6.5 | <0.001 |
| 总节数 No. of total nodes | 24.8 | <0.001 | 158.9 | <0.001 | 16.4 | <0.001 |
| 总茎长 Total stem length | 22.6 | <0.001 | 193.9 | <0.001 | 13.2 | <0.001 |
| 总叶片数 No. of total leaves | 42.0 | <0.001 | 72.6 | <0.001 | 20.1 | <0.001 |

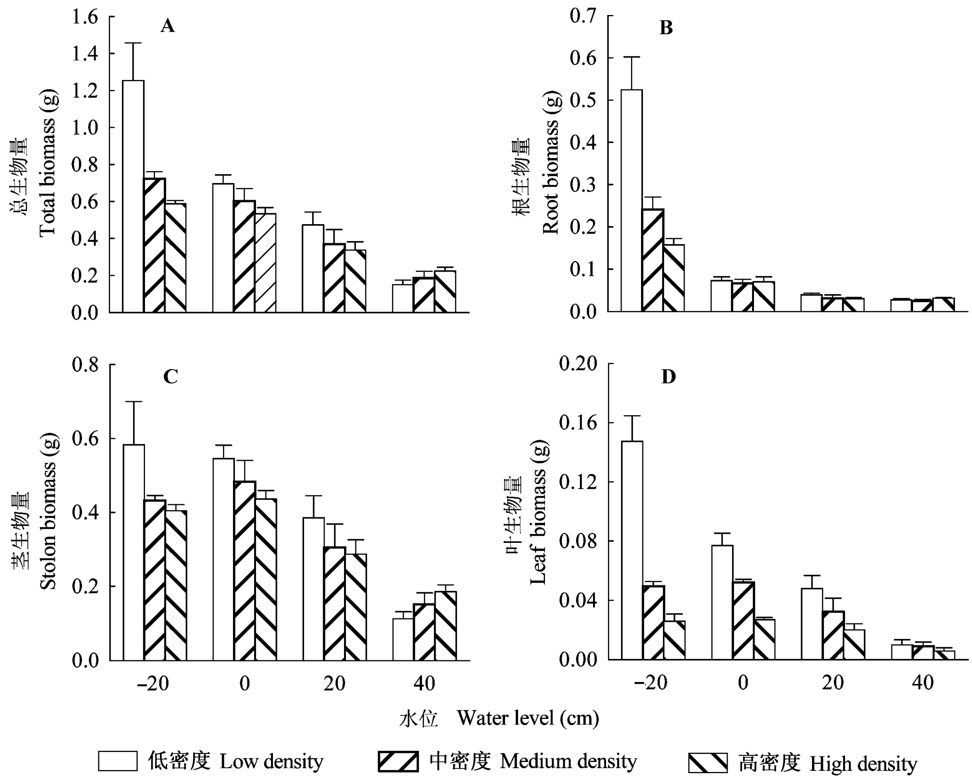


**图1** 水淹(水位)和植株密度对空心莲子草植株总生物量(**A**)、根生物量(**B**)、茎生物量(**C**)和叶生物量(**D**)的影响(平均值±标准误差)。
**Fig. 1** Effects of waterlogging (water level) and plant density on total biomass (**A**), root biomass (**B**), stolon biomass (**C**) and leaf biomass (**D**) per *Alternanthera philoxeroides* plant (mean ± *SE*).

0.088)对*RNE*没有显著的效应(图3)。

## 3 讨论

完全水淹显著抑制了空心莲子草的生长, 这与以前对许多植物的研究结果相一致(曾淑华等, 2004; 胡田田和康绍忠, 2005; 王海峰等, 2008)。完全水淹可能是通过削弱光照强度和空气含量, 从而抑制了植物光合作用(Zaerr, 1983)。在完全水淹的情况下, 空心莲子草的节间显著伸长, 比节间长增加, 而分枝数减少。这些形态上的反应, 有利于空心莲子草保持直线性生长, 从而尽快伸出水面, 进行高效的光合作用(江红英等, 2007; 罗芳丽等, 2007; Luo *et al.*, 2011)。

整体而言(主效应), 相对于低密度处理(不存在

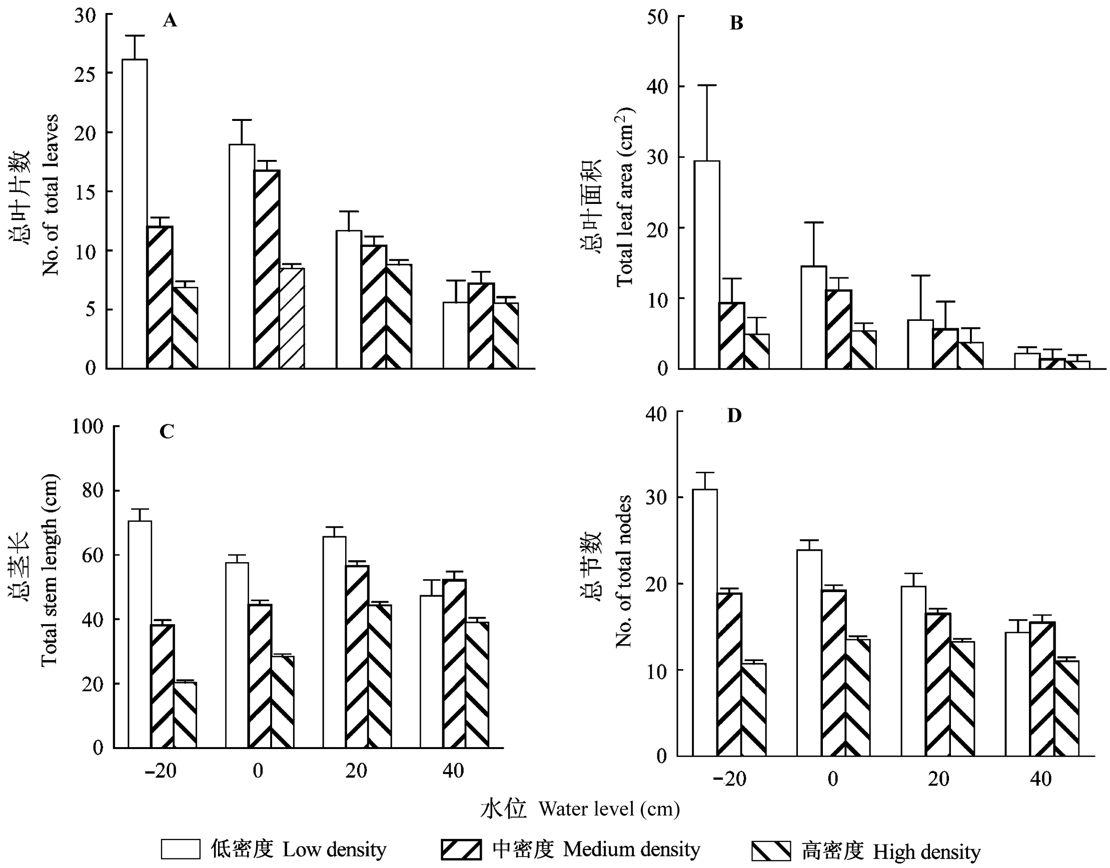


**图2**　水淹(水位)和植株密度对空心莲子草植株总叶片数(**A**)、总叶面积(**B**)、总茎长(**C**)和总节数(**D**)的影响(平均值±标准误差)。
**Fig. 2**　Effects of waterlogging (water level) and plant density on total number of leaves (**A**), total leaf area (**B**), total stem length (**C**) and total number of nodes (**D**) per *Alternanthera philoxeroides* plant (mean ± *SE*).

种内关系), 中密度和高密度下空心莲子草的生长显著削弱, 表明整体上空心莲子草植株之间的作用关系为竞争关系。但这种效应随着水淹程度的增加而改变: 在不淹水的情况下, 植株之间的表现为负(竞争)效应, 并且强度很高; 在水位为0和20 cm的情况下, 植株之间的关系仍为竞争关系, 但作用强度相对减少; 而在水位为40 cm的情况下, 空心莲子草植物总生物量和茎生物量随着密度的增大而倾向于增加, 即植株间的关系表现为易化(facilitation)作用。进一步分析度量植物之间作用强度和类型的相对邻体效应(*RNE*)发现, 随着水淹程度的增加, 相对邻体效应显著改变, 其数值由不水淹情况下的负值逐渐增加到在40 cm完全水淹下的正值。这些结果支持“胁迫梯度假说” (Bertness & Callway, 1994), 表明随着环境胁迫强度的增加, 空心莲子草植物个体之间的竞争强度逐渐减弱, 而易化作用逐渐增强。

关于植物间互作类型和互作强度与环境压力的关系, 在不同空间尺度和时间梯度上有了一定的研究(Buttery *et al.*, 1965; Bertness & Yeh, 1994; Bertness & Hacker, 1994; Bertness & Ewanchuk, 2002)。一般认为, 植物在竞争性与耐受性之间存在着权衡(trade-off)。当环境比较适宜, 植物能自由获取资源时, 竞争比较重要; 而当环境压力较大时, 植物的耐受能力占主导地位, 并将大部分资源分配到相应的性状或器官, 或通过形态和生理的变化适应和影响环境(Bosse & Frenzel, 1997; Visser *et al.*, 2000), 从而提高其适合度。本实验中, 在40 cm完全水淹的条件下, 空心莲子草的茎生物量和叶生物量随着密度增大, 分别呈现出增加和减少的趋势, 这正是空心莲子草通过改变资源分配格局适应水淹环境的表现。但尚未发现空心莲子草的形态方面与“胁迫梯度假说”存在显著相关性。

目前, 对于胁迫梯度假说还没有提出明确的解

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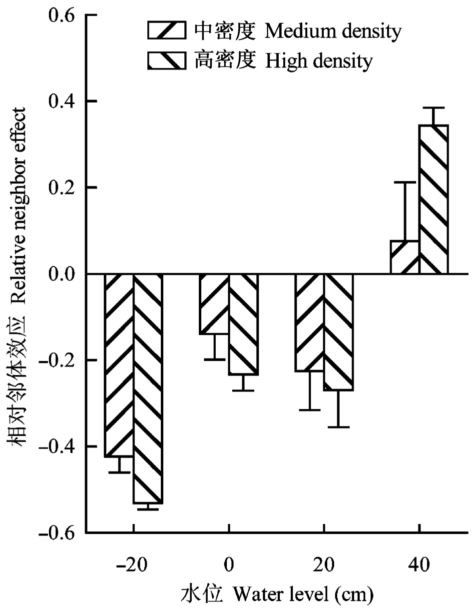


**图3** 水淹(水位)和植株密度对空心莲子草相对邻体效应(*RNE*)的影响(平均值±标准误差)。

**Fig. 3** Effects of waterlogging (water level) and plant density on the relative neighbor effect (*RNE*) of *Alternanthera philoxeroides* plant (mean ± *SE*).

释。Visser等(2000)发现, 在水淹条件下, 植物可以通过减少放射氧损失(radial oxygen loss, ROL)适当提高土壤中的$O_2$浓度, 改善环境。Bertness (1989)发现在恶劣环境下, 密度的提高有助于增加橡子藤壶(*Semibalanus balanoides*)的适合度, 说明相对于较低的密度, 高密度下物种更能改善周围的环境, 或者分散在种群边缘的个体为其他个体提供了缓冲, 削弱了胁迫程度。本实验中, 在胁迫程度很高的40 cm完全水淹的情况下, 空心莲子草植株之间发生易化作用的原因可能在于: (1)高密度下根的呼吸作用对土壤温度的提高作用较低密度的大; (2)空心莲子草通过其减少根系的放射性氧损失提高土壤中的$O_2$浓度, 而高密度下这种作用更明显; (3)基质中厌氧微生物产生有害产物(Flessa & Fischer, 1992), 高密度下单株空心莲子草分担的有害产物压力较小; (4)分散在种群边缘的个体可为其他个体提供缓冲, 从而削弱了胁迫程度(Bertness, 1989)。

本研究表明, 水淹能够改变植物的种内关系。然而, 完全水淹下空心莲子草的种内易化作用的确切机制目前并不清楚, 有待于进一步的研究。在今后的实验过程中, 对水体中的光照、$O_2$和温度进行监测, 并开展相关的生理生态学研究, 将有利于揭示这一机制。

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