

• 研究报告 •

# 不同土壤质地和淤积深度对大米草生长繁殖的影响

刘琳<sup>1</sup> 安树青<sup>2</sup> 智颖飙<sup>3</sup> 张明祥<sup>1</sup> 李红丽<sup>1\*</sup><sup>1</sup> (北京林业大学自然保护区学院, 北京 100083)<sup>2</sup> (南京大学生命科学学院, 南京 210093)<sup>3</sup> (内蒙古大学环境与资源学院, 呼和浩特 010021)

**摘要:** 盐沼湿地生态系统中的土壤质地和淤积深度由于受到潮汐和生物的协同作用会发生相应的变化, 将对植物个体生长与湿地植被分布产生影响。本文通过智能温室人工模拟控制土壤质地和淤积深度实验, 分析了不同土壤质地(粘土和混合土)及淤积深度(无淤积、淤积植株高度1/4、淤积植株高度1/2及淤积植株高度3/4)对外来克隆植物大米草(*Spartina anglica*)种群的生长繁殖特征及生物量积累的影响。结果表明: 粘土促进叶面积、叶片数及根状茎数的增加, 并增加根状茎总长、根状茎生物量及地上生物量的积累; 而混合土(粘土与沙土体积比为1:1)增加了克隆分株数、总生物量、地下生物量及根生物量。除叶面积在淤积株高3/4处理下达到最大值外, 其他指标均在淤积株高1/2处理下达到最大值。由此推断, 大米草种群较适宜的土壤质地及淤积深度为粘土淤积株高的1/2处。据此推测, 可通过相应的生物及工程措施来改良土壤质地及通过改变淤积深度来有效管理我国海岸带大米草的分布, 为控制大米草在海岸带盐沼中的入侵与种群扩张提供了理论依据。

**关键词:** 盐沼湿地; 大米草; 种群衰退与扩张; 生物量积累

## Effects of different sediment type and burial depth on growth traits and biomass accumulation of *Spartina anglica*

Lin Liu<sup>1</sup>, Shuqing An<sup>2</sup>, Yingbiao Zhi<sup>3</sup>, Mingxiang Zhang<sup>1</sup>, Hongli Li<sup>1\*</sup><sup>1</sup> School of Nature Conservation, Beijing Forestry University, Beijing 100083<sup>2</sup> School of Life Sciences, Nanjing University, Nanjing 210093<sup>3</sup> College of Environment and Resources, Inner Mongolia University, Hohhot 010021

**Abstract:** Soils in salt marsh ecosystems have been undergoing certain changes including those related to sediment types and burial depths due to tidal activity and a variety of biotic factors. The changes in sediment type affect water-retaining properties, permeability and organic content while those in burial depth alter soil humidity, nutrition content, oxygen content, light intensity and temperature. Although many previous studies have focused on the effects of soil properties on plant growth and reproduction, few have explicitly tested the impacts of sediment type and burial depth on plants in salt marsh ecosystems. The exotic species *Spartina anglica* found in coastal China has been experiencing increased mortality over the past decade, however the mechanism of this mortality remains unclear. This study mainly focused on the effects of sediment type and burial depth on growth traits and biomass accumulation of *S. anglica* and was conducted under greenhouse conditions. The experiment included two types of sediments with clay and clay-sand mixtures (the volume of 1:1). Furthermore, four treatments were established with burial depths from 0 cm to one quarter of the plant height, one half of the plant height and three quarters of the plant height. Results indicated that clay increased leaf area, number of leaves, number of rhizomes, total length of rhizomes, rhizome mass and aboveground mass, while the clay-sand mixture led to an increase in the number of ramets, total mass, underground mass

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\* 通讯作者 Author for correspondence. E-mail: lihongli327@163.com

and root mass. All of the measures, except for leaf area, peaked at one half of the plant height burial treatment among all treatments. Overall, burial depth at one half of the plant height in clay was the most suitable combination for *S. anglica*. The results indicate that changes in sediment properties and subsequent changes in burial depth for *S. anglica* may assist with management of its populations over the species range.

**Key words:** salt marsh; *Spartina anglica*; population invasion and decline; biomass accumulation

土壤是湿地生态系统获取化学物质的最初场所及生物地球化学循环的中介,是诸多湿地生态过程的重要参与者与载体;其理化性质是湿地生态系统的重要指征,决定着湿地植物的分布类型、数量和质量(田应兵等, 2002; 姜明等, 2006; 张玉兰和陈利军, 2010)。

由于受到潮汐的作用,盐沼湿地常出现淤积。淤积程度由输沙量、固体悬浮物的浓缩及接收水体中泥浆的分配决定(Nielsen et al, 2002)。淤积作用、潮汐运动及地形对盐沼湿地海岸质地类型具有重要的影响(Kim et al, 2013),如在江苏盐城盐沼湿地海岸,从海水到陆地土壤质地类型依次为粗砂、细砂、砂土混合基质及粘土(Ren, 1986)。盐沼湿地土壤质地类型的差异导致其理化性状如土壤pH值、盐度、土壤含水量及土壤紧实度发生改变。而土壤理化性状在很大程度上决定着植被的分布(Kim et al, 2013)。如在美国乔治亚州,盐沼湿地的土壤容重大,土壤含水量下降在一定程度上导致了互花米草(*Spartina alterniflora*)在海岸带的衰退(Crawford & Stone, 2015)。另一方面,植物的生长反过来也会影响盐沼湿地土壤的沉积作用(Sánchez et al, 2001),植被类型及其覆盖率会调节盐沼湿地土壤的沉积动态及质地类型,植物与土壤二者间形成反馈,共同影响着盐沼湿地的发展(Kent et al, 2001)。

随着土壤的不断淤积,盐沼湿地植物会被沉积物掩埋(Pye, 1995),而不同植物物种对掩埋土壤的质地类型及淤积深度的适应能力和反应各不相同(Kent et al, 2001)。例如,研究表明粘土掩埋深度降低了大叶藻(*Zostera marina*)种子的萌发率(Jarvis & Moore, 2015)。对于幼苗来说,有些植物如灰株藎草(*Carex rostrata*)被掩埋后不久就会死亡(Ewing, 1996),也有些植物如盐草(*Distichlis spicata*)被掩埋后并没有影响正常生长(Brown, 1997),甚至掩埋会促进一些植物的生长,如互花米草和加拿大披碱草(*Elymus canadensis*) (Pezeshki et al, 1992; Perumal & Maun, 2006; Maun, 2011)。这些反应主要因物种、

掩埋质地及掩埋深度而异(Kent et al, 2001; Owen et al, 2004; Walls et al, 2005)。

大米草(*Spartina anglica*)是欧洲米草(*S. maritima*)和互花米草的自然杂交种,它能在广阔的滩涂生长,具有较强的耐盐耐淹能力(仲崇信, 1985; An et al, 2007)。由于大米草具有较强的克隆生长特性,而且可以作为饲料,具有稳定堤坝及保护海岸线等生态功能,我国于1963年从英国埃塞克斯将其引入,之后它便在我国海岸带逐步定居且成功建立了种群(An et al, 2007),曾成为我国海岸带湿地植被的优势植物之一(李湘萍等, 1998; 沈永明等, 2005)。

然而,大米草的扩张对海岸的生态系统有显著的负面效应,对当地的植物种群、濒危鸟类及许多软体动物都具威胁,在一定程度上降低了生物多样性(An et al, 2007; Cutajar et al, 2012)。互花米草自1979年被引入我国后迅速在海岸带大面积扩张(邓自发等, 2006; Li et al, 2014b),由于其秆密集粗壮、地下根系更加发达,能够促进泥沙的快速沉降与淤积(王卿等, 2006),入侵后造成地势升高,海岸淤积程度加重,微生物环境发生变化(Chen et al, 2012)。随着土壤的淤积,土壤质地组成及其性质也会发生改变。与互花米草相反,自20世纪90年代以来,大米草在我国海岸带出现了严重的自然衰退(An et al, 2007),主要表现为分布面积减少、植株矮化、有性繁殖率低下(An et al, 2007),但在欧洲及其他许多地方它仍属入侵性很强的物种(Nehring & Hesse, 2008; Balke et al, 2012)。

对于大米草种群在我国海岸带的自然衰退机理,已经进行了种间竞争、密度效应及潮汐淹没时间等方面的研究(Zhi et al, 2007; Li et al, 2009; 李红丽等, 2010; Li et al, 2014a),而关于土壤质地和淤积深度对大米草种群影响的研究相对缺乏。本文通过探讨大米草种群自然衰退与土壤质地和淤积深度的关系,研究大米草对不同土壤质地下不同淤积深度处理的生态响应,探讨不同的土壤环境条件如土

壤质地及淤积深度对大米草的克隆繁殖性状和生长性状的影响。

## 1 材料与方法

### 1.1 材料来源

实验材料大米草采自江苏省盐城海岸带湿地(32°34'–34°28' N, 119°48'–120°56' E)的新洋港(33°37.8' N, 120°34.6' E), 该地区受到古长江和古黄河携带泥沙的共同堆积作用, 其泥沙淤积相对严重(闵凤阳和汪亚平, 2008; 高祥宇, 2013)。该滩涂是典型的淤泥质海岸, 根据沉积、地貌、动力及发育演替特征, 自海向陆可分为4个土壤类型和植被带: (1)低潮粉沙滩(光滩); (2)泥–粉沙混合滩; (3)高潮位泥沙滩; (4)草滩地。滩涂受潮汐以及其他因素的影响, 其中滩面植物依次为互花米草、互花米草+大米草、碱蓬(*Suaeda salsa*)+大米草等。其中实验所用材料取自互花米草和大米草植被带。

### 1.2 实验方法

2009年4月3日, 在我国盐城海岸滨海湿地大米草生长区, 选取一定数量的克隆苗带根土取样。去除部分不健康植株和死根后, 移植于南京大学智能温室(32°10.6' N, 118°41.9' E)。5月10日, 将大米草克隆苗分成独立的克隆分株, 并从中选取高度 $6 \pm 0.5$  cm的分株, 移植于内直径28 cm、高20 cm的塑料培养钵容器内, 每个实验容器内定植两株。培养一周后, 开始实验。

采用双因素完全随机实验设计, 包括土壤质地(2种类型)和淤积深度(4个水平)两个因素, 共计8个处理。根据盐城国家级自然保护区大米草分布区土壤的质地特点, 将实验设计为粘土和混合土两种土壤质地类型。其中, 混合土为体积比1:1的粘土与沙土(混合土比例根据野外样地的监测结果而设计); 粘土主要取自盐城海岸带湿地的新洋港, 而沙土选用南京附近的河沙。河沙先以盐度15‰的人工海水淋透, 以模拟大米草野外生长的盐沼土壤环境。粘土和混合土的土壤有效氮含量分别为 $76.34 \pm 1.23$  mg/kg和 $52.50 \pm 3.59$  mg/kg; 有效磷含量分别为 $8.31 \pm 0.76$  mg/kg和 $5.09 \pm 0.18$  mg/kg。4种淤积深度分别对应为基质不淤积、淤积株高的1/4、淤积株高的1/2和淤积株高的3/4 (缩写代号依次为CK、株高1/4、株高1/2和株高3/4), 后3个处理的淤积深度随植株的生长而调整。为了便于处理, 将实验容器置入略

大容器中。实验结束时, 大米草株高约40 cm, 因此淤积深度依次约为10、20及30 cm左右, 各处理淤积深度能在一定程度上反映盐沼湿地的基质及淤积情况。每种处理设置6个重复。整个实验在智能温室内进行, 最初土壤深度约为12 cm, 实验中保持土壤表层积水状态, 自然光照, 盐度保持为15‰, 每2 d检测一次淤积深度。

### 1.3 指标测定

10月18日, 将培养钵倒置, 将植株完整取出, 每重复随机取1株, 每处理共取6株。用水冲洗干净后主要测定克隆繁殖和生长指标参数(克隆分株数、根状茎数、根状茎生物量、根状茎总长、叶片数及叶面积)及生物量参数(总生物量、地上生物量、地下生物量及根生物量)。用LI-3000A叶面积仪(LI-COR公司, Lincoln, NE, USA)随机测量6片克隆系代表性功能叶片的叶面积, 取其均值。随后, 将大米草植株分解为地上、根和根状茎3部分, 放置在60°C烘箱内烘干72 h, 测定生物量。

### 1.4 数据分析

采用双因素方差分析(Two-Way ANOVA)检验土壤质地、淤积深度及二者的交互效应对大米草克隆繁殖、叶性状及生物量积累各指标的影响, 并采用Duncan法对均值进行多重比较( $P = 0.05$ )。在方差分析前, 对数据进行正态性检验和方差齐性检验(Levene's test)。对于不满足方差齐性的数据进行对数转换。采用SPSS 19.0软件进行数据统计分析, 利用Sigmaplot 11.0软件作图。

## 2 结果

### 2.1 土壤质地及淤积深度对大米草克隆繁殖和叶性状指标的影响

土壤质地对大米草克隆分株数、根状茎数、根状茎总长、叶片数及叶面积均有显著影响( $P < 0.05$ ), 而对根状茎生物量影响不显著( $P > 0.05$ ); 淤积深度对克隆繁殖和叶性状指标均有极显著影响( $P < 0.001$ ); 土壤质地和淤积深度的交互作用对根状茎数、根状茎生物量、根状茎总长和叶片数具有显著影响( $P < 0.05$ ) (表1)。

两种土壤质地的分株数、根状茎数、根状茎生物量和根状茎总长均在淤积株高1/2处理下达到最大值, 其中粘土在CK、淤积株高1/4、淤积株高1/2处理下的各指标均大于混合土处理; 除分株数外,

表1 土壤质地及淤积深度对大米草克隆繁殖、叶性状指标以及生物量积累影响的方差分析结果  
Table 1 Results of ANOVAs testing the effects of sediment type and burial depth on clonal and growth traits, and biomass accumulation of *Spartina anglica*

性状指标 Traits	土壤质地 Sediment type (S)		淤积深度 Burial depth (B)		土壤质地×淤积深度 S × B	
	<i>F</i> <sub>1, 40</sub>	<i>P</i>	<i>F</i> <sub>3, 40</sub>	<i>P</i>	<i>F</i> <sub>3, 40</sub>	<i>P</i>
(A)克隆繁殖和叶性状指标 Clonal and leaf traits						
分株数 No. of ramets	7.9	0.008	9.8	<0.001	1.1	0.359
根状茎数 No. of rhizomes	6.5	0.014	25.4	<0.001	4.5	0.008
根状茎生物量 Rhizome biomass	3.9	0.057	28.5	<0.001	5.2	0.004
根状茎总长 Total length of rhizomes	9.8	0.003	18.1	<0.001	3.6	0.023
叶片数 No. of leaves	6.4	0.015	17.5	<0.001	3.4	0.028
叶面积 Leaf area	6.5	0.014	32.9	<0.001	2.0	0.127
(B)生物量积累 Biomass accumulation						
总生物量 Total biomass	1.0	0.328	49.4	<0.001	10.8	<0.001
地上生物量 Aboveground biomass	0.1	0.770	48.0	<0.001	12.1	<0.001
地下生物量 Belowground biomass	6.6	0.014	44.1	<0.001	7.3	<0.001
根生物量 Root biomass	11.0	0.002	23.8	<0.001	2.6	0.064

上述指标在淤积株高3/4处理下小于混合土(图1A–D)。两种土壤质地的叶片数在淤积株高1/2处理下达到最大值,且显著大于淤积株高3/4处理( $P < 0.05$ ) (图1E),而两种土壤质地的叶面积在淤积株高3/4处理下达到最大值,且粘土类型显著大于其他处理,而混合土则显著大于CK处理(图1E, F)。

2.2 土壤质地及淤积深度对大米草生物量积累的影响

不同的土壤质地对大米草种群的地下生物量及根生物量影响显著( $P < 0.05$ ),对总生物量及地上生物量则无显著影响( $P > 0.05$ );而不同的淤积深度处理对大米草种群的生物量积累均有极显著影响( $P < 0.001$ );此外,除根生物量外,土壤质地和淤积深度的交互作用对其他生物量指标均影响显著( $P < 0.001$ ) (表1)。

两种土壤质地的总生物量、地上生物量、地下生物量和根生物量均在淤积株高1/2处理下达到最大值,且除根生物量外,均显著大于CK和淤积株高3/4处理( $P < 0.05$ ) (图2)。其中总生物量、地下生物量和根生物量以混合土处理时最大,而地上生物量以粘土处理时最大。

3 讨论

湿地土壤质地对植物种群的生长和发育有着显著影响。由于潮汐流速改变,导致基质的悬浮物

质发生变化,进而引发土壤质地组分的改变,在一定程度上引发了植被的变化(Kim et al, 2013)。本研究结果表明,粘土显著促进大米草的克隆生长及植株生物量积累,而混合土仅促进大米草生物量的积累。虽然粘土透气性差、排水能力不强、易限制植株根部的生长,但相对于混合土而言,粘土的蓄水能力更强,有机质含量也更加充足,并且能增加土壤中无机磷酸盐和铵浓聚物的含量,提供给植物充足的养分(Jarvis & Moore, 2015),有利于根系获取足够的养分以保证地上部的生物量积累,因而更有利于大米草的许多形态指标的生长及其克隆繁殖,从而有利于克隆植物获得更多的阳光,使其具有较强的生长优势,有利于大米草的种群延续(Willis & Hester, 2004; 李红丽等, 2007; Li et al, 2014a; Jarvis & Moore, 2015)。与粘土相比,混合土的透气性增加,有利于植物根部的生长,但其土壤养分相对缺乏,不利于地上部生物量积累(Mariska et al, 2009)。总的看来,粘土更有利于大米草的生长和总生物量的积累。这与部分有关互花米草的研究结果(何军等, 2009; Crawford & Stone, 2015)一致:随着土壤淤积深度的增加,土壤质地以粘土为主,土壤的保水性有所提高,含沙量下降,粘土相对于混合土更有利于互花米草的生长繁殖,能维持其种群延续及扩张,而混合土可增加互花米草地下生物量尤其是根生物量的积累。但在美国乔治亚州海岸,互花米

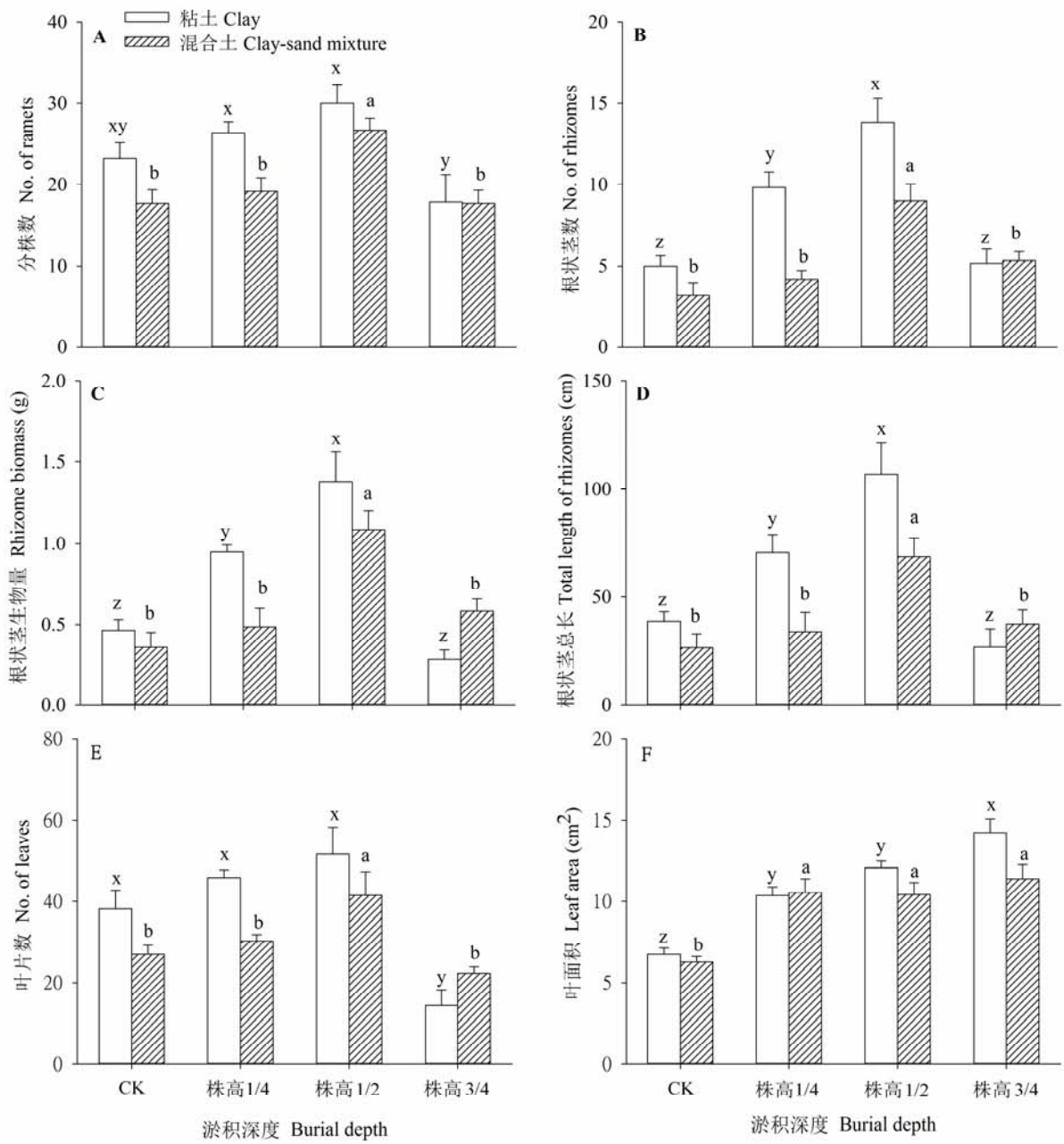


图1 不同土壤质地及淤积深度处理下大米草种群的克隆繁殖及叶性状指标(平均值+标准误)。相同字母表明同一土壤质地淤积深度处理间无显著差异(Duncan检验,  $P = 0.05$ )。淤积深度处理CK、株高1/4、株高1/2和株高3/4分别对应为基质不淤积、淤积株高1/4、淤积株高1/2和淤积株高3/4。

Fig. 1 Clonal and leaf traits of *Spartina anglica* under different soil types and the four burial depth treatments (Mean + SE). Means sharing the same letter are not different at  $P = 0.05$  within sediment type treatments (Duncan tests). Furthermore, CK, 1/4 plant height, 1/2 height and 3/4 height were established with unburied, 25% buried, 50% buried and 75% buried, respectively.

草的衰退区相比植被覆盖区土壤容重从 $0.33\text{ g/cm}^3$ 增加为 $0.69\text{ g/cm}^3$ , 土壤含水率下降, 土壤透气性增加, 粉砂性增加。土壤质地的这种改变在一定程度上导致了该区域互花米草的衰退(Crawford &

Stone, 2015)。本研究表明, 土壤质地也可能引发我国海岸大米草种群的衰退, 进而引发植物群落类型的演变。

虽然不同土壤质地间大米草的生长繁殖性状

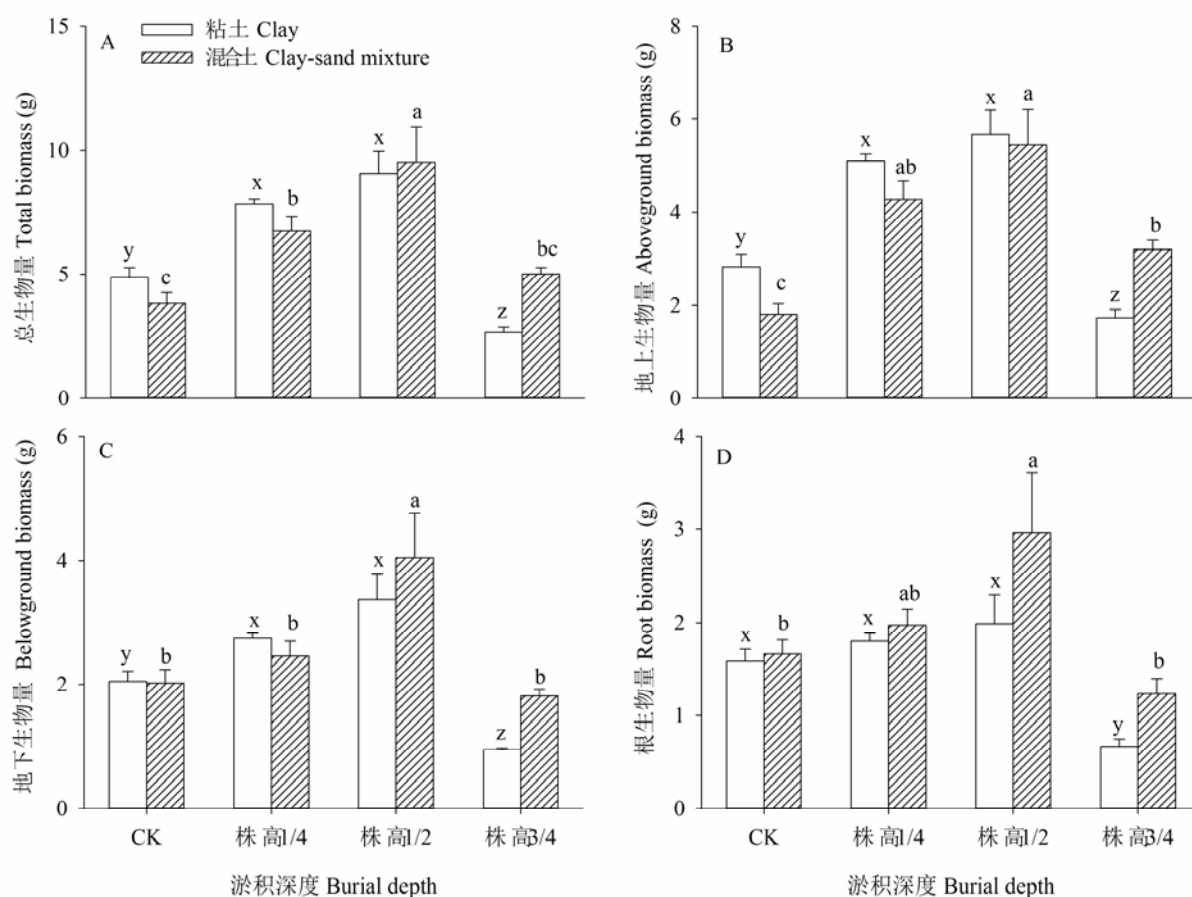


图2 不同土壤质地及淤积深度处理下大米草种群的生物量积累(平均值+标准误)。相同字母表明同一土壤质地淤积深度处理间无显著差异(Duncan检验,  $P = 0.05$ )。淤积深度处理CK、株高1/4、株高1/2和株高3/4分别对应为基质不淤积、淤积株高1/4、淤积株高1/2和淤积株高3/4。

Fig. 2 Biomass of *Spartina anglica* under different soil types and the four burial depth treatments (Mean + SE). Means sharing the same letter are not different at  $P = 0.05$  within sediment type treatments (Duncan tests). Furthermore, CK, 1/4 plant height, 1/2 plant height and 3/4 plant height were established with unburied, 25% buried, 50% buried and 75% buried, respectively.

指标间有一定差异,但对淤积深度的响应呈现一致规律。持续淤积深度处理对大米草种群的生长繁殖性状均有极显著影响,并且适中或者稍浅的淤积处理有利于大米草的生长和繁殖。本研究结果与关于土壤淤积对盐地碱蓬(*Suaeda salsa*)的形态指标影响的研究结果相类似(Sun et al, 2014)。此外,研究表明互花米草除了在完全淤积处理下以外,株高、总生物量、营养繁殖体数均随着淤积深度的增加而显著增加,并且在淤积株高1/2和重复淤积下达最大值(Deng et al, 2008),即淤积株高1/2时最能促进互花米草在我国海岸的扩张。然而,随着土层淤积深度的继续增加,其对大米草的生长和生物量积累由促进转变为抑制,这可能是因为土壤环境中的湿度及容积密度增加,土壤透气性减弱,导致植株生长受

抑,无氧呼吸加剧,不利于植物生长。因此轻度和适中的淤积能促进大米草的生长和生物量的积累,而随着淤积深度的增加,氧气、光照和温度会逐渐减少和降低,造成植株能量代谢失调(李秋艳和赵文智, 2006; 聂华丽等, 2006; Sciegienka et al, 2011),进而影响了大米草的生长,甚至造成大米草种群的死亡(Koch, 2001)。

综上所述,粘土相对于混合土更有利于大米草种群的生长,且淤积株高1/2为大米草种群较适宜的淤积深度。在自然盐沼生态系统中,互花米草有极高的繁殖系数及强大的造淤能力,能够在我国海岸迅速扩张与繁殖,并且使得海岸的淤积程度不断加深(Chung et al, 2004; 杨东和万福绪, 2014),土层深度越来越大,逐渐超过大米草的最佳淤积状态,

并且使得湿地土壤的各项养分指标、通透性及保水性明显下降, 土壤生态化学性质发生明显的变化(张祥霖等, 2008), 这在一定程度上不适宜大米草种群的生长及繁殖。此外, 在我国海岸带, 大米草由于花粉活力降低、花粉管伸长受阻导致有性繁殖能力低下, 其种子实生苗比例较低(Li et al, 2008)。大米草种群生长主要依赖克隆苗, 因此克隆苗对土壤质地及淤积深度的响应, 以及其他环境因素的协同作用如淹水时间、淹水梯度等, 最终可能引起其种群的自然衰退(Li et al, 2008, 2009, 2011, 2014a)。

根据本研究结果, 可以通过采取适当的工程措施及生物措施促淤(喻国华和鲍曙东, 1992), 合理改变土壤质地(如改变粘土与沙土的比例关系)及控制土层深度过度减少或增加淤积深度来控制大米草种群的衰退或者暴发。

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