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模拟干旱和盐碱胁迫对碱蓬、盐地碱蓬种子萌发的影响*

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摘 要: 为研究干旱和盐碱胁迫对碱蓬(*Suaeda glauca*)、盐地碱蓬(*Suaeda salsa*)种子萌发的影响, 比较碱蓬和盐地碱蓬逆境生理特性的异同, 本研究利用 PEG6000、NaCl 和 Na_2CO_3 分别模拟干旱、盐和碱胁迫, 配制相同渗透势的 PEG6000、NaCl、Na_2CO_3 处理液, 以蒸馏水处理为对照, 对碱蓬、盐地碱蓬种子的萌发与胚的生长进行比较研究。结果表明: 1)低渗处理(−0.46 MPa)对碱蓬、盐地碱蓬种子的萌发无显著影响; 高渗处理(−1.38 MPa、−1.84 MPa)抑制碱蓬、盐地碱蓬种子的萌发。2)当溶液渗透势相等时, NaCl 处理下碱蓬种子的萌发率显著大于 PEG、Na_2CO_3 处理; 而等渗 PEG、NaCl、Na_2CO_3 处理对盐地碱蓬种子萌发率的影响无显著差异。3)PEG、NaCl、Na_2CO_3 处理组碱蓬、盐地碱蓬种子的最终萌发率与对照无显著差异。4)在幼苗形成阶段, PEG、Na_2CO_3 处理对碱蓬、盐地碱蓬胚的抑制作用显著大于等渗 NaCl 处理。5)碱蓬、盐地碱蓬胚的生长对 NaCl、Na_2CO_3 胁迫的响应存在差异。−0.92 MPa NaCl 处理抑制碱蓬胚的生长, 却对盐地碱蓬产生促进作用; −0.46 MPa Na_2CO_3 处理对碱蓬胚的抑制作用小于盐地碱蓬。综合分析表明: 碱蓬、盐地碱蓬均具有很强的抗盐性。在种子萌发阶段, 碱蓬种子的抗旱、抗碱能力低于盐地碱蓬; 在幼苗形成阶段, 碱蓬胚的抗盐性小于盐地碱蓬, 但对轻度碱胁迫的抗性高于盐地碱蓬。

关键词: 种子萌发; 碱蓬; 盐地碱蓬; NaCl 胁迫; Na_2CO_3 胁迫; PEG 胁迫
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Effects of PEG, NaCl and Na_2CO_3 stresses on *Suaeda glauca* and *Suaeda salsa* seed germination*

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Abstract: *Suaeda glauca* and *S. salsa* are native halophytes in China with a key role in the improvement and restoration of salt marsh ecologies. There is a lot of works on the response of *Suaeda* plants to salinity, but works are limited about the effects of drought and

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alkali stress on *S. glauca* and *S. salsa*, especially at germination stage. The aim of this study was to evaluate the impacts of PEG, NaCl and Na_2CO_3 stress on the germination of *S. glauca* and *S. salsa* seeds. The *in-vitro* seed germination test was carried out with various solutions of PEG-6000 (29 mmol·L^{-1}, 38 mmol·L^{-1}, 45 mmol·L^{-1}and 50 mmol·L^{-1}), NaCl (100 mmol·L^{-1}, 200 mmol·L^{-1}, 300 mmol·L^{-1} and 400 mmol·L^{-1}) and Na_2CO_3 (70 mmol·L^{-1}, 140 mmol·L^{-1}, 210 mmol·L^{-1}and 280 mmol·L^{-1}) in iso-osmotic concentrations (–0.46 MPa, –0.92 MPa, –1.38 MPa and –1.84 MPa). We measured the germination rate, germination index, mean germination time, early seedling growth after 7-day treatment and final germination rate after another 7-day recovery. The results showed that with increasing osmotic stress intensity, the germination rates of two species were depressed under PEG, NaCl and Na_2CO_3 treatments, while –0.46 MPa treatment did not differ significantly from that of the control (fresh water). The negative effect of NaCl on *S. glauca* seed germination was less than iso-osmotic PEG and Na_2CO_3 treatments. By contrast, the effects of iso-osmotic PEG, NaCl or Na_2CO_3 treatments on *S. salsa* seed germination were not significantly different. The germination rate of *S. salsa* was positively related to osmotic potential. Recovery study indicated that PEG, NaCl and Na_2CO_3 stress had no negative effects on the final germinate rate of *S. glauca* and *S. salsa*, meaning that the inhibition of PEG, NaCl and Na_2CO_3 stress on seed germination was due to osmotic pressure rather than ion toxicity. In addition, mild NaCl treatments (–0.46 MPa for *S. glauca*, and –0.46 and –0.92 MPa for *S. salsa*) promoted *S. glauca* and *S. salsa* seedling elongation, while PEG and Na_2CO_3 treatments inhibited it. In iso-osmotic conditions, radicle and hypocotyl lengths of *S. glauca* and *S. salsa* seedlings under NaCl treatment were greater than those under PEG and Na_2CO_3 treatments. Compared with *S. glauca*, *S. salsa* seedlings grew better under –0.46 MPa and –0.92 MPa NaCl treatments, but worse under –0.46 MPa Na_2CO_3 treatment. The findings suggested that, 1) *S. salsa* seeds exhibited strong resistance to PEG, NaCl and Na_2CO_3 stress, and its resistance to PEG and Na_2CO_3 stress was greater than that of *S. glauca*. 2) *S. salsa* had stronger capacity to establish seedlings under NaCl stress than *S. glauca*, but its tolerance to mild Na_2CO_3 stress was weaker than that of *S. glauca*.

Keywords: Seed germination; *Suaeda glauca*; *Suaeda salsa*; NaCl stress; Na_2CO_3 stress; PEG stress

环渤海地区是我国重要的经济发展区，但由于该地区分布有大量的盐碱荒地，土壤贫瘠、植被稀疏、生态环境恶劣[1]，迫切需要加快当地的植被建设，以满足社会经济快速发展需求[2]。在盐碱地植被建设中，客土绿化由于成本高、可持续性差等局限性[3]，难于大面积应用到盐碱地的生态治理。相比之下，利用耐盐植物重建植被，完成原土绿化日益受到重视。

碱蓬(*Suaeda glauca*)和盐地碱蓬(*Suaeda salsa*)属于藜科(Chenopodiaceae)碱蓬属的一年生草本，是我国本土盐生植物。研究表明种植碱蓬、盐地碱蓬具有改善土壤性状、降低土壤含盐量、修复土壤重金属污染、净化富营养水体等多种生态效益[3-8]。碱蓬、盐地碱蓬作为重要的物种资源，在盐碱地的生态治理与修复领域具有重要的开发潜力。碱蓬、盐地碱蓬在自然界的分布具有明显的地带性：碱蓬多分布于东北、西北等内陆盐碱地区[9]，盐地碱蓬在辽河三角洲、黄河三角洲等滨海地区的分布明显多于碱蓬；在小地形区域，碱蓬多分布于土坡、沙丘的高处，盐地碱蓬多分布于低洼地带[10]。

在盐碱地中，种子萌发是植物生长与种群建成的重要阶段，同时也是对逆境的敏感时期[11-13]。植物萌发阶段受到的胁迫主要包括干旱胁迫、盐胁迫和碱胁迫。盐地碱蓬作为典型的盐生植物，前人关于盐地碱蓬的报道多局限于盐胁迫[14-17]，已有研究表明盐地碱蓬对 NaCl 具有高度的适应性，离子区隔化与叶片肉质化是盐地碱蓬重要的耐盐机制[18-19]。碱蓬作为盐地碱蓬的近缘物种，其形态与盐地碱蓬多有相似之处，但目前鲜有对碱蓬逆境生理研究的报道。因此，本文利用 PEG 6000、NaCl、Na_2CO_3 分别模拟旱、盐、碱胁迫，对碱蓬、盐地碱蓬种子萌发及胚的生长特性进行比较研究，旨在探讨二者地带性分布的可能机制，为碱蓬、盐地碱蓬在盐碱地上的种群建植提供理论依据。

1 材料与方法

1.1 试验材料

碱蓬和盐地碱蓬种子于 2016 年 11 月采自河北省海兴县盐碱地(117°32′~117°58′E，38°19′~38°29′N)，经干燥和清理后，保存于纸袋，放置于 4 ℃冰箱保存。

1.2 试验设计

挑选饱满、大小均匀的碱蓬、盐地碱蓬黑色种子，在 5%次氯酸钠溶液中浸泡 5 min，随后用蒸馏水冲洗除去残留，置于铺 2 层滤纸的直径 90 mm 的培养皿中，每个培养皿放 50 粒种子，加入处理液 10 mL，各处理 3 个重复。试验设计以蒸馏水处理为对照，以 PEG 6000、NaCl、Na_2CO_3 溶液为处理组，分别配制–0.46 MPa、–0.92 MPa、–1.38 MPa、–1.84 MPa 4 个溶液渗透势梯度。由 WP4C 露点水势仪(美国 Decagon 公司)测定溶液的渗透势、pH 仪(Sartorius，PB-10)测定溶液

的 pH(表 1)。本文所有试验均在人工智能气候箱中完成, 光照 14 h·d^{-1}, 光强≥56.6 μmol·s^{-1}, 温度 25 ℃/20 ℃(昼/夜), 相对湿度 75%~80%。每 24 h 统计种子萌发数, 以可见胚根为萌发标准。第 7 d 测量已萌发种子的胚轴与胚根长度, 拍照, 并将未萌发种子清洗后移至蒸馏水处理复水, 7 d 后计算种子最终萌发数。

表 1　不同胁迫处理液的浓度、渗透势和 **pH**
Table 1　Concentration, osmotic potential and pH of the treatment solutions

处理 Treatment	浓度 Concentration (mmol·L^{-1})	渗透势 Osmotic potential (MPa)	pH
对照 Control	0	0	6.76
PEG 6000	29	−0.46	6.75
	38	−0.92	6.72
	45	−1.38	6.70
	50	−1.84	6.69
NaCl	100	−0.46	6.75
	200	−0.92	6.72
	300	−1.38	6.69
	400	−1.84	6.68
Na_2CO_3	70	−0.46	11.53
	140	−0.92	11.60
	210	−1.38	11.62
	280	−1.84	11.64

1.3　萌发指标计算公式

萌发率=(试验种子萌发个数/待测种子总数)×100%　　(1)

最终萌发率=[(试验种子萌发个数+复水后新萌发的种子个数)/待测种子总数]×100%　　(2)

萌发指数=∑(第 t 天种子萌发个数/相应的萌发天数 t)　　(3)

平均萌发时间=∑(第 t 天种子萌发个数×相应的萌发天数 t)/试验种子萌发个数　　(4)

1.4　数据处理和分析

采用 SPSS 16.0 软件对实验数据进行邓肯多重比较, P<0.05 为差异显著, 用 Origin 9.1 作图。

2　结果与分析

2.1　PEG、NaCl、Na_2CO_3 胁迫对碱蓬、盐地碱蓬种子萌发率、最终萌发率的影响

由图 1 可知, 碱蓬和盐地碱蓬种子在蒸馏水处理中的萌发率分别为 96.7%和 84.7%。低渗处理(−0.46 MPa)下, PEG、NaCl 和 Na_2CO_3 对碱蓬和盐地碱蓬的种子萌发无显著影响。−0.92 MPa NaCl 处理的碱蓬和盐地碱蓬种子的萌发率与对照无显著差异; 等渗的 PEG、Na_2CO_3 处理未显著影响盐地碱蓬种子的萌发, 但显著抑制了碱蓬种子的萌发, 且 Na_2CO_3 的抑制作用大于 PEG。高渗处理(−1.38 MPa、−1.84 MPa)明显抑制碱蓬、盐地碱蓬种子的萌发率, 且溶液渗透势越低, 种子萌发受抑制程度越大。−1.38 MPa NaCl 处理下, 碱蓬和盐地碱蓬种子萌发率分别比对照降低 16.7%和 14.7%。高渗 PEG、Na_2CO_3 处理对碱蓬种子萌发率的抑制作用明显大于盐地碱蓬, −1.38 MPa PEG、Na_2CO_3 处理中碱蓬种子的萌发率比对照降低 84.7%和 86.7%, 同处理条件下, 盐地碱蓬种子萌发率比对照分别降低 28.0%和 30.7%。

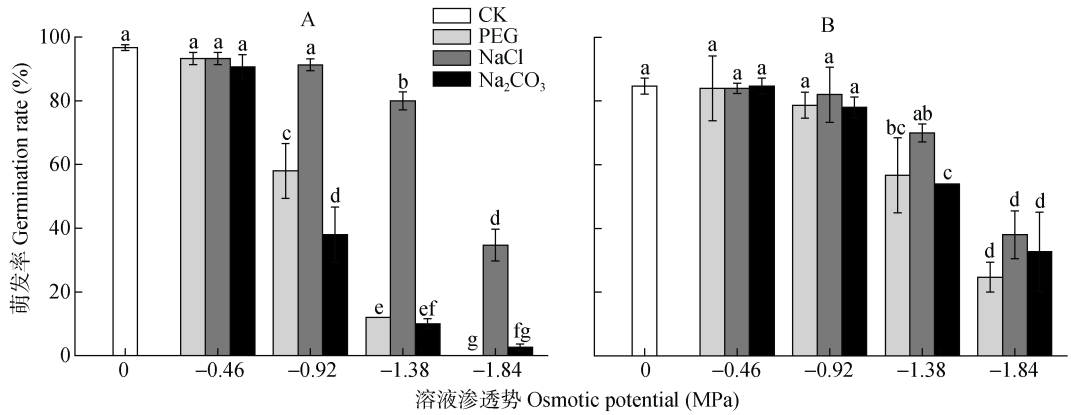

图 1　不同渗透势 **PEG**、**NaCl** 和 **Na_2CO_3** 处理对碱蓬**(A)**和盐地碱蓬**(B)**萌发率的影响
Fig. 1　Effects of PEG, NaCl and Na_2CO_3 with different ostimotic potentials on the germination rates of *Suaeda glauca* (A) and *Suaeda salsa* (B)
不同小写字母表示不用处理间 0.05 水平差异显著。Different lowercase letters mean significant differences among treatments at P < 0.05.

复水 7 d 后, 所有处理组碱蓬和盐地碱蓬种子的最终萌发率与对照均无显著差异(图 2), 但随着 Na_2CO_3 胁迫的加重, 盐地碱蓬种子的最终萌发率呈现下降的趋势, −1.38 MPa 和−1.84 MPa Na_2CO_3 处理下, 盐地碱蓬种子最终萌发率比对照分别降低 7.1%和 15.8%。

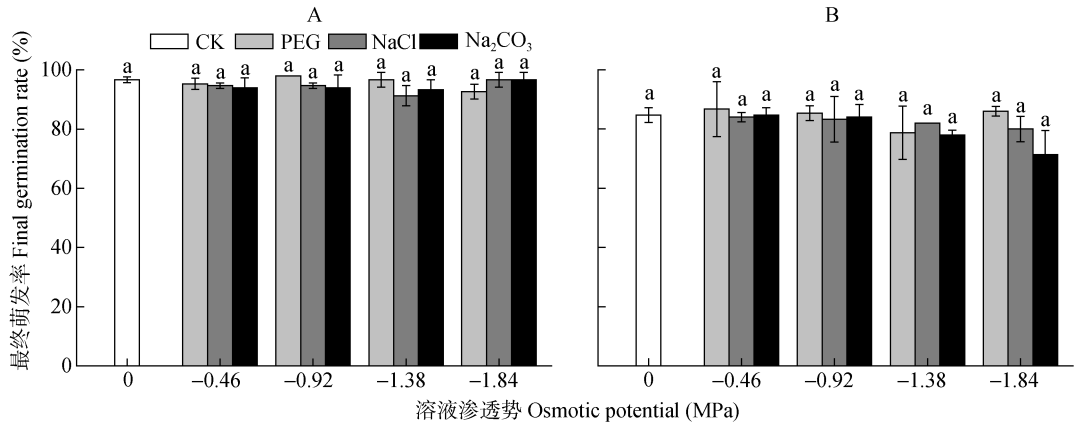

图 2 不同渗透势 PEG、NaCl 和 Na_2CO_3 处理对碱蓬(A)和盐地碱蓬(B)最终萌发率的影响

Fig. 2 Effects of PEG, NaCl and Na_2CO_3 with different ostimotic potentials on the final germination rates of *Suaeda glauca* (A) and *Suaeda salsa* (B)

不同小写字母表示不用处理间 0.05 水平差异显著。Different lowercase letters mean significant differences among treatments at $P < 0.05$.

2.2 PEG、NaCl、Na_2CO_3 胁迫对碱蓬、盐地碱蓬种子萌发指数、种子平均萌发时间的影响

萌发指数是种子重要的活力指标, 种子活力由遗传因素决定, 但环境因素决定种子活力的现实性, 因此萌发指数可以很好地反映逆境对种子萌发的影响程度[20-21]。碱蓬、盐地碱蓬种子萌发指数随溶液渗透势的降低而降低, 不同处理组种子的萌发指数与溶液渗透势均呈线性相关关系(图 3)。参考回归方程的斜率发现: 溶液渗透势每下降 1 MPa, PEG、NaCl、Na_2CO_3 处理组碱蓬种子的萌发指数分别下降 11.20、7.24、10.76, 碱蓬种子的萌发指数在 NaCl 处理中随溶液渗透势下降的程度明显小于 PEG 和 Na_2CO_3 处理; 对于盐地碱蓬, 溶液渗透势每下降 1 MPa, PEG、NaCl、Na_2CO_3 处理组种子的萌发指数分别下降 16.38、17.12、15.82, 各处理间种子萌发指数变化趋势相似。碱蓬、盐地碱蓬萌发指数对 PEG、NaCl、Na_2CO_3 胁迫的响应与萌发率部分的结论高度一致。

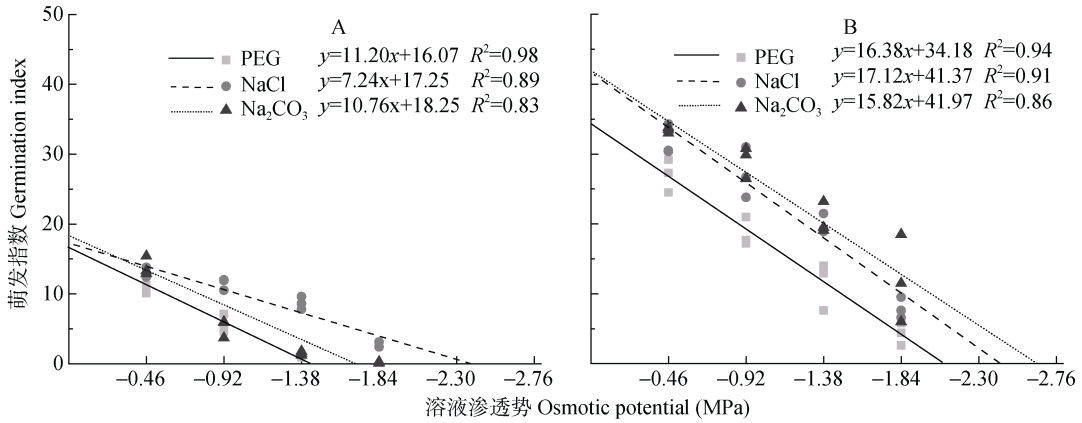

图 3 不同渗透势 PEG、NaCl 和 Na_2CO_3 处理对碱蓬(A)和盐地碱蓬(B)萌发指数的影响

Fig. 3 Effects of PEG, NaCl and Na_2CO_3 with different ostimotic potentials on the germination indexes of *Suaeda glauca* (A) and *Suaeda salsa* (B)

由图 4 可知, 对照组碱蓬和盐地碱蓬种子的平均萌发时间分别为 3.5 d 和 1.7 d。随着 PEG 胁迫的加重,碱蓬、盐地碱蓬种子平均萌发时间逐渐升高。当溶液渗透势为−0.92 MPa、−1.38 MPa 时, NaCl、Na_2CO_3 处理组碱蓬、盐地碱蓬种子的平均萌发时间明显小于等渗 PEG 处理, 并且与对照无显著差异。

2.3 PEG、NaCl、Na_2CO_3 胁迫对碱蓬、盐地碱蓬胚生长特性的影响

在 PEG 和 Na_2CO_3 处理中, 碱蓬、盐地碱蓬胚轴、胚根长度随溶液渗透势降低而下降, 低渗 NaCl 处理(−0.46 MPa)处理对碱蓬、盐地碱蓬胚的生长具有促进作用, 高渗 NaCl 处理(−1.38 MPa、−1.84 MPa)对碱蓬和盐地碱蓬胚轴、胚根的生长具有抑制

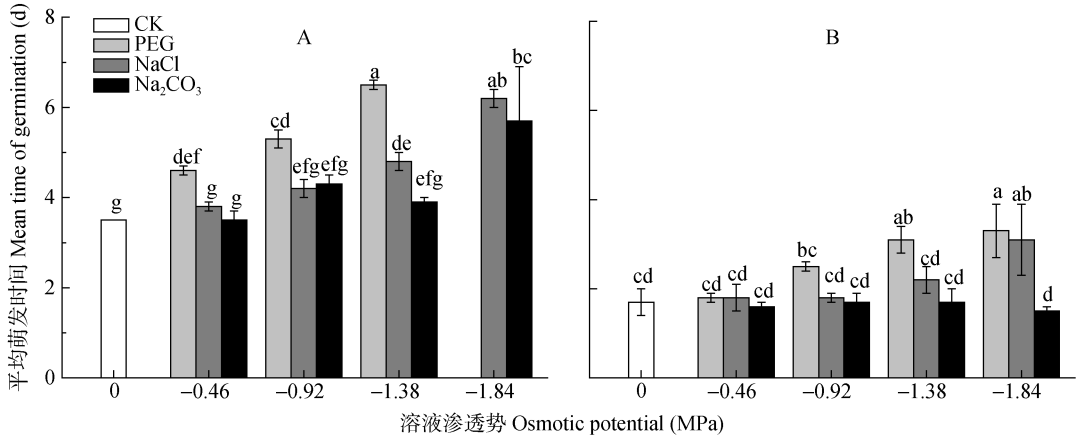

图 4　不同渗透势 PEG、NaCl 和 Na_2CO_3 处理对碱蓬(A)和盐地碱蓬(B)平均萌发时间的影响

Fig. 4　Effects of PEG, NaCl and Na_2CO_3 with different ostimotic potentials on the mean germination times of *Suaeda glauca* (A) and *Suaeda salsa* (B)

不同小写字母表示不用处理间 0.05 水平差异显著。Different lowercase letters mean significant differences among treatments at $P < 0.05$.

作用，但 NaCl 处理对碱蓬和盐地碱蓬胚生长的抑制作用明显小于等渗 PEG 和 Na_2CO_3 处理(图 5，图 6)。碱蓬、盐地碱蓬胚的生长对 NaCl 和 Na_2CO_3 胁迫的响应存在差异：−0.92 MPa NaCl 处理对盐地碱蓬胚根生长具有明显的促进作用，而碱蓬胚根的生长受到抑制；−0.46 MPa Na_2CO_3 处理下，碱蓬的胚轴和胚根长度分别比对照降低 13.0%和 12.9%，而盐地碱蓬胚轴和胚根长分别降低 33.9%和 64.0%，−0.46 MPa Na_2CO_3 处理对盐地碱蓬胚的生长抑制作用大于碱蓬(图 5，图 6)。

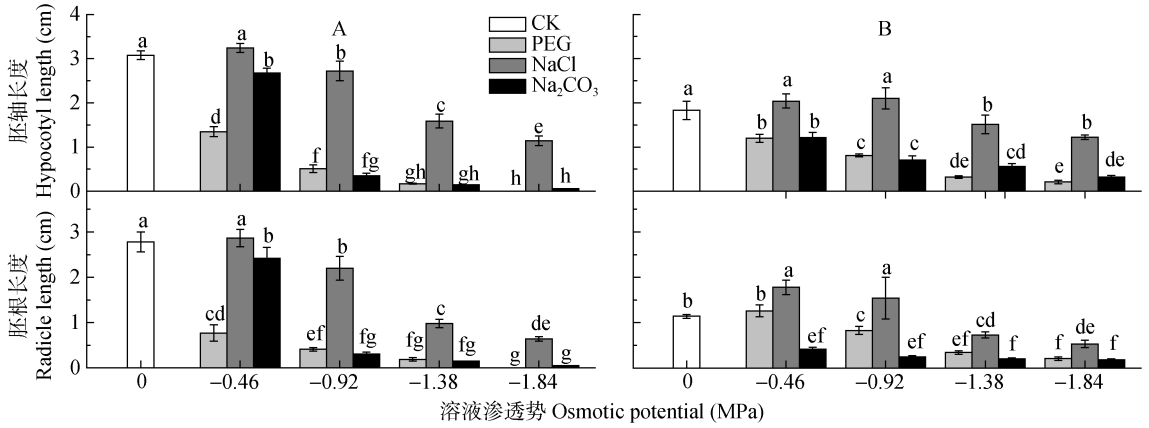

图 5　不同渗透势 PEG、NaCl 和 Na_2CO_3 处理对碱蓬(A)和盐地碱蓬(B)胚轴、胚根长度的影响

Fig. 5　Effects of PEG, NaCl and Na_2CO_3 with different ostimotic potentials on the hypocotyl and radicle lengths of *Suaeda glauca* (A) and *Suaeda salsa* (B)

不同小写字母表示不用处理间 0.05 水平差异显著。Different lowercase letters mean significant differences among treatments at $P < 0.05$.

3　讨论与结论

植物的抗逆性不仅取决于植物种类，在不同的生长阶段，植物的抗逆性也存在较大差异。植物在种子萌发期与幼苗形成期对逆境敏感，成株抗性普遍较高[22]，因此种子萌发与幼苗形成期是研究植物抗逆性的最佳时期。与棉花(*Gossypium* spp.)、茄子(*Solanum melongena*)、芝麻(*Sesamum indicum*)的研究一致[23-25]，碱蓬、盐地碱蓬在种子萌发时期抗性较高，在幼苗形成期的抗逆性明显低于种子萌发期。本研究表明，低渗 PEG、Na_2CO_3 处理(−0.46 MPa)对种子萌发率影响不显著，但对碱蓬、盐地碱蓬胚的生长产生显著的抑制作用；高渗 PEG、NaCl、Na_2CO_3 胁迫(−1.38 MPa、−1.84 MPa)对碱蓬、盐地碱蓬的萌发与生长均产生不同程度的抑制作用。

种子萌发率与萌发指数结果表明：在等渗条件下，PEG 与 Na_2CO_3 胁迫对碱蓬种子萌发的抑制作用无显著差异，NaCl 胁迫对碱蓬种子萌发的抑制程度明显小于等渗 PEG、Na_2CO_3 胁迫；盐地碱蓬种子的萌发主要受渗透胁迫的影响，对 PEG、NaCl、Na_2CO_3 胁迫的响应无显著差异。有研究表明，在等渗条件

图 6 不同渗透势 PEG、NaCl 和 Na_2CO_3 处理对碱蓬和盐地碱蓬幼苗形成的影响

Fig. 6 Effects of PEG, NaCl and Na_2CO_3 with different ostimotic potentials on the seedlings establishment of *Suaeda glauca* and *Suaeda salsa*

下细茎针茅(*Stipa tenacissima*)、长角豆(*Ceratonia siliqua*)种子在 NaCl 溶液中的萌发率高于 PEG[26-27]。本研究中碱蓬、盐地碱蓬也出现类似现象，这可能是由于 NaCl 起到了渗透调节作用。NaCl 作为无机离子，在机体的富集有助于减缓渗透胁迫的负面影响[28]。Cavallaro 等[29]研究表明长角豆种子在 NaCl 溶液中的吸胀速率明显高于在等渗 PEG 溶液中。NaCl 胁迫下碱蓬、盐地碱蓬种子的吸胀与萌动过程还有待深入研究。对牛至(*Origanum compactum*)、羊草(*Leymus chinensis*)的研究表明，高 pH 是抑制种子萌发的重要因素[30-31]。本研究中尽管 Na_2CO_3 胁迫对碱蓬、盐地碱蓬种子萌发产生了明显的抑制作用，但在等渗条件下，Na_2CO_3 胁迫与 PEG 胁迫的抑制作用无显著差异。由此可知，对于碱蓬、盐地碱蓬，Na_2CO_3 胁迫对种子萌发的抑制作用主要是由于渗透胁迫，高 pH 胁迫没有产生显著影响。

植物种子在高盐逆境下存活，雨季后集中萌发并建立种群是盐生植物适应盐生境的重要策略[32-33]。大部分盐生植物种子具有较强的恢复萌发能力，也有物种如驼蹄瓣(*Zygophyllum simplex*)、异子蓬(*Borszczowia aralocaspica*)、地肤(*Kochia scoparia*)种子的萌发活性被盐胁迫永久抑制[34-36]。复水试验表明 PEG、NaCl 胁迫下碱蓬、盐地碱蓬种子均具有良好的恢复萌发能力，虽然 Na_2CO_3 处理组种子的复水萌发率与对照差异不显著，但 Na_2CO_3 胁迫有降低盐地碱蓬种子最终萌发率的趋势，Na_2CO_3 胁迫对盐地碱蓬种子产生了毒害作用。

对碱蓬、盐地碱蓬早期生长特性的研究表明，碱蓬、盐地碱蓬均表现喜盐的特征，但盐地碱蓬对 NaCl 的抗性高于碱蓬。轻度 NaCl 处理对盐地碱蓬胚根伸长的促进作用明显大于碱蓬，高 NaCl 处理对盐地碱蓬根长的抑制作用小于碱蓬，这与前人研究结果一致[37]。与盐胁迫相比，碱胁迫还会对植物产生高 pH 伤害，金属离子与磷的沉淀会阻碍植物对矿质营养的吸收，从而扰乱机体的离子平衡与 pH 稳态[38-39]，对植物产生更严重的损伤。与苍耳(*Xanthium sibiricum*)、碱地肤(*Kochia sieversiana*)、灰绿藜(*Chenopodium glaucum*)[40-42]等盐生植物一样，Na_2CO_3 胁迫对碱蓬、

盐地碱蓬生长的抑制作用明显大于 NaCl 胁迫, 重度碱胁迫(–0.92 MPa、–1.38 MPa、–1.84 MPa)下, 碱蓬、盐地碱蓬根尖出现变黑死亡的现象。比较碱蓬与盐地碱蓬发现, 二者在幼苗形成期对轻度 Na_2CO_3 胁迫(–0.46 MPa)的抗性存在差异, 轻度 Na_2CO_3 胁迫(–0.46 MPa)对碱蓬胚生长的抑制作用明显小于盐地碱蓬。碱蓬与盐地碱蓬在幼苗形成期抗盐、抗碱性的差异可能是导致二者地带性分布的重要原因。我国东北盐渍区属于苏打碱土, 西北黄河中上游盐渍土主要盐分为碳酸盐, 土壤都明显偏碱性[43-44], 碱蓬对轻度 Na_2CO_3 胁迫的抗性优于盐地碱蓬, 因此碱蓬更偏向分布于内陆轻度碱土地区; 而辽河、黄河等滨海盐碱地是土壤盐分以 NaCl 为主的盐土, 盐地碱蓬对 NaCl 的高度适应性可能是盐地碱蓬种群从内陆向沿海发展以及低洼地带分布的重要原因。

本研究通过对碱蓬、盐地碱蓬在种子萌发及幼苗形成期逆境响应的综合分析, 发现碱蓬和盐地碱蓬对旱、盐、碱胁迫的响应趋势基本一致, 碱蓬和盐地碱蓬均具有很强的抗盐性, 并且抗盐能力明显高于抗旱、抗碱能力。比较碱蓬和盐地碱蓬, 在种子萌发期, 碱蓬种子的抗旱、抗碱能力低于盐地碱蓬; 在幼苗形成期, 碱蓬的抗盐性小于盐地碱蓬, 但对轻度碱胁迫的抗性高于盐地碱蓬。

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