Natural and Tissue Culture–Generated Variation in the Salt Marsh Grass *Sporobolus virginicus*: Potential Selections for Marsh Creation and Restoration

Denise M. Seliskar

Halophyte Biotechnology Center, College of Marine Studies, University of Delaware, 700 Pilottown Road, Lewes, DE 19958

Sporobolus virginicus (L.) Kunth. is a halophytic grass that inhabits salt marshes and sandy beaches of subtropical coasts. It is tolerant to salinities as high as $80 \text{ g} \cdot \text{kg}^{-1}$ (Gallagher, 1979) and tolerates flooding and hypoxic soils (Donovan and Gallagher, 1984, 1985). This plant has two distinct growth forms: a coarse, robust form found most commonly on sandy beaches and dunes, and a fine, soft form found typically in salt marshes (Blits and Gallagher, 1991; Hitchcock, 1971). The purpose of the research presented here was to compare selections of *S. virginicus* collected from natural populations with selections produced through tissue culture for morphological characteristics with the potential to affect marsh function in created or restored salt marshes.

Wetland creation and restoration are widespread practices used to prevent further net loss of valuable wetland ecosystems. Vascular plants are primary regulators of salt marsh ecosystems due to their high productivity and their large three-dimensional structure. The plants determine the amount of above- and below-ground organic material contributed to a marsh system. Dead shoots primarily fuel the aerial and aquatic phases of the detritus-based food web of a salt marsh, while the organic matter directed below-ground fuels the edaphic community (Gallagher and Plumley, 1979; Howes et al., 1984). Structure of the plant canopy, e.g., canopy height and stem density, affects the amount of light that reaches the marsh surface and therefore the benthic algal community and the temperature and water balance of the wetland system (Gallagher and Daiber, 1974; Van Raalte et al., 1976; Whitney and Darley, 1983). The canopy's structure also affects the use of the area by fish and other organisms (Kneib, 1984; Minello and Zimmerman, 1983). Root and rhizome sys-

tems are important in stabilizing the marsh sediment. Two wetlands with the same species of dominant plant, but with genotypes of different plant structure and form, may function differently (Seliskar, 1995).

MATERIALS AND METHODS

Natural populations. *Sporobolus virginicus* plants from natural marshes and dune populations in Georgia and Florida were collected and maintained as stock plants in a greenhouse where they were propagated vegetatively. The natural marsh fine-form plant populations denoted as CC, BH, and NSS are from different locations on Sapelo Island, Ga., JI is from Jekyll Island, Ga., MF is from Fort Matanzas, Fla., and NSB is from New Smyrna Beach, Fla. Likewise, the coarse-form populations NG and UN are from Sapelo Island, Ga., and PC is from Port Canaveral, Fla.

Tissue culture–generated plants. Regenerants of *S. virginicus* used in this study were propagated vegetatively in the greenhouse from regenerants originally developed by Straub (1990). Original cultures had been established using immature inflorescences as explant tissue, with callus grown on PP medium (Chandler and Vasil, 1984) plus $0.5 \text{ mg} \cdot \text{L}^{-1}$ 2,4-dichlorophenoxyacetic acid, $1.0 \text{ mg} \cdot \text{L}^{-1}$ 1-naphthaleneacetic acid, $1.0 \text{ mg} \cdot \text{L}^{-1}$ benzyladenine, $30 \text{ g} \cdot \text{L}^{-1}$ sucrose, and 5% coconut water; plant regeneration was initiated by auxin removal (Straub et al., 1992). In the regenerant graphs depicted in this paper (Figs. 1–3), the first six regenerants (R24, R28, R58, R22, R09, R101) came from one parent plant collected on Jekyll Island, Ga., and the last two (R43 and R55) came from another parent plant collected on Sapelo Island, Ga.

Field studies. Two-gallon plastic buckets were modified by drilling 25 evenly distributed drainage holes on sides and bottom, and cutting an $8 \times 2\text{-cm}$ slit 3 cm down from the top rim to allow for water to flow into and out of the bucket; these were similar to the units described by Gallagher and Wolf (1980). They were filled with sieved field soil, and each was planted with four plants with attached rhizome sections, using six replicate buckets for each plant selection. Buckets were planted during early June in a simulated marsh field plot such that the bottom of the slit was level with the soil surface. They were flood-irrigated thrice weekly with saltwater pumped from a nearby tidal creek, and harvested in early November, after one growing season, since *S. virginicus* is not winter hardy in Delaware.

After the buckets were harvested, the shoots were cut off at the soil surface and placed in plastic bags and stored in a refrigerator until morphological and biomass measurements could be made. The soil portion was removed from the bucket and placed on a sieve where roots and rhizomes were washed free of soil. Roots and rhizomes were separated, dried at 60°C , and weighed. Morphological measurements made later on the shoots included plant height, stem density, leaf length and width, internode length, and stem diameter. Shoots were then dried at 60°C and weighed. Root : shoot ratios and root : rhizome ratios were also determined.

RESULTS

Shoot biomass varied significantly among natural populations of *Sporobolus virginicus*, as well as among the regenerants of this species. The first six natural populations (CC, BH, NSS, JI, MF, NSB) are the fine marsh form of this species, while the last three (NG, PC, UN) are the coarse dune form (Figs. 1–3). Dry mass in the fine form ranged from ≈ 400 to $800 \text{ g} \cdot \text{m}^{-2}$, while that in the coarse form ranged from 1000 to $1200 \text{ g} \cdot \text{m}^{-2}$ (Fig. 1A). There were significant differences in biomass among the various populations, with population CC producing the least shoot biomass. With the regenerants (Fig. 1B), the first six are from one parent and the last two from another. Somaclonal variation was evident in that there were significant differences among the regenerants coming from the first parent, with R22 producing the most shoot biomass.

Among the natural populations, the coarse-form plants produced the most below-ground biomass (Fig. 1C). Significant variation in below-ground biomass is evident among the fine-form populations, as well as among the regenerants, with R09 producing significantly less biomass than the other regenerants (Fig. 1D).

Stem density varied from ≈ 5000 to $8000 \text{ stems} \cdot \text{m}^{-2}$ in the fine-form natural populations and was $\approx 2000 \text{ stems} \cdot \text{m}^{-2}$ in the three coarse-form populations (Fig. 2A). The regenerants R22 and R09 produced significantly fewer stems than did any of the other regenerants (Fig. 2B) or the fine-form natural populations. Canopy height was greatest in the NSB fine-form natural population and in the NG and UN coarse-form populations (Fig. 2C). Regenerant R22 produced the tallest canopy of all the tissue culture and natural selections tested (Fig. 2D).

In the natural fine-form populations, the CC and NSB populations produced the high-

Received for publication 6 Oct. 1997. Accepted for publication 8 Nov. 1997. Support for this research came from the Coastal Ocean Program Office of the National Oceanic and Atmospheric Administration through Grant No. NA90AA-D-SG457 to the Univ. of Delaware Sea Grant Program. The original genotypes used for this project were developed under Grant No. NA83AA-D-00017, Project R/B-22 of the University of Delaware Sea Grant Program. I am grateful to Jack Gallagher for his participation in the project, and to Mike Gross, Xianggan Li, Laurie Mutz, Divakar Rao, Ron Smith, Tonny Wijte, and Jinglan Wu for their assistance with various aspects of the field work and data collection. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.

Fig. 1. Shoot (A, B) and below-ground (C, D) biomass of natural populations of *Sporobolus virginicus* (A, C) and selections regenerated from tissue culture (B, D). The first six natural populations are the fine form and the last three the coarse form plants. The first six regenerants were propagated from one parent plant and the last two from another. Bars represent mean $\pm$ standard error. Based upon one-way analysis of variance, statistically significant differences exist among the natural populations and among the regenerants ($P \leq 0.05$).

Fig. 2. Stem density (A, B) and canopy height (C, D) of natural populations of *Sporobolus virginicus* (A, C) and selections regenerated from tissue culture (B, D). The first six natural populations are the fine form and the last three the coarse form plants. The first six regenerants were propagated from one parent plant and the last two from another. Bars represent mean $\pm$ standard error. Based upon one-way analysis of variance, statistically significant differences exist among the natural populations and among the regenerants ($P \leq 0.05$).

est percentage of flowering stems (Fig. 3A). Among the regenerants, R22 produced a much higher percentage of flowering stems than did any of the others, while R101 and R43 produced significantly fewer flowering stems (Fig. 3B).

Other morphological parameters are also important in determining the architecture of the canopy (Table 1). Leaf length varied from 5.22 cm in the NSB natural fine-form population to 6.78 cm in Regenerant R58. Leaf width was greatest in the coarse-form plants, ranging up to 5.23 mm in the UN population. Among the fine-form natural population plants and regenerants, leaf width varied from 2.10 to 2.78 mm. Internode length was greatest in the tallest plants, the NSB natural population and Regenerants R22 and R09. That these two regenerants were both significantly taller with longer internodes than the other regenerants is evidence of somaclonal variation in this characteristic. Stem diameter, which can affect the stability and uprightness of the canopy, was greatest in the coarse-form natural populations, almost twice that of the fine form.

Root : shoot ratios illustrate how photosynthate is allocated to above- and below-ground portions of the plant, with a value >1.0 indicating more roots and rhizomes than shoots and a value <1.0 indicating that more resources were directed to shoots than to below-ground parts. There was more variation among the regenerants in this characteristic than among the natural populations (Table 1). In the first six regenerants, all of which come from the same parent, values ranged from 0.38 to 1.25, indicating a significant difference in how these plants manage their photosynthate. It is also evidence of somaclonal variation. Among the fine-form natural populations, the root : rhizome ratio varied significantly from 0.31 to 0.80 and among the regenerants from 0.31 to 0.57. The lower numbers may indicate more resources were being stored in rhizomes than were used to produce roots.

DISCUSSION

Biomass and structure can vary significantly among genotypes of a single species of salt marsh plant, as seen when the various genotypes are planted in a common garden (Gallagher et al., 1988) or when planted together in a created wetland (Seliskar, 1995). These differences can affect the functional aspects of the ecosystem in which the plants are a component (Seliskar, 1995). We can take advantage of these genetically based differences in plant phenotype when planting newly created or restored marshes by selecting plants with particular attributes to suit a particular site.

Similar variation can be generated through tissue culture via somaclonal variation (Larkin and Scowcroft, 1981; McClintock, 1984). Changes take place while the plant is in callus culture and more variation occurs the longer the cells are kept in this stage (Lee and Phillips, 1987). Numerous examples exist in the literature of improving crop cultivars via somaclonal variation (Adkins et al., 1995; Arnold et al.,

Fig. 3. Percent flowering of natural populations of *Sporobolus virginicus* (A) and selections regenerated from tissue culture (B). The first six natural populations are the fine form and the last three the coarse form plants. The first six regenerants were propagated from one parent plant and the last two from another. Bars represent mean $\pm$ standard error. Based upon one-way analysis of variance, statistically significant differences exist among the natural populations and among the regenerants ($P \leq 0.05$).

1995; Racchi et al., 1995; Roylance et al., 1994; Winicov, 1991). Thus this approach could be used to produce noncrop plants with characteristics valuable for other purposes, such as marsh restoration.

Since the salt marsh ecosystem is detritus-based, the productivity of the system may be limited by the amount of dead organic matter formed to fuel detritus formation, especially in a newly created system where plant density is low. Therefore, if one could select lines of a given species that produce more above-ground biomass than others, they could be used to stimulate the aerial and aquatic phases of the newly created marsh. With *Sporobolus virginicus*, the coarse-form populations produce the most shoot biomass; however, since this form is not the native marsh form, the remaining discussion relative to marsh cre-

ation will focus primarily on the fine-form plants, i.e., the first six natural populations represented in the figures, and all the regenerants. Among the fine-form plants tested, the NSB, BH, and NSS natural populations and the regenerants, R22, R28, and R09, produced the most biomass (Fig. 1) and would therefore be the best choices for planting in a new marsh to enhance detritus production.

If development of below-ground processes is of high concern at a newly excavated site, where the soil may be poor due to removal of the top soil, then choosing plants that put significant resources into the production of organic matter below-ground is important. This will enhance the rate at which the soil community, the microbial and invertebrate populations, will develop, thereby hastening the transition to natural marsh equivalency. In

this case, natural populations BH, NSS, MF, and NSB and regenerants R24, 28, 58, 101, 43, and 55 would be good choices (Fig. 1). However, if the input of organic matter to produce detritus is as important as putting organic matter below-ground, then natural population NSB or regenerant R22 should be the plants of choice. Although regenerant R09 produces large amounts of shoot biomass, it would not be the best choice since it produces less root and rhizome material than any of the other selections.

Erosion control is also often a significant concern along coastlines. Selecting plant varieties that produce a large network of roots would obviously be best for holding sand or sediment in place, thereby stabilizing the shoreline. For beaches and dunes, of course, the coarse-form plants, NG, PC, and UN, would be the best choices, all of which produce a large below-ground network. For marshes, the fine forms mentioned above that produce the most roots and rhizomes would be the plants of choice for preventing erosion.

Marshes are important in providing habitat for nursery and feeding grounds, as well as refuge from predators, for fish and other fauna (Kneib, 1984, 1987). The structure of the vegetation canopy significantly affects these marsh functions. Stem density is a significant factor in providing marsh fauna with protection from predation (Minello and Zimmerman, 1983, 1992). Three natural populations and four regenerated plant lines of *S. virginicus* in our study produced more than 6000 stems per m^2 (Fig. 2) and therefore may offer better protection from predators than the other plant lines tested. However, this density may be higher than optimal depending on the size and nature of the organisms to be protected, in which case regenerants R22 and R09 offer lower density options in the fine-form *S. virginicus*.

Canopy height is also important in marsh functioning, for example, in bird nesting (Zedler, 1993), and may be important in protecting young fish from avian predators. In our study, the fine-form natural population, NSB, and two regenerant lines, R22 and R09, provided the tallest canopy (Fig. 2). The canopy also has significant effects on the quantity of light reaching the soil surface and therefore on the edaphic algal community. With this factor, not only stem density and height play a role, but so does leaf structure, i.e., length and width, along with stem diameter and internode length (Table 1).

Although the spread of *S. virginicus* is almost entirely vegetative via rhizome growth, choosing plants that direct some effort into flowering may be desirable in a newly created marsh where the plant density is very low and seed distribution may be a means of hastening plant coverage. If this is the case, then Regenerant R22 offers the best choice, since it produced a significantly greater percentage of flowering stems than did any of the other selections, natural populations or regenerants (Fig. 3). However, if vegetative reproduction is desired to maintain particular plant characteristics, then the best choices for planting

Table 1. Morphological characteristics of *Sporobolus virginicus* populations. Values are means with SEs in parentheses. Within groups (natural populations, regenerants) statistically significant differences exist for each morphological characteristic below (one-way analysis of variance, $P \leq 0.05$).

Population	Type/Parent	Leaf length (cm)	Leaf width (mm)	Internode length (cm)	Stem diam (mm)	Root : shoot ratio	Root : rhizome ratio
<i>Natural populations</i>							
CC	fine	6.00 (0.15)	2.38 (0.09)	5.85 (0.73)	1.03 (0.05)	1.18 (0.09)	0.31 (0.04)
BH	fine	6.77 (0.36)	2.46 (0.07)	5.80 (0.77)	1.07 (0.02)	1.12 (0.14)	0.39 (0.05)
NSS	fine	6.05 (0.23)	2.32 (0.10)	5.90 (0.65)	0.98 (0.03)	0.98 (0.16)	0.54 (0.06)
JI	fine	6.60 (0.24)	2.65 (0.11)	6.12 (0.29)	1.06 (0.02)	0.98 (0.13)	0.51 (0.06)
MF	fine	5.69 (0.12)	2.78 (0.08)	7.49 (0.39)	1.09 (0.02)	1.08 (0.09)	0.54 (0.04)
NSB	fine	5.22 (0.22)	2.10 (0.13)	12.29 (0.91)	1.08 (0.02)	0.77 (0.10)	0.80 (0.14)
NG	coarse	6.61 (0.24)	4.70 (0.15)	9.97 (1.09)	2.05 (0.04)	0.85 (0.06)	0.32 (0.03)
PC	coarse	5.63 (0.13)	5.20 (0.09)	6.21 (0.55)	2.08 (0.04)	0.88 (0.07)	0.25 (0.02)
UN	coarse	6.27 (0.15)	5.23 (0.14)	9.46 (0.66)	2.04 (0.06)	0.95 (0.10)	0.40 (0.08)
<i>Regenerants</i>							
R24	1	6.39 (0.17)	2.27 (0.15)	5.87 (0.38)	0.98 (0.04)	1.25 (0.13)	0.44 (0.08)
R28	1	6.68 (0.25)	2.35 (0.08)	6.57 (0.27)	1.07 (0.02)	1.15 (0.13)	0.37 (0.02)
R58	1	6.78 (0.10)	2.50 (0.04)	7.07 (0.44)	1.05 (0.03)	1.24 (0.09)	0.33 (0.03)
R22	1	6.01 (0.28)	2.40 (0.11)	11.99 (1.16)	1.08 (0.03)	0.74 (0.05)	0.43 (0.03)
R09	1	5.65 (0.32)	2.58 (0.11)	11.16 (0.41)	1.04 (0.05)	0.38 (0.02)	0.57 (0.06)
R101	1	6.28 (0.29)	2.68 (0.12)	4.70 (0.34)	0.96 (0.04)	1.14 (0.09)	0.33 (0.04)
R43	2	6.04 (0.28)	2.37 (0.09)	4.63 (0.27)	1.01 (0.03)	1.42 (0.14)	0.31 (0.03)
R55	2	5.71 (0.11)	2.21 (0.07)	4.60 (0.20)	1.03 (0.03)	1.40 (0.10)	0.35 (0.04)

would be Regenerants R101 and R43 and natural population NSS.

Of the plant selections tested, the natural population, NSB, and regenerant line R22, appear to offer the best all-around combination of characteristics for planting in a newly created marsh: high shoot biomass, fairly high root plus rhizome biomass, and a tall canopy with a moderate stem density.

CONCLUSIONS

This research demonstrates that there is significant variation in plant structure and biomass of *Sporobolus virginicus* collected from natural populations in different geographic locations. Also evident from this study is the fact that similar amounts of variation can be produced from any one natural population selection using tissue culture techniques, i.e., via somaclonal variation in plants regenerated from callus culture. The latter provides a low-cost method of generating variation without the need for travel to numerous geographic locations, and the types of changes that occur in tissue culture are ones that could also occur in nature. Vegetative reproduction is by far the dominant form of reproduction in salt marsh grasses. Thus, for purposes of marsh creation and restoration, whether characteristics of first generation tissue culture regenerants are sexu-

ally stable or not is of no concern, because by reproducing vegetatively the original morphological and structural characteristics are maintained. The different phenotypic characteristics of the various plant selections can affect the development of newly created marshes in distinctively different ways. The amount of detritus production, the development of the soil community, the growth of the edaphic algal community, and the use of the marsh for refuge, nursery, and feeding grounds by fish and other fauna are all dependent on the productivity and three-dimensional structure of the dominant vascular plant. The plants chosen for a given site will affect the functioning of the whole marsh ecosystem.

Literature Cited

- Adkins, S.W., R. Kuranuvatchaidach, and I.D. Godwin. 1995. Somaclonal variation in rice—Drought tolerance and other agronomic characters. *Aust. J. Bot.* 43:201–209.
- Arnold, D., A. Flegmann, J.M. Clarkson. 1995. Somaclonal variation in watercress for resistance to crook root disease. *Plant Cell Rpt.* 14:241–244.
- Blits, K.C. and J.L. Gallagher. 1991. Morphological and physiological responses to increased salinity in marsh and dune ecotypes of *Sporobolus virginicus* (L.) Kunth. *Oecologia* 87:330–335.
- Chandler, S.F. and I.K. Vasil. 1984. Selection and characterization of NaCl tolerant cells from embryogenic cultures of *Pennisetum purpureum* Schum (Napier grass). *Plant Sci. Lett.* 37:157–164.

- Donovan, L.A. and J.L. Gallagher. 1984. Anaerobic substrate tolerance in *Sporobolus virginicus* (L.) Kunth. *Amer. J. Bot.* 71:1424–1431.
- Donovan, L.A. and J.L. Gallagher. 1985. Morphological responses of a marsh grass, *Sporobolus virginicus* (L.) Kunth., to saline and anaerobic stresses. *Wetlands* 5:1–13.
- Gallagher, J.L. 1979. Growth and elemental compositional responses of *Sporobolus virginicus* (L.) Kunth. to substrate salinity and nitrogen. *Amer. Mid. Nat.* 102:68–75.
- Gallagher, J.L. and F.C. Daiber. 1974. Primary production of the edaphic algal communities in a Delaware salt marsh. *Limnol. Oceanogr.* 19:390–395.
- Gallagher, J.L. and F.G. Plumley. 1979. Underground biomass profiles and productivity in Atlantic coastal marshes. *Amer. J. Bot.* 66:151–161.
- Gallagher, J.L., G.F. Somers, D.M. Grant, and D.M. Seliskar. 1988. Persistent differences in two forms of *Spartina alterniflora*: A common garden experiment. *Ecology* 69:1005–1008.
- Gallagher, J.L. and P.L. Wolf. 1980. Field bioassays for the role of plants as vectors in contaminant transfer from dredged material, p. 445–463. In: R.H. Baker (ed.). *Contaminants and sediments*, vol. 2. Chemistry, biology, toxicology. Ann Arbor Science Publ., Ann Arbor, Mich.
- Hitchcock, A.S. 1971. *Manual of the grasses of the United States*. Dover Publications, New York.
- Howes, B.L., J.W.H. Dacey, and G.M. King. 1984. Carbon flow through oxygen and sulfate reduction pathways in salt marsh sediments. *Limnol. Oceanogr.* 29:1037–1051.
- Kneib, R.T. 1984. Patterns in the utilization of the intertidal salt marsh by larvae and juveniles of *Fundulus heteroclitus* (Linnaeus) and *Fundulus luciae* (Baird). *J. Expt. Marine Biol. Ecol.* 83:41–51.
- Kneib, R.T. 1987. Predation risk and use of intertidal habitats by young fishes and shrimp. *Ecology* 68:379–386.
- Larkin, P.J. and W.R. Scowcroft. 1981. Somaclonal variation—A novel source of variability from cell culture for plant improvement. *Theor. Appl. Genet.* 60:197–214.
- Lee, M.L. and L.R. Phillips. 1987. Genetic variability in progeny of regenerated maize (*Zea mays* L.) plants. *Genome* 29:344–355.
- McClintock, B. 1984. The significance of responses of the genome to challenge. *Science* 226:792–801.
- Minello, T.J. and R.J. Zimmerman. 1983. Fish predation on juvenile brown shrimp, *Penaeus aztecus* Ives: The effect of simulated *Spartina* structure on predation rates. *J. Expt. Marine Biol. Ecol.* 72:211–231.
- Minello, T.J. and R.J. Zimmerman. 1992. Utilization of natural and transplanted Texas salt marshes by fish and decapod crustaceans. *Mar. Ecol. Prog. Ser.* 90:273–285.
- Racchi, M.L., M. Rebecchi, G. Todesco, E. Nielsen, and G. Forlani. 1995. Glyphosate tolerance in maize (*Zea mays* L.). 2. Selection and characterization of a tolerant somaclone. *Euphytica* 82:165–173.
- Roylance, J.T., N.S. Hill, and W.A. Parrott. 1994. Detection of somaclonal variation in tissue-culture regenerants of tall fescue. *Crop Sci.* 34:1369–1372.
- Seliskar, D.M. 1995. Exploiting plant genotypic diversity for coastal salt marsh creation and restoration, p. 407–416. In: M.A. Khan and I.A. Ungar (eds.). *Biology of salt-tolerant plants*. Dept. of Botany, Univ. of Karachi, Pakistan.
- Straub, P.F. 1990. Tissue culture and somatic cell genetics of the salt-tolerant grasses *Distichlis spicata* and *Sporobolus virginicus* (L.) Kunth. PhD Diss., Univ. of Delaware, Lewes.
- Straub, P.F., D.M. Decker, and J.L. Gallagher. 1992. Characterization of tissue culture initiation and plant regeneration in *Sporobolus virginicus* (Gramineae). *Amer. J. Bot.* 79:1119–1125.
- Van Raalte, C.D., I. Valiela, and J.M. Teal. 1976. Production of epibenthic salt marsh algae: Light and nutrient limitation. *Limnol. Oceanogr.* 21:862–872.
- Whitney, D.E. and W.M. Darley. 1983. Effect of light intensity upon salt marsh benthic microalgal photosynthesis. *Mar. Biol.* 75:249–252.
- Winicov, I. 1991. Characterization of salt tolerant alfalfa (*Medicago sativa* L.) plants regenerated from salt tolerant cell lines. *Plant Cell Rpt.* 10:561–564.
- Zedler, J.B. 1993. Canopy architecture of natural and planted cordgrass marshes: Selecting habitat evaluation criteria. *Ecol. Applic.* 3:123–138.