Estuaries Vol. 28, No. 5, p. 761–766 October 2005

Environmental Determination of Shoot Height in Populations of the Cordgrass *Spartina maritima*

J. M. CASTILLO[1,*], S. REDONDO[1], C. WHARMBY[1], M. E. FIGUEROA[1], T. LUQUE[1], E. M. CASTELLANOS[2], and A. J. DAVY[3]

[1] *Departamento de Biología Vegetal y Ecología, Facultad de Biología, Universidad de Sevilla, Apartado 1095, 41080-Sevilla, Spain*

[2] *Departamento de Biología Ambiental y Salud Pública, Facultad de Ciencias Experimentales, Universidad de Huelva, Spain*

[3] *Centre for Ecology, Evolution and Conservation, School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, U.K.*

ABSTRACT: *Spartina* species tend to exhibit a range of phenotypes, often with short and tall growth forms. Such differences have been attributed variously to environmentally induced phenotypic plasticity and genetic differentiation between populations. This work examines the basis of height variation in *Spartina maritima* (Curtis) Fernald at Odiel salt marshes, southwest Spain. Populations from sites with lower sediment redox potentials tended to have significantly taller shoots. Thirty-four natural populations with an 8-fold range of shoot height were transplanted to a common environment on an unvegetated, intertidal plain and shoot height was measured annually for 3 yr. There was a striking convergence in height across populations after transplantation and the change in height in each year of a population was linearly related to its initial height. Most populations grew taller after transplantation, suggesting environmental limitation in their natural habitats. Populations that were originally tall tended to become shorter. The change in shoot height was negatively related to the difference in surface sediment redox potential between their natural sites and the common transplant site. Hypoxic sediments may stimulate stem growth, resulting in improved photosynthetic gas exchange and internal aeration of roots and rhizomes. Although height variation in *S. maritima* appears mainly to be a result of phenotypic plasticity, a genetic component cannot be ruled out. This study emphasizes the importance of long-term studies, preferably longer than turnover time of shoot populations. The highly plastic growth form of *S. maritima* allows it to colonize a wide range of habitats in environmentally heterogeneous salt marshes.

Introduction

Several species of *Spartina* clearly show distinguishable tall and short growth forms (Shea et al. 1975; Mendelssohn 1979; Howes et al. 1986; Pezeshki and DeLaune 1991). Some studies have concluded that the observed variability in growth forms among *Spartina* populations may be the result of genetic differentiation (Gallagher et al. 1988; Sanchez et al. 1997; Proffitt et al. 2003), identifying ecotypes with different canopy heights (Seliskar et al. 2002). Other studies have attributed different growth forms to phenotypic plasticity in response to differences in environmental factors (Anderson and Treshow 1980), such as the availability of nutrients (Dai and Wiegert 1997; Wigand et al. 2003) or salinity (Phelger et al. 1971; Trnka and Zedler 2000). The consequence is that the different growth forms are only ecophenes. Variation in canopy height of a dominant *Spartina* species can influence ecological functions and the structure of plant and animal communities in a marsh (Seliskar et al. 2002).

Spartina maritima is an important pioneer and ecosystem engineer in salt marshes on the Atlantic coast of southern Europe (Castellanos et al. 1994; Castillo et al. 2000). It produces extensive stands, in a range of marsh environments (Castellanos et al. 1998), that also differ greatly in their shoot height. Collateral transplantation to a common environment has proved a particularly informative approach to investigating the origins of such morphological variation in a large number of local populations and has been used in other species of *Spartina* (Thompson et al. 1991).

The work described in this paper aimed to assess the importance of plasticity in response to environmental variation and genetic differentiation as determinants of shoot height in a large sample of local populations of *S. maritima* with a wide range of phenotypes. The specific objectives were to examine the environmental correlates of shoot height and the response of shoot height in these populations after transplantation to a generally favorable common environment.

---

* Corresponding author; tele: +34 954557165; fax: +34 954615780; e-mail: manucas@us.es

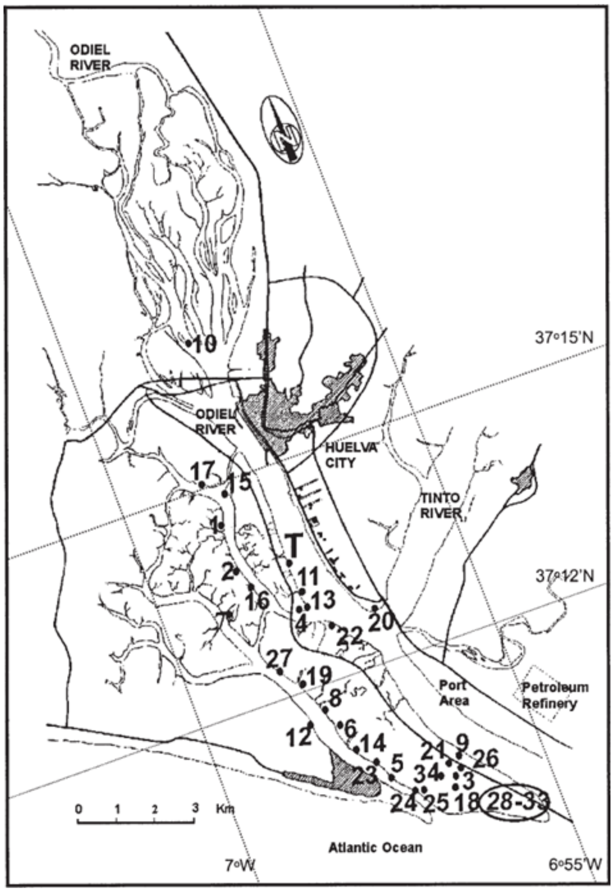

Fig. 1. Location of Odiel marshes on the Atlantic coast of southwest Spain, showing the sites of 34 natural populations of *Spartina maritima* and the intertidal plain transplant site (T) within Odiel marshes.

Materials and Methods

STUDY LOCATION

The study was carried out at Odiel marshes, in the joint estuary of the Odiel and Tinto rivers at Huelva, on the Atlantic coast of southwest Spain (Fig. 1). This coast is mesotidal; tides are semidiurnal with a mean range of 2.10 m and a mean spring tidal range of 2.97 m, representing 0.40–3.37 m above Spanish Hydrographic Zero (SHZ). Mean sea level at Huelva is +1.85 m relative to SHZ.

ENVIRONMENTAL CHARACTERISTICS OF NATURAL POPULATIONS

Elevation and sediment data were obtained, before transplantation, for 29 monospecific stands representing natural populations of *S. maritima*. Elevation relative to SHZ was determined using a theodolite (Leica NA 820). Redox potential of the sediment was determined in the field with a portable meter and electrode system (Crison pH/mV p-506). Sediment salinity was measured as conductivity of the interstitial water (conductivity meter, Crison-522) in the laboratory. Five replicate measurements were made of all sediment characteristics, at two depths (0–2 and 3–10 cm) during June and July 1999.

TRANSPLANT EXPERIMENT

Thirty-four natural *S. maritima* populations (including the 29 for which environmental data were obtained) were selected to represent the range of shoot height at various sites at Odiel (Fig. 1). Two or three clumps with homogeneous shoot height were removed from each population and transplanted to a common environment in the same marsh system during October 2001. Clumps were planted in rows parallel to the tidal line, 1 m apart, on an unvegetated and gently sloping intertidal plain (mean elevation +1.62 m SHZ) that faces southeast at the edge of the principal channel of the estuary (Fig. 1). This position is within the normal elevational range of *S. maritima* and where conditions are generally favorable for its growth and survival (Castillo et al. 2000). Clumps were chosen primarily to have similar amounts of underground reserves as rhizomes and roots and 20–40 shoots extracted where possible from different tussocks in the natural populations. No attempt was made to remove local sediment adhering to the clumps. Individual clumps were planted to a depth of 10–15 cm.

HEIGHT MEASUREMENTS

Shoot height was measured from the base of the shoot to the tip of the tallest leaf. Measurements (n = 30) were taken in the natural *S. maritima* populations before transplanting and in the transplanted clumps after 1, 2, and 3 yr during October (10 shoots in each clump, chosen at random among the population of mature, taller shoots without a flowering spike; n = 20–30). The median survival time of *S. maritima* shoots has been estimated at 9–12 months (Castellanos et al. 1998), so shoots alive 2 yr after transplantation were likely to be new recruits in the common environment of the intertidal plain.

STATISTICAL ANALYSIS

Analysis was carried out using Statistica release 5.1 (Statsoft Inc. Tulsa, Oklahoma). Analysis of variance (ANOVA) was used to compare heights in different planting rows to determine whether the planting scheme affected the height response. Pearson correlation coefficients and regressions were calculated between shoot heights before and after transplanting to examine relative changes in height

TABLE 1. Mature shoot height (cm) of *Spartina maritima* in 34 natural populations from Odiel marshes, southwest Spain, and in plants from the same populations 1, 2, and 3 yr after transplantation to a common environment. Values are means (± SE). n = 20–30.

	Shoot Height (cm)			
Population	Natural Population	Year 1	Year 2	Year 3
1	8.5 (0.4)	26.4 (0.7)	38.5 (1.0)	43.7 (0.7)
2	13.3 (0.6)	23.2 (0.3)	30.0 (0.9)	33.9 (0.8)
3	14.2 (0.5)	33.4 (0.9)	42.0 (0.8)	41.5 (0.9)
4	14.8 (0.6)	25.9 (0.8)	38.2 (1.5)	45.8 (1.2)
5	15.3 (0.6)	22.3 (0.7)	28.0 (0.6)	30.7 (0.8)
6	15.5 (0.5)	21.2 (0.6)	34.5 (1.0)	39.0 (0.6)
7	15.5 (0.7)	21.2 (0.7)	32.9 (0.7)	36.3 (0.6)
8	15.6 (0.6)	20.8 (0.9)	35.9 (1.8)	36.7 (0.9)
9	16.7 (0.8)	34.4 (0.6)	40.3 (0.8)	48.0 (0.9)
10	16.7 (0.8)	24.6 (0.9)	38.0 (0.9)	44.8 (0.9)
11	16.7 (0.7)	25.4 (0.8)	33.1 (0.7)	34.4 (0.4)
12	17.6 (0.9)	24.0 (0.6)	29.4 (0.5)	35.3 (0.8)
13	17.9 (0.6)	31.0 (1.2)	39.8 (1.4)	45.0 (0.8)
14	18.1 (0.7)	23.0 (1.0)	39.0 (1.3)	43.9 (1.0)
15	21.5 (1.0)	28.9 (0.6)	42.0 (0.6)	47.1 (1.1)
16	22.0 (0.9)	29.8 (0.8)	41.0 (0.8)	43.8 (0.9)
17	25.0 (0.8)	22.9 (0.6)	31.5 (0.7)	30.6 (0.6)
18	26.5 (1.2)	32.0 (0.4)	43.7 (0.7)	44.9 (0.9)
19	28.8 (0.9)	30.4 (0.7)	40.7 (0.6)	44.7 (0.9)
20	30.3 (0.7)	33.5 (1.0)	40.9 (1.5)	51.9 (1.6)
21	30.7 (0.8)	34.6 (0.7)	40.5 (1.2)	43.4 (1.3)
22	31.1 (0.7)	30.7 (0.8)	48.7 (1.4)	53.3 (1.1)
23	31.9 (1.4)	32.5 (0.8)	44.9 (0.8)	50.0 (0.9)
24	33.9 (0.8)	24.6 (0.7)	33.0 (0.9)	37.8 (1.0)
25	34.6 (1.1)	25.5 (1.0)	39.5 (0.9)	46.5 (0.8)
26	35.8 (0.8)	25.3 (0.9)	37.5 (1.6)	34.3 (0.9)
27	36.5 (1.5)	24.0 (1.4)	35.2 (0.5)	37.1 (0.6)
28	46.9 (1.0)	36.1 (1.0)	44.9 (1.3)	46.2 (1.3)
29	48.2 (1.3)	38.4 (1.6)	50.4 (1.5)	54.0 (0.6)
30	48.4 (1.3)	25.4 (1.3)	46.1 (2.5)	42.2 (1.9)
31	49.7 (0.9)	24.3 (0.8)	43.6 (1.0)	42.7 (1.5)
32	52.9 (0.7)	27.0 (1.0)	49.4 (1.0)	50.0 (1.1)
33	60.3 (1.1)	28.9 (1.0)	49.9 (0.6)	43.4 (0.9)
34	66.9 (0.9)	22.5 (0.7)	37.9 (0.8)	36.0 (0.7)
Mean	28.8 (2.6)	27.5 (0.8)	39.4 (1.0)	42.3 (1.1)

and between changes in shoot height and changes in abiotic environmental factors after transplanting to identify environmental factors related to shoot height. Student's *t*-test for dependent samples was used to compare mean shoot height between years.

Results

The mean mature shoot height in 34 natural *S. maritima* populations from different parts of Odiel ranged from 8.5 to 66.9 cm (nearly 8-fold) at the time of collection (Table 1). Mean mature shoot height per population was negatively related to surface (0–2 cm) sediment redox potentials at the natural population sites ($r = -0.38$, $p < 0.04$). Populations on sediments of lower redox potential tended to have taller shoots. Shoot height showed no significant correlations with sediment salinity or elevation over SHZ.

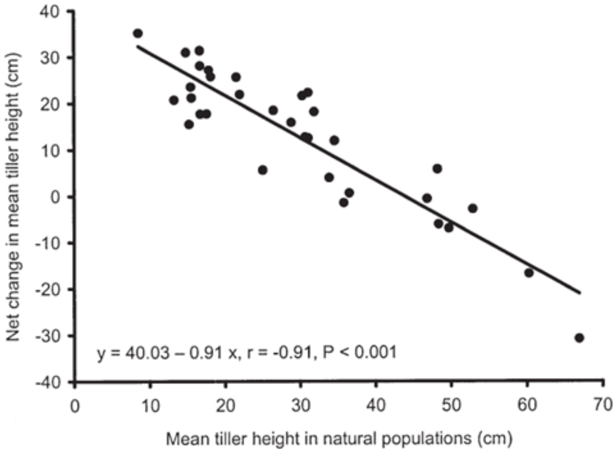

Fig. 2. Relationship between mean net change in mature shoot height of 34 populations of *Spartina maritima* from Odiel marshes, 3 yr after transplantation to an intertidal plain, and initial mature shoot height in their natural populations.

The planting scheme at the transplant site had no significant effect on shoot height at the end of the experiment (ANOVA, $p = 0.84$). After transplantation to a common environment, there was an overall tendency for height to increase, as the initial mean of 28.8 ± 2.6 cm increased to 42.3 ± 1.1 cm after 3 yr. The variation between populations also declined after transplantation. At the end of the experiment mean mature shoot height ranged from 30.6 ± 0.6 to 54.0 ± 0.6 cm (Table 1). Three years after transplantation it was clear that, although initially short populations had become taller, the populations that had been tall initially had tended to become shorter. There was negative, linear relationship between net change in height and initial population height (Fig. 2).

This pattern of change did not occur gradually or progressively over the 3 yr (Fig. 3). The greatest accommodation took place during year 1 after transplantation, when 95% of the populations with an initial mean mature shoot height over 30 cm suffered a significant reduction in their height (mean change −13.6 ± 3.6 cm). In contrast, 90% of populations with shoots initially shorter than 30 cm increased in height (mean change 8.4 ± 1.3 cm). There was a highly significant negative relationship between net change in height and initial height. During year 2, every population grew taller and the increase in height was positively correlated with the initial shoot height in natural populations. During year 3, a negative relationship between net change in height and initial height in the natural population reasserted itself, although with a much gentler slope than in year 1. Despite this, 68% of the populations increased their shoot height in year 3 (mean change 2.9 ± 0.6 cm).

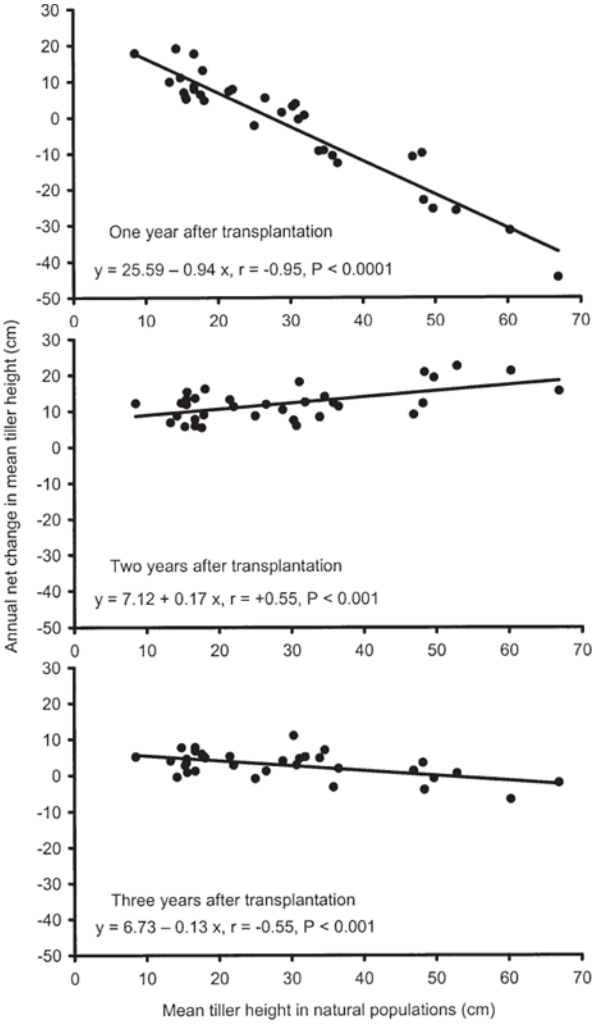

Fig. 3. Relationship between annual net change in mature shoot height of 34 populations of *Spartina maritima* from Odiel marshes in the 3 yr after transplantation to an intertidal plain and initial mature shoot height in their natural populations.

Mature shoot height 3 yr after transplanting had decreased only in the 5 tallest natural populations (*t*-test, $p < 0.05$). Mean height change in these populations was -12.6 ± 5.6 cm. Shoot height did not change significantly in 3 populations. It increased significantly in the other 26 populations (*t*-test, $p < 0.05$), with a mean change of $+20.2 \pm 1.6$ cm.

The transplant site at +1.62 m above SHZ had a sediment surface (0–2 cm) redox potential of -124 ± 7 mV and a redox potential of -171 ± 5 mV at 3–10 cm depth 3 yr after transplantation. There was a striking negative relationship ($r = -0.53$, $p < 0.003$) between the mean change in shoot height of a population and the difference in surface redox potential between its natural site and the transplant site (Fig. 4). The greatest decreases in sediment redox potential were associated with the greatest increases in shoot height and vice versa.

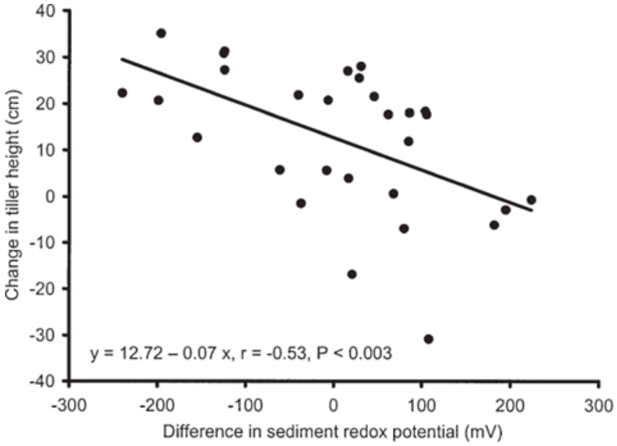

Fig. 4. Relationship between change in shoot mature height after transplantation for 3 yr to a common environment, and the difference between natural site and transplant site in surface sediment redox potential (0–2 cm) for 29 natural populations of *Spartina maritima* at Odiel marshes.

Discussion

Large height differences have been found between populations within several of the species of *Spartina* that form monospecific stands on salt marshes. The relative importance of genetic and environmental factors influencing such differences has been the subject of much controversy (Anderson and Treshow 1980; Proffitt et al. 2003). Considerable evidence has accumulated for ecotypic and other genetically determined variation in height, particularly between the distinct short-form and tall-form plants of *S. alterniflora* (Gallagher et al. 1988; Daehler et al. 1999; Seliskar et al. 2002) in North America. There are many environmental influences on height, and they have been shown to be the dominant effect in *S. foliosa* (Trnka and Zedler 2000) and *S. anglica* (Thompson et al. 1991). *S. maritima* shows a wide range of growth forms in European marshes.

The 34 local populations of *S. maritima* that were examined displayed a range of mean shoot height of 58.4 cm in their natural habitats but a range of only 23.3 cm 3 yr after transplanting. There was a striking convergence between populations in shoot height after transplantation. Collateral transplantation to a common intertidal environment at Odiel marshes suggests the dominance of environmental conditions in influencing their shoot height; most of the *S. maritima* populations in Odiel marshes (77%) were demonstrably limited in their shoot height by environmental conditions in their natural habitats, and the shortest populations tended to respond most to transplantation. This considerable plasticity of growth form is in agreement with that found in *S. anglica* (Thompson et al. 1991) and *S. foliosa* (Trnka and Zedler 2000).

The idea of environmental determination is further supported by the relatively close association of height with sediment redox potential in the 29 populations for which data were obtained, both in the natural populations and in their responses to transplantation. An increase in shoot height is a commonly reported growth strategy for increased water depth in emergent plants (Grace 1989; Sorrel et al. 2002) including the genus *Spartina* (Lessmann et al. 1997). Our results suggest that oxygenation level of the surface sediment may be a major environmental influence on shoot height of *S. maritima* at Odiel marshes. Shoots might grow taller in response to sediment anoxia, a response possibly signalled by ethylene (Pezeshki et al. 1993), or in response to increased nutrient mobilization in the sediment under more reducing conditions (Lenssen et al. 1999). Our results do not agree with Sanchez et al. (1997) who did not find any relationship between shoot height and sediment redox potential in 3 natural populations of *S. maritima* in northwest Spain. Previous studies have identified plastic responses that increase shoot height with longer flooding periods and anoxic sediments in other wetland species (Vandersman et al. 1991; Insausti et al. 2001). This could be a phenotypic adaptation to low elevation in tidal frame. It would increase the effective photoperiod (i.e., average leaf emergence from tidal waters during daylight hours), a potent environmental factor in limiting the survivorship of *S. maritima* clumps on low marshes, where a few centimeters of elevation in the tidal frame determine its lower distribution limit (Castillo et al. 2000). Taller shoots may play a role in improving the oxygenation of rhizomes and roots via aerenchyma in anoxic environments, as in certain nontidal wetland species (Sorrel et al. 2002); such internal ventilation might be associated with internal pressurization, as has been described for *S. alterniflora*, a salt marsh cordgrass that colonizes habitats similar to *S. maritima* (Hwang and Morris 1991). It is perhaps surprising that we found no significant correlation of shoot height with elevation in the tidal frame but local drainage conditions also have substantial effects on sediment redox potential (Castellanos et al. 1994; Crooks et al. 2002).

The adjustment of the shoot height in transplanted clumps of *S. maritima* to the new location with different sediment and hydrodynamic conditions was slow, taking more than 3 yr, a period long enough to allow substantial turnover and replacement of the shoot populations at Odiel marshes (with median shoot survival times of 9–12 mo, see Castellanos et al. 1998). This might also have been the result of long-term carry over effects, from the nutrient and carbohydrate reserves in the transplanted clumps.

Although environmental conditions appear largely to determine shoot height in *S. maritima*, a genetic component influencing this trait cannot be excluded, since substantial differences in shoot height after 3 yr in a common environment were still evident. The transplant site with an intermediate environment may not necessarily have provided conditions for different genotypes to express distinct shoot-height phenotypes (Thompson 1991). The convergence in shoot height between populations after transplantation does suggest a relatively low level of genetic variation for this trait in *S. maritima* populations, in agreement with previous studies that recorded high genetic similarity between *S. maritima* populations (Ayres and Strong 2001; Yannic et al. 2004). Our study also emphasizes the importance of long-term studies, preferably longer than turnover time of shoot populations, to investigate the genetic basis of *Spartina* growth forms. Knowledge of the effects of parental growth form on ramets introduced to new sites has broad implications for ecological restoration, since it would allow selection of genotypes to achieve the particular goals of marsh creation and restoration projects. Although we provide a basis for predicting an important aspect of the outcome of *S. maritima* transplantations, more detailed studies to identify the determinants of growth form are needed.

ACKNOWLEDGMENTS

This study was carried out through an investigation agreement with the oil refinery of C.E.P.S.A. (Compañía Española de Petróleos, Sociedad Anónima) in Huelva, the Port Authority of Huelva, and the General Directorate of Environmental Protection of the Junta de Andalucía. We also thank the Directorate of the Odiel Marshes Natural Park for collaboration.

LITERATURE CITED

ANDERSON, C. M. AND M. TRESHOW. 1980. A review of environmental and genetic-factors that affect height in *Spartina alterniflora* Loisel (salt-marsh cord grass). *Estuaries* 3:168–176.

AYRES, D. R. AND D. R. STRONG. 2001. Origin and genetic diversity of *Spartina anglica* (Poaceae) using nuclear DNA markers. *American Journal of Botany* 88:1863–1867.

CASTELLANOS, E. M., M. E. FIGUEROA, AND A. J. DAVY. 1994. Nucleation and facilitation in saltmarsh succession: Interactions between *Spartina maritima* and *Arthrocnemum perenne*. *Journal of Ecology* 82:239–248.

CASTELLANOS, E. M., C. HEREDIA, M. E. FIGUEROA, AND A. J. DAVY. 1998. Tiller dynamics of *Spartina maritima* in successional and non-successional Mediterranean salt marsh. *Plant Ecology* 137:213–225.

CASTILLO, J. M., L. FERNÁNDEZ-BACO, E. M. CASTELLANOS, C. J. LUQUE, M. E. FIGUEROA, AND A. J. DAVY. 2000. Lower limits of *Spartina densiflora* and *S. maritima* in a Mediterranean salt marsh determined by different ecophysiological tolerances. *Journal of Ecology* 88:801–812.

Crooks, S., J. Schutten, G. D. Sheern, K. Pye, and A. J. Davy. 2002. Drainage and elevation as factors in the restoration of salt marsh in Britain. *Restoration Ecology* 10:591–602.

Daehler, C. C., C. K. Anttila, D. R. Ayres, D. R. Strong, and J. P. Bailey. 1999. Evolution of a new ecotype of *Spartina alterniflora* (Poaceae) in San Francisco Bay, California, USA. *American Journal of Botany* 86:543–546.

Dai, T. and R. G. Wiegert. 1997. A field study of photosynthetic capacity and its response to nitrogen fertilization in *Spartina alterniflora*. *Estuarine Coastal and Shelf Science* 45:273–283.

Gallagher, J. L., G. F. Somers, D. M. Grant, and D. M. Seliskar. 1988. Persistent differences in 2 forms of *Spartina alterniflora*—A common garden experiment. *Ecology* 69:1005–1008.

Grace, J. B. 1989. Effects of water depth on *Typha latifolia* and *Typha dominguensis*. *American Journal of Botany* 76:762–768.

Howes, B. L., J. W. H. Dacey, and D. D. Goehringer. 1986. Factors controlling the growth form of *Spartina alterniflora*—Feedbacks between aboveground production, sediment oxidation, nitrogen and salinity. *Journal of Ecology* 74:881–898.

Hwang, I. H. and J. T. Morris. 1991. Evidence for hygrometric pressurization in the internal gas space of *Spartina alterniflora*. *Plant Physiology* 96:166–171.

Insausti, P., A. A. Grimoldi, E. J. Chaneton, and V. Vasellati. 2001. Flooding induces a suite of adaptive plastic responses in the grass *Paspalum dilatatum*. *New Phytologist* 152:291–299.

Lenssen, J. P. M., F. B. J. Menting, W. H. van der putten., and C. W. P. M. Blom. 1999. Effects of sediment type and water level on biomass production of wetland plant species. *Aquatic Botany* 64:151–165.

Lessmann, J. M., I. A. Mendelssohn, M. W. Hester, and K. L. McKee. 1997. Population variation in growth response to flooding in three marsh species. *Ecological Engineering* 8:31–47.

Mendelssohn, I. A. 1979. Influence of nitrogen level, form, and application method on the growth-response of *Spartina alterniflora* in North Carolina. *Estuaries* 2:106–112.

Pezeshki, S. R. and R. D. Delaune. 1991. A comparative-study of aboveground productivity of dominant United States Gulf Coast marsh species. *Journal of Vegetation Science* 2:331–338.

Pezeshki, S. R., J. H. Pardue, and R. D. Delaune. 1993. The influence of soil oxygen deficiency on alcohol-dehydrogenase activity, root porosity, ethylene production and photosynthesis in *Spartina patens*. *Environmental and Experimental Botany* 33:565–573.

Phleger, C. F. 1971. Effect of salinity on growth of a salt marsh grass. *Ecology* 52:908–911.

Proffitt, C. E., S. E. Travis, and K. R. Edwards. 2003. Genotype and elevation influence Spartina alterniflora colonization and growth in a created salt marsh. *Ecological Applications* 13: 180–192.

Sanchez, J. M., X. L. Otero, J. Izco, and F. Macías. 1997. Growth form and population density of *Spartina maritima* (Curtis) Fernald in northwest Spain. *Wetlands* 17:368–374.

Seliskar, D. M., J. L. Gallagher, D. M. Burdick, and L. A. Mutz. 2002. The regulation of ecosystem functions by ecotypic variation in the dominant plant: A *Spartina alterniflora* salt-marsh case study. *Journal of Ecology* 90:1–11.

Shea, M. L., R. S. Warren, and W. A. Niering. 1975. Biochemical and transplantation studies of growth form of *Spartina alterniflora* on Connecticut salt marshes. *Ecology* 56:461–466.

Sorrel, B. K., C. C. Tanner, and J. P. S. Sukias. 2002. Effects of water depth and substrate on growth and morphology of *Eleocharis sphaceolata*: Implications for culm support and internal gas transport. *Aquatic Botany* 73:93–106.

Thompson, J. D. 1991. Phenotypic plasticity as a component of evolutionary change. *Tree* 6:246–249.

Thompson, J. D., T. McNeilly, and A. J. Gray. 1991. Population variation in *Spartina anglica* Hubbard,C.E.1. Evidence from a common garden experiment. *New Phytologist* 117:115–128.

Trnka, S. and J. B. Zedler. 2000. Site conditions, not parental phenotype, determine the height of *Spartina foliosa*. *Estuaries* 23:572–582.

Vandersman, A. J. M., L. A. C. J. Voesenek, C. W. P. M. Blom, F. J. M. Harem, and J. Reuss. 1991. The role of ethylene in shoot elongation with respect to survival and seed output of flooded *Rumex maritimus* L plants. *Functional Ecology* 5:304–313.

Wigand, C., R. A. McKinney, M. A. Charpentier, M. M. Chintala, and G. B. Thursby. 2003. Relationships of nitrogen loadings, residential development, and physical characteristics with plant structure in New England salt marshes. *Estuaries* 26:1494–1504.

Yannic, G., A. Baumel, and M. Ainouche. 2004. Uniformity of the nuclear and chloroplast genomes of *Spartina maritima* (Poaceae), a salt-marsh species in decline along the western European coast. *Heredity* 93:182–188.

Received, February 8, 2005
Revised, June 3, 2005
Accepted, June 7, 2005