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Author(s): Robert I. Lonard, Frank W. Judd, and Richard Stalter

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The Biological Flora of Coastal Dunes and Wetlands: *Spartina patens* (W. Aiton) G.H. Muhlenberg

Robert I. Lonard[†], Frank W. Judd[‡], and Richard Stalter[‡]

[†]Department of Biology
The University of Texas-Pan American
Edinburg, Texas 78539-2999, U.S.A.
rlonard@utpa.edu

[‡]Department of Biological Sciences
St. John's University
8000 Utopia Parkway
Queens, New York 11439, U.S.A.



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ABSTRACT



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Spartina patens (W. Aiton) G.H. Muhlenberg is a New World tropical-, subtropical-, and temperate-zone rhizomatous grass that often is a dominant species in coastal environments. It occurs in habitats ranging from foredunes to saturated soil conditions in high marshes and swales. Herein, we present a review of the extensive literature of this important species. *Spartina patens* occurs where salinity ranges from 1 to 27 ppt, but it will tolerate salinities up to 40 ppt for brief periods. It tolerates moderate tidal inundation, low nutrient levels, and low to moderate sand coverage. Also known as marshhay cordgrass, it may account for almost all net productivity in high marshes on the Gulf of Mexico coast of Louisiana. High marshes dominated by *S. patens* are affected by flooding depths associated with global warming and rising sea levels. It is a valuable species for coastal restoration projects for it quickly invades dredged material and storm washover sites. *Spartina patens* provides cover for wildlife and forage for livestock.

ADDITIONAL INDEX WORDS: Marshhay cordgrass, morphology, habitats, communities, population ecology, productivity and decomposition, reproduction, geomorphological interactions, economic importance.

INTRODUCTION

The grass genus *Spartina* is represented by 15 to 17 species in the tropics, subtropics, and temperate zones. Nine native and two introduced species occur in wetlands in North America north of Mexico (Barkworth, 2003). *Spartina patens*, which often is a dominant species in coastal environments, occurs along a moisture gradient from arid foredunes and primary dunes to tidal saturated conditions in salt marshes and in isolated brackish swales. Global warming and subsequent sea-level rise are affecting coastal wetlands. Monotypic low salt marsh plant communities dominated by *Spartina alterniflora* are moving landward and are replacing high marsh zones dominated by *S. patens*, *Distichlis spicata*, and *Juncus gerardii* on northern New England coastlines (Donnelly and Bertness, 2001).

Wetlands adjacent to the Gulf of Mexico represent one of the most productive ecosystems in North America, and *S. patens* may account for 97% of the productivity of this ecosystem (Pezeshki and DeLaune, 1991; White and Simmons, 1988). Standing dead shoots are resistant to decay (Frasco and Good, 1982).

Spartina patens is a rhizomatous species that represents phalanx growth (Bertness and Ellison, 1987). It quickly colonizes disturbed sites. Therefore, this species is important for coastal conservation and reclamation projects.

TAXONOMY AND VARIATION

Name

Spartina patens (W. Aiton) G.H. Muhlenberg, family Poaceae (Gramineae), subfamily Chloridoideae, tribe Cynodonteae, Synonyms: *S. juncea* (A. Michaux) C. von Willdenow, *S. patens* var. *juncea* (A. Michaux) A.S. Hitchcock, *S. patens* (W. Aiton) G.H. Muhlenberg var. *monogyna* (M.A. Curtis) M. Fernald; marshhay cordgrass, saltmarsh cordgrass, saltmeadow cordgrass, marsh hay, wiregrass, foxgrass, couchgrass, rush saltgrass, spartine étalée.

Taxonomic Description

The following taxonomic description has been assembled from Barkworth, 2003; Gould, 1975; Hatch, Schuster, and Drawe, 1999; and Lonard, 1993, and from live plants (R.I. Lonard and F.W. Judd, personal observations, unless otherwise cited).

Seed Morphology

In *S. patens* and in most other grasses, the seed coat and ovary wall (pericarp) are coalesced. They form an indehiscent one-seeded fruit, a caryopsis. The caryopsis includes the embryo, endosperm, and the united seed coat and pericarp (Gould and Shaw, 1983).

Seedling Morphology

Germination is initiated by the enlargement of the sheath-like coleorhizae, which protects the primary root and the

expansion of the coleoptiles, which enclose the embryonic shoot system (Gould and Shaw, 1983). Initial leaf blades are similar to those on mature shoots; they are linear, simple, alternately arranged, and glabrous, and have a parallel venation pattern.

Shoot Morphology

Plants are perennial, and cespitose or with elongated rhizomes 1–6 mm thick. Culms are 20–150 cm, 1–6 mm thick, usually erect, solitary, glabrous, terete in cross section. Leaf blades are 10–70 cm, 0.5–2.5 mm wide, indurate, involute, glabrous, grayish green, with scabrous margins. Ligules are 0.5–1.5 mm, membranous with pubescent margins. Sheaths are glabrous.

Root Morphology

Spartina patens has a fibrous root system typical of monocots. It may occur 15–42.5 cm below the soil surface (Cooke, Butler, and Madole, 1993; Stalter, 1974). Stalter (1974) reported the deepest penetration at 61.0 cm. Adventitious roots are formed at the lower nodes in plants that are partially covered by moving sand.

Inflorescence

The laterally compressed spikelets containing one floret are the basic unit of the terminal panicle that has unilateral spikelike branches; branches: one per node, 2–12 in the inflorescence, 3.5–5 cm long, appressed, and spreading at maturity; inflorescence axes are winged and scabrous. Spikelets are 6–10 mm, 2.5 to <3 mm wide, lanceolate, subsessile. Glumes are usually glabrous, midvein scabrous, apices acute; disarticulation below the glumes; lower glumes are 3–3.5 mm, one-veined, linear; upper glumes are as long as the spikelets, three-veined, often purple tinged. Lower lemmas are about as long as the spikelets, glabrous, hispid on veins near the apices. Paleas are about as long as the lemmas, membranous, glabrous, apices lacerate. There are three stamens; anthers are 3–4 mm, yellow or cream colored (Figure 1).

Caryopses

The caryopsis is 3 to <3.5 mm, ellipsoidal, fusiform, and dark brown or olivaceous at maturity. Caryopses are seldom produced in dense populations that occur in brackish marshes and swales (Silander, 1979; Silander and Antonovics, 1979).

Variability

Spartina patens is closely related to *S. gracilis* C. von Trinius and *S. bakeri* E. Merrill (Silander and Antonovics, 1979). Panicle branches are appressed in *S. bakeri* and divergent in *S. patens* at maturity. *Spartina* × *caespitosa* A.A. Eaton is a putative hybrid between *S. patens* and the more inland *S. pectinata* J. Link (Gleason and Cronquist, 1991). The hybrids occur in drier disturbed sites of saline marshes in the northeastern United States and adjacent Canada.

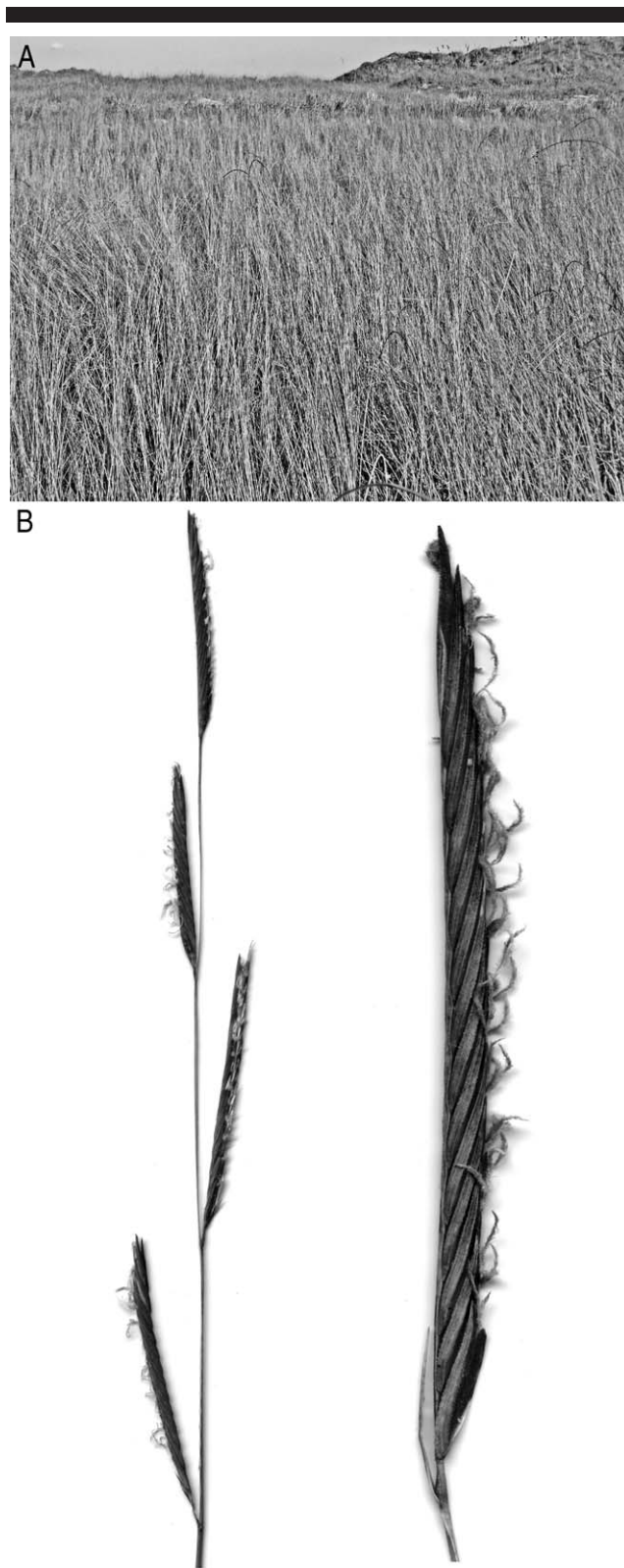


Figure 1. *Spartina patens* in a brackish swale on (A) South Padre Island, Texas and (B) inflorescences in anthesis.

Chromosome Number

Spartina patens is a tetraploid and has a chromosome number of $2n = 40$ (Marchant, 1968; Silander and Antonovics, 1979). Ainouche *et al.* (2003) reported that the basic chromosome number in the genus *Spartina* is $x = 10$ and that no diploids have been found.

GEOGRAPHIC DISTRIBUTION

Spartina patens has an extensive range from temperate Atlantic shorelines in Newfoundland, Canada (Stalter, 1993), to subtropical coastlines in Florida and to South Padre Island, Texas, adjacent to the Gulf of Mexico (Gould, 1975; Lonard, 1993). In Mexico its distribution extends from subtropical coastlines on the Gulf of Mexico in Tamaulipas to tropical shorelines at Quintana Roo (Sauer, 1967). Populations occur sporadically along the shoreline of Lake Huron in Michigan (Gould, 1975; Voss, 1972) and in southern Ontario, Canada (Catling, Reznicek, and Riley, 1977).

Spartina patens is recognized as an invasive species in California, Oregon, Washington, and British Columbia, Canada (Baird and Thieret, 1993; Barkworth, 2003; Daehler and Strong, 1996; Douglas, Straley, and Meidinger, 1994), and it has been reported in the West Indies and North Africa (Hester, Mendelssohn, and McKee, 1996). Recently, *S. patens* has been reported as an invasive weed in salt marshes in Spain (Campos *et al.*, 2004; San Leon, Izco, and Sanchez, 1999) and in China (An *et al.*, 2007) (Figure 2).

RANGE OF HABITATS

Spartina patens is an important species of the coastal zone vegetation in a wide variety of habitats throughout its geographic range. It is found along a moisture gradient from arid foredunes and primary dunes to saturated soil conditions in salt marshes (Stalter, 1974; Stalter and Lamont, 1997; van der Valk, 1975). Ehrenfeld (1990) reported that marshhay cordgrass occurs in all habitats across barrier islands including bayside salt marshes, high marshes, swales, and foredunes. North of 43°N latitude in Maine and Nova Scotia, Canada, *S. patens* is present only in salt marshes, and south of 25°N latitude, it typically is restricted to dunes and beaches (Silander and Antonovics, 1979).

Spartina patens occurs in the most diverse array of habitats on the Florida coastline of any halophytic angiosperm. It is the dominant or an important species in dunes, on strand-beaches, on storm washover sites, in savanna and scrub zones, and on the inner margins of salt marshes (Anderson and Alexander, 1985; Craig, 1975; Stalter *et al.*, 1999).

Marshhay cordgrass occurs on foredunes and primary dunes on temperate Atlantic coastlines from North Carolina to New Jersey (Oosting and Billings, 1942; van der Valk, 1975). Oosting and Billings (1942) indicated that it is a dominant species in flats in the lee of foredunes that are inundated by storm surges. *Spartina patens* often is a dominant species in brackish and intertidal salt marshes (Hardaway *et al.*, 2002; Hill, 1986; Stalter and Lamont, 1990; Tyndall *et al.*, 1987). On coastlines in Connecticut and Maryland, *S. patens* occurs typically in tidal wetlands where it is the dominant species and

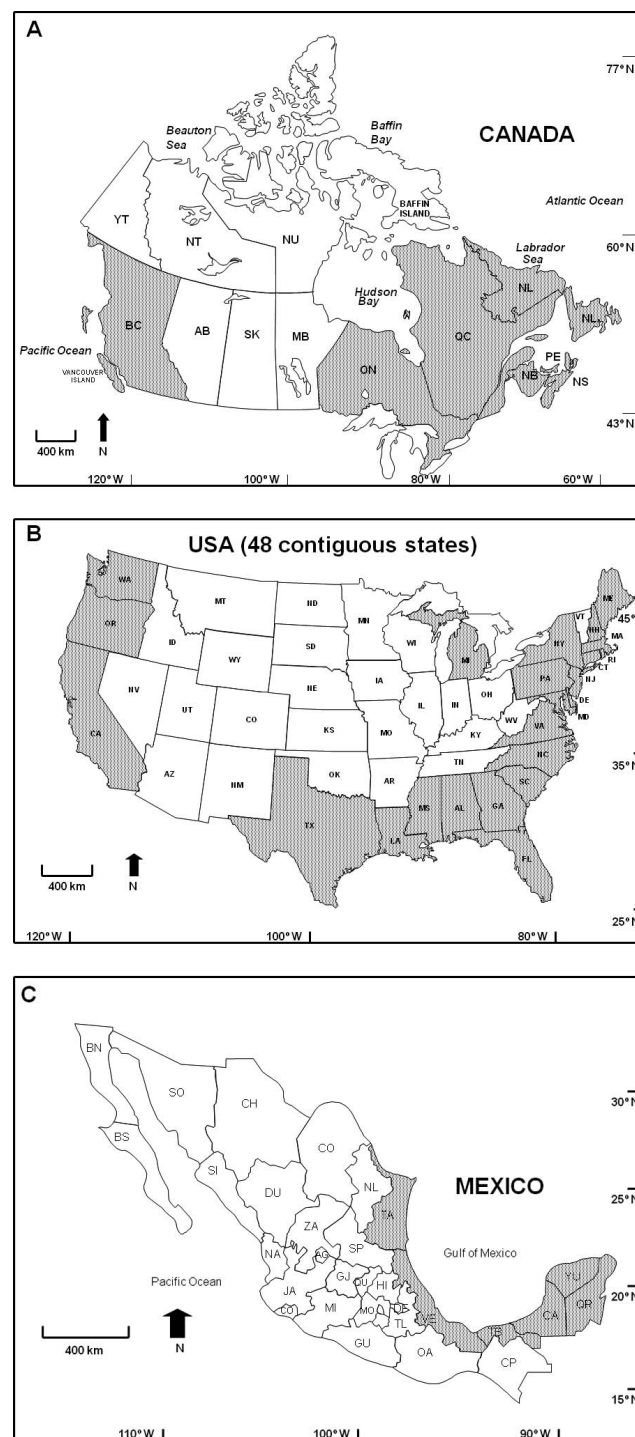


Figure 2. Distribution of *Spartina patens* in (A) Canada, (B) the contiguous 48 states of the United States, and (C) Mexico. The species also occurs in Puerto Rico, the Virgin Islands, and West Indies. It has been introduced into China, North Africa, and Spain. Likewise, populations in California, Oregon, Washington, and British Columbia, Canada, have invaded from introductions. *Spartina patens* is absent in Alaska and Hawaii.

S. alterniflora is of secondary importance (Martin, 1959). Marshhay cordgrass is present in habitats from mean high tide to 10 cm to 1.1 m above mean high tide (Cooke, Butler, and Madole, 1993; Hardaway *et al.*, 2002). Burger and Shisler (1983) reported that *S. patens* readily colonizes dredged materials.

In Mississippi, Louisiana, and the upper Texas Gulf Coast, *S. patens* occurs in a wide variety of habitats including foredunes, primary dunes, secondary dunes, swales, brackish marshes, and intermediate salinity marshes (Burdick and Mendelssohn, 1987; Eleuterius, 1972; Hester, Spalding, and Franze, 2005; Stutzenbaker, 1999). Barbour *et al.* (1987) reported that it is common in sites that have minimal sand accretions, and Eleuterius (1972) noted stands of *S. patens* on dredged materials.

Further south on the lower Texas coastline where the climate is semi-arid, marshhay cordgrass usually becomes less important in the vegetation. Salt marshes in this region are replaced by barren tidal flats topographically where freshwater inflow is curtailed.

The vegetation of South Padre Island, Texas, is topographically zoned in conjunction with exposure to wind, aerosol salt spray, and depth to the water table (Judd, Lonard, and Sides, 1977). *Spartina patens* is rare or absent in foredunes and in the primary dune complex. However, it is present in swales and in brackish wetlands in the secondary dunes and vegetated flats (Judd and Lonard, 2009; Judd, Lonard, and Sides, 1977). It is common in the transition zone between the secondary dunes and vegetated flats, and the tidal flats; it also colonizes roadside margins and the margins of storm washover channels (Judd, Lonard, and Sides, 1977).

Marshhay cordgrass is present in similar habits on North Padre Island because of its close proximity to South Padre Island. It occurs on the leeward faces of foredunes and primary dunes, and in swales in the secondary dunes and vegetated flats (Carls, Lonard, and Fenn, 1991; Nelson *et al.*, 2000). Gillespie (1976) reported it in disturbed sites including roadside margins on Mustang Island adjacent to North Padre Island.

Substrate Characteristics

Spartina patens occurs on coastlines that have a pH range from 4.5 to 7.1 (Martin, 1959). Substrates consist of white and dark quartz sand, calcareous oolitic sand, and coral sand on the coastlines of eastern Mexico (Sauer, 1967). In North America north of Mexico, soils usually consist of sand particles. In South Carolina and northern Florida, marshhay cordgrass colonies are common on coastal pre-Columbian Indian shell middens that consist primarily of oyster shell fragments (Stalter and Kincaid, 2004; Stalter, Leyva, and Kincaid, 1999).

On South Padre Island, 85.9% of sand particle sizes in the secondary dunes and vegetated flats range between 0.18 and 0.25 mm, and 80.2% of the particles were in the same size class on the margins of the tidal flats (Judd, Lonard, and Sides, 1977). At a depth of 25 cm, mean water content of sand samples in the secondary dunes and vegetated flats was 11% and 18.1% on the margins of the tidal flats (Judd, Lonard, and Sides, 1977). Oosting and Billings (1942) reported maximum soil temperatures of 52°C to 53°C on the dunes of North Carolina.

Marshhay cordgrass is a dominant species on the Louisiana coastline where soil salinity ranges from 2.0 ppt (g/kg) of solution up to 15.2 ppt of solution. Lethal levels of soil salinity, where death of 50% of aboveground tissue occurs, ranges from 63 to 93 ppt of solution (Hester, Spalding, and Franze, 2005). On the Atlantic coastline, marshhay cordgrass occurs where salinity ranges from 1.0 to 27 ppt (Cooke, Butler, and Madole, 1993; Martin, 1959; Oosting and Billings, 1942; Roman and Daiber, 1984; Stalter and Batson, 1969). Judd and Lonard (2009) found *S. patens* in brackish swales where salinity ranged from 2 to 12 ppt. Soils typically are nutrient-poor and usually are low in N, P, and K (Hester and Mendelssohn, 1990).

Climatic Requirements

The geographical distribution of *S. patens* extends from the tropics at 16°N latitude in the West Indies to a humid continental climate with cool summers at 50°N in Québec and Newfoundland provinces in Canada (Hester, Mendelssohn, and McKee, 1996; Silander, 1984; Silander and Antonovics, 1979; Stalter, 1993). The northern distribution in the Canadian Shield is limited by a subarctic climate characterized by long, cold winters and short, cool summers.

Aerial shoots usually are dormant during the winter months, and the perennial intercalary meristems in the rhizome system are protected by scalelike leaves. Ruber, Gillis, and Montagna (1981) found live culms as late as December 30th at Cape Cod, Massachusetts (42°N). Stalter (1974) noted most rhizome depths ranging between 15 and 20 cm below the soil surface. Lonard and Judd (personal observations) have seen vegetative growth at all seasons on the Texas coast.

PLANT COMMUNITIES

Spartina patens is a dominant or an important species in a wide variety of coastal plant communities. The salt marsh and high marsh communities characterize large segments of Atlantic shorelines in Rhode Island, New York, Connecticut, New Jersey, Virginia, North Carolina, South Carolina, northern Florida, and Louisiana (Crain, Albertson, and Bertness, 2008; Harvill, 1965; Hester, Spalding, and Franze, 2005; Martin, 1959; Silander and Antonovics, 1979; Stalter and Lamont, 1990, 2002; Stalter *et al.*, 1999, 2006; Warren and Niering, 1993). Table 1 includes common species associated with *S. patens* in salt marsh communities throughout its range in the United States.

Martin (1959) reported that marshhay cordgrass is the dominant species in more inland coastal sites characterized by grasses, trees, shrubs, and forbs. He referred to this community in New Jersey as a Saltgrass–Sea Myrtle–Red Cedar (*Distichlis spicata*–*Morella pensylvanica*–*Juniperus virginiana*) savanna. Representative species in this community are *Acer rubrum*, *Baccharis halimifolia*, *Distichlis spicata*, *Juniperus virginiana*, *Morella pensylvanica*, *Panicum virgatum*, *Vulpia octoflora*, *Rhus copallina*, *Rhus radicans*, and *Schizachyrium scoparium*.

In temperate and subtropical sites in North Carolina, Florida, and Louisiana, *S. patens* is found in communities designated as beach, foredunes and dunes, dune grass, salt

Table 1. Representative species associated with *Spartina patens* in a salt marsh community.

Species	NY	CN	NJ	VA	SC-NFL	LA	TX
<i>Atriplex patula</i>				×			
<i>Avicennia germinans</i>					×		
<i>Baccharis hamifolia</i>					×		
<i>Bassia hirsuta</i>				×			
<i>Batis maritima</i>					×		×
<i>Blutaparon vermiculare</i>							×
<i>Borrichia frutescens</i>				×	×	×	×
<i>Cladium mariscoides</i>				×			
<i>Coreopsis tinctoria</i>							×
<i>Distichlis spicata</i>	×	×		×	×	×	×
<i>Fimbristylis caroliniana</i>				×			
<i>F. castanea</i>				×			
<i>Heliotropium curassavicum</i>					×		
<i>Iva frutescens</i>	×			×	×		
<i>I. texensis</i>							×
<i>Juncus gerardii</i>	×	×					
<i>J. roemerianus</i>				×	×		
<i>Limonium carolinianum</i>	×			×	×		
<i>Machaeranthera phyllocephala</i>							×
<i>Monanthochloë littoralis</i>							×
<i>Plantago hookeri</i>							×
<i>P. maritima</i>				×			
<i>Polypogon monspeliensis</i>							×
<i>Ruppia maritima</i>				×			
<i>Salicornia bigelovii</i>							×
<i>S. europaea</i>	×		×	×	×		
<i>S. virginica</i>				×			×
<i>Sesuvium maritimum</i>				×			
<i>S. portulacastrum</i>							×
<i>Spartina alterniflora</i>	×	×	×	×	×	×	
<i>S. cynosuroides</i>				×			
<i>Spergularia marina</i>				×			×
<i>Sporobolus pyramidatus</i>				×			×
<i>S. virginicus</i>			×	×	×		×
<i>Suaeda linearis</i>					×		×
<i>S. maritima</i>	×						
<i>Symphyotrichum tenuifolium</i>	×						
<i>Triglochin maritima</i>		×					
<i>Zostera marina</i>				×			

NY=New York (Stalter and Lamont, 2002); CN=Connecticut (Warren and Niering, 1993); NJ=New Jersey (Martin, 1959); VA=Virginia (Harvill, 1965); Stalter and Lamont, 1990; Stalter and Odom, 1993); SC-NFL=South Carolina-Northern Florida (Stalter, Leyva, and Kincaid, 1999); LA=Louisiana (Hester, Spalding, and Franze, 2005); TX=Texas (Lonard, Judd, and Smith, 2003).

spray, and strand beach (Barbour *et al.*, 1987; Hester, Spalding, and Franze, 2005; Silander and Antonovics, 1979; Stalter and Lamont, 1997; Stalter *et al.*, 1999; van der Valk, 1975). Representative species are listed in Table 2.

Spartina patens occurs also in a swale community. This community is in shallow, moist depressions in the vegetated flats leeward of the primary dune complex. A swale community or a marshhay cordgrass series is common on coastlines of North Carolina, Louisiana, and Texas (Diamond, Riskind, and Orzell, 1987; Hester, Spalding, and Franze, 2005; Hester, Wilsey, and Mendelssohn, 1994; Judd and Lonard, 2009; Lonard *et al.*, 1999; Nelson *et al.*, 2000; Silander and

Table 2. Representative species associated with *Spartina patens* in foredunes and dunes, dune grass, salt spray, and strand beach.

Species	VA	NC	FL	LA
<i>Ammophila breviligulata</i>	×	×		
<i>Andropogon virginicus</i>		×		
<i>Argusia gnaphaloides</i>			×	
<i>Atriplex arenaria</i>		×		
<i>Cakile edentula</i>	×	×		
<i>C. lanceolata</i>			×	
<i>Cakile sp.</i>				×
<i>Carduus spinosissimus</i>		×		
<i>Cenchrus spinifex</i>				×
<i>C. tribuloides</i>		×		
<i>Chamaesyce polygonifolia</i>		×	×	
<i>Commelina erecta</i>		×		
<i>Conyza canadensis</i>	×	×		
<i>Croton punctatus</i>		×		×
<i>Cynodon dactylon</i>		×		
<i>Cyperus esculentus</i>		×		
<i>Diodia teres</i>		×		
<i>Eragrostis spectabilis</i>		×		
<i>Fimbristylis castanea</i>		×		×
<i>Gnaphalium obtusifolium</i>		×		
<i>Heterotheca subaxillaris</i>	×			
<i>Hydrocotyle bonariensis</i>		×		
<i>Ipomoea imperati</i>				×
<i>I. pes-caprae</i>				×
<i>Iva imbricata</i>		×		
<i>Lactuca canadensis</i>		×		
<i>Oenothera humifusa</i>	×	×		
<i>Panicum amarum</i>	×	×		
<i>P. amarum var. amarulum</i>		×		
<i>Paspalum vaginatum</i>				×
<i>Physalis viscosa</i>		×		
<i>Sabatia stellaris</i>	×			
<i>Salsola kali</i>	×			
<i>Sesuvium maritimum</i>			×	
<i>S. portulacastrum</i>			×	
<i>Solidago sempervirens</i>		×		
<i>Sporobolus virginicus</i>			×	×
<i>Strophostyles helvola</i>	×	×		
<i>S. umbellata</i>	×			
<i>Suaeda linearis</i>				×
<i>Suriana maritima</i>				×
<i>Triplasis purpurea</i>	×	×		
<i>Uniola paniculata</i>	×	×		
<i>Waltheria indica</i>				×
<i>Xanthium strumarium</i>				×

VA=Virginia (Stalter and Lamont, 1990); NC=North Carolina (Silander and Antonovics, 1979; Stalter and Lamont, 1997; van der Valk, 1975); FL=Florida (Stalter *et al.*, 1999); LA=Louisiana (Barbour *et al.*, 1987; Hester, Spalding, and Franze, 2005).

Antonovics, 1979). Table 3 shows species common in this community type.

A unique topographic feature referred to as tidal flats replaces salt marshes along the semi-arid coastal zone of south Texas where freshwater inflow is curtailed (White *et al.*, 1983; Withers, 2002). Vascular plants are excluded from this harsh environment. However, halophytic species occur in a narrow band adjacent to the tidal flats. Judd, Lonard, and Sides (1977) and Lonard, Judd, and Smith (2003) refer to this zone as a tidal flats community. *Spartina patens* has a patchy distribution in this community.

Table 3. Representative species associated with *Spartina patens* in a Swale Community.

Species	VA	NC	LA	NPI	SPI
<i>Agalinus maritima</i>	×				×
<i>Andropogon glomeratus</i>				×	×
<i>Baccharis hamillifolia</i>			×		
<i>Bacopa monnieri</i>	×				×
<i>Blutaparon vermiculare</i>					×
<i>Borrichia frutescens</i>				×	×
<i>Cenchrus tribuloides</i>	×				
<i>Conoclinium betonicifolium</i>					×
<i>Distichlis spicata</i>			×		
<i>Eleocharis geniculata</i>					×
<i>E. halophila</i>	×				
<i>E. parvula</i>	×				
<i>Eragrostis pilosa</i>		×			
<i>E. secundiflora</i>					×
<i>Fimbristylis castanea</i>				×	×
<i>Flaveria brownii</i>					×
<i>Fuirena simplex</i>					×
<i>Heterotheca subaxillaris</i>	×				
<i>Hydrocotyle bonariensis</i>			×	×	
<i>Iva frutescens</i>			×		
<i>I. texensis</i>					×
<i>Kosteletzkya virginiana</i>	×				
<i>Lippia nodiflora</i>			×		
<i>Lythrum alatum</i>					×
<i>Morella cerifera</i>			×		
<i>Muhlenbergia capillaris</i>		×			
<i>Panicum amarum</i>					×
<i>Phragmites australis</i>	×				
<i>Rhynchospora colorata</i>					×
<i>Samolus ebracteatus</i>			×		×
<i>Schizachyrium littorale</i>					×
<i>S. scoparium</i>		×			
<i>Schoenoplectus americanus</i>	×				
<i>S. pungens</i>			×	×	×
<i>Sesbania drummondii</i>			×		
<i>Solidago sempervirens</i>	×	×			×
<i>Sporobolus tharpai</i>					×
<i>S. virginicus</i>					×
<i>Strophostyles helvola</i>	×				
<i>S. umbellata</i>	×				
<i>Symphyotrichum subulatum</i>	×				
<i>Teucrium canadense</i>	×				
<i>Typha domingensis</i>					×

VA=Virginia (Stalter and Lamont, 1990); NC=North Carolina (Silander and Antonovics, 1979); LA=Louisiana (Hester, Spalding, and Franze, 2005); NPI=North Padre Island, Texas (Nelson *et al.*, 2000); SPI=South Padre Island, Texas (Judd and Lonard, 2009; Lonard *et al.*, 1999).

PHYSIOLOGICAL ECOLOGY

Physiology

Spartina patens occurs where aerosol salt spray deposition is high, and Boyce (1954) noted that salt spray adheres readily to narrow leaf blades. However, plants are resistant to injury. Blades have a thick cuticle and usually are involute when fully developed (Oosting, 1945).

An abundance of glycolipids and sterols in cell membranes indicates that these short-chain fatty acids play a role in salinity tolerance in marshhay cordgrass (Wu, Seliskar, and Gallagher, 2005). Indicators of salt tolerance are high CO₂ assimilation rates, efficient water usage, and low rhizome-to-

aerial shoot and dead total aerial biomass ratios (Hester, Mendelssohn, and McKee, 2001).

Salt spray intensity is reduced in mixed plant communities where marshhay cordgrass culms range between 20 and 30 cm. These lower stature plants receive protection from salt spray from much taller plants including *Panicum amarum* and *Uniola paniculata* (Boyce, 1954).

Marshhay cordgrass occurs along a moisture continuum from arid dunes to water logged marshes. Seneca (1972) found that seedlings of *S. patens* exhibited symptoms of salinity stress but survived for 1 month at salinities of 40 ppt. He noted that optimal growth occurred in freshwater. Aerobic respiration occurs in root systems of dune and swale populations, and anaerobic respiration characterizes colonies growing in marshes (Burdick and Mendelssohn, 1987). Flooding inhibits growth of new adventitious roots and increases mortality of older roots (Burdick, 1989). A limited number of root hairs develop adjacent to the apical meristem, but parenchyma cells in the root cortex deteriorate and form a loose aerenchyma tissue arrangement (Anderson, 1974). Development of aerenchyma increases root porosity and facilitates oxygen diffusion to water logged roots. However, aerenchyma is insufficient for aerobic respiration as indicated by the enzyme alcohol dehydrogenase in roots (Burdick and Mendelssohn, 1987). Aerenchyma is a significant, but incomplete, adaptation to saturated soil conditions. However, this adaptation allows *S. patens* to tolerate some flooding conditions, and it imparts competitive ability of the species to sites along a saturation gradient (Burdick, 1989; Burdick and Mendelssohn, 1987; Naidoo, McKee, and Mendelssohn, 1992).

Ewing, McKee, and Mendelssohn (1997) evaluated environmental stress indicators including levels of adenine nucleotide concentrations, leaf proline concentrations, shoot elongation, and leaf spectral reflectance. They concluded that no single environmental stress parameter limited the occurrence of *S. patens* in harsh environments.

Spartina patens is a C₄ plant in its mode of carbon fixation in the light independent reactions of photosynthesis. Leaf anatomy features are consistent with Kranz anatomy (Anderson, 1974; Barbour *et al.*, 1987).

Phenology

Flowering and fruiting cycles for marshhay cordgrass range from May to November in North America north of Mexico (Anderson and Alexander, 1985; Lonard and Judd, 1989; Radford, Ahles, and Bell, 1968; Stalter, 1993). Caryopses mature in August and September on the coastline of North Carolina, but germination does not follow until May (Plyler and Proseus, 1996).

PRODUCTIVITY AND DECOMPOSITION

The marshes of the Gulf Coast have been identified as one of the most productive ecosystems in North America (Pezeshki and DeLaune, 1991). Carbon fixation occurs in Louisiana wetlands throughout the year. In some brackish marshes, *S. patens* may account for 97% of a marsh's total biomass (White and Simmons, 1988). As expected, a gradual increase in leaf

biomass occurs in spring and summer followed by a growth plateau from September to November and a decline in winter (Pezeshki and De Laune, 1991). White *et al.* (1978) estimated net production of *S. patens* in Louisiana marshes ranging from 1342 to 1428 g/m²/y of live and dead material with a peak standing crop of 2194 g/m²/y. *Distichlis spicata*, *Juncus roemerianus*, *S. patens*, and *S. alterniflora* produce an estimated 146×10^5 metric tons of biomass per year in these wetlands (White *et al.*, 1978). Burdick, Mendelssohn, and McKee (1989) suggested that a combination of parameters including soil aeration and higher nutrient levels may be significant in biomass production.

At higher latitudes tidal marsh productivity of *S. patens* is slightly lower than in the wetlands listed earlier. Aerial primary productivity of marshhay cordgrass in Delaware ranged from 1089 to 1147 g/m²/y. Belowground primary productivity was estimated at 3.3 kg/m²/y (Roman and Daiber, 1984). In salt marshes of northern Massachusetts, standing crop productivity of *S. patens* ranks second in importance to *S. alterniflora*, which is a dominant species in the low marsh environment (Ruber, Gillis, and Montagna, 1981). Further north in the Bay of Fundy, Canada, net aerial production in the high marsh is estimated at only 172 g/m²/y (Gordon, Cranford, and Despland, 1985). Belowground biomass is confined primarily to the upper 20 cm of moist soil. Most of the root biomass (70% to 84%) is in the <2.0 mm size class in barrier island sites in Virginia (Conn and Day, 1993).

The biology of *S. patens* is best understood for the northeastern United States and the Louisiana coastal zones. Gaps in the knowledge of primary productivity of *S. patens* exist for the south Atlantic coast, Florida, Texas Gulf Coast, and Mexico. *Spartina patens* is usually not a dominant species in the barrier island ecosystems of the lower Gulf Coast of Texas and Mexico, which may explain why data are not available from these areas. Biomass data are not available for regions where marshhay cordgrass is recognized as an invasive species.

Spartina patens is resistant to decomposition (Frasco and Good, 1982). Shoots are tough and heavily lignified. In Louisiana, Foote and Reynolds (1997) found 50% of plant material remaining after 2 years, whereas White *et al.* (1978) indicated that only 36% of standing dead marshhay cordgrass plants decomposed in 1 year. In the same area, all *S. alterniflora* plants decayed within 7 months. Gordon, Cranford, and Despland (1985) indicated that vegetation turnover time is 2 years for the high marsh in the Bay of Fundy.

POPULATION BIOLOGY

Perennation

Marshhay cordgrass is a long-lived cespitose or rhizomatous perennial. Rhizomatous forms occur on sandy beaches, sandy flats, and on low dune margins. Cespitose forms are found in marshes and muddy bayous (Hatch, Schuster, and Drawe, 1999). Colonies in dunes and storm washover sites where changes in sand coverage are common reproduce from rhizomes (Silander, 1979; Silander and Antonovics, 1979). Rhizomatous forms quickly colonize dredged material provided that the depth of coverage is not excessive (Burger and Shisler, 1983).

Population Dynamics

Natural disturbance and anthropogenic perturbations are significant features of population dynamics in coastal ecosystems (Judd and Lonard, 1987). Populations of *S. patens* recover rapidly after storms. Judd and Lonard (1987) noted that marshhay cordgrass was the sole colonizing species after vegetation removal in hurricane simulated experiments in the harsh environment on the margins of tidal flats on South Padre Island, Texas.

Wildfires usually do not affect population dynamics in coastal areas. However, Lonard, Judd, and Smith (2003) found that *S. patens* on the margins of tidal flats recovered from rhizomes 9 months after a wildfire on North Padre Island, Texas.

REPRODUCTION

Sexual Reproduction

Pollination and Fertilization

Spartina patens pollen is produced over a period of 2 to 4 days per floret in Rhode Island salt marshes and is disseminated by the wind (Bertness, Wise, and Ellison, 1987). Marshhay cordgrass, as well as other perennial grasses, is cross fertilized and is self-sterile (Gould and Shaw, 1983).

Caryopsis

Spikelets in the genus *Spartina* contain one floret. The lemma and palea of the floret enclose the caryopsis and usually disarticulate from the spikelet as a unit.

Dispersal

The dispersal unit in *S. patens* is the floret containing a caryopsis. Dispersal may occur during the flowering and fruiting phenophases that extend from May until November. Lonard and Judd (1980) reported that caryopses are dispersed by water, and grazing animals likely serve as dispersal agents. Florets or caryopses have a flotation time of 26 days (Else-Quirk, Middleton, and Proffitt, 2009).

Seed Bank and Floret Weights

Spartina patens is the dominant species in oligohaline (0.5 to 5 ppt) marshes in Louisiana. However, this species was not found in the seed bank (Baldwin, McKee, and Mendelssohn, 1996). The most common species in the marshes was the annual, herbaceous dicot *Ammania latifolia*. LaPeyre *et al.* (2005) emphasized that seed banks of *S. patens* and other species are unreliable sources for marsh restoration projects in Louisiana. Mean spikelet weight ($n = 75$) at Galveston Island is 0.00103 g (R.I. Lonard and F.W. Judd, personal observations).

Germination Ecology and Establishment of Seedlings

Barkworth (2003) reported that reproduction in the genus *Spartina* is primarily vegetative. Stalter and Batson (1973) found that 7% of marshhay caryopses were viable in salt marsh populations in South Carolina. However, Seneca (1969) noted that greater than 70% of the grains germinated at constant temperature and in alternating thermoperiods ranging from

18°C to 35°C. Prechilling also proved to be effective in breaking dormancy (Plyler and Proseus, 1996). Cold treatment at 6.1°C for 30 days prior to germination increased germination success (Seneca, 1969). Surgical injury to the endosperm enhances germination rates to 92% (Plyler and Proseus, 1996).

GEOMORPHOLOGICAL INTERACTIONS

Response to Burial

Sand accretion in dune systems and in storm wash over sites plays a major role in population dynamics of *S. patens*. Marshhay cordgrass colonies are easily buried and killed by sand accumulation of 100 cm (Courtemanche, Hester, and Mendelssohn, 1999; McKann *et al.*, 1991). *Spartina patens* survives only in areas with minimal sand coverage (Barbour *et al.*, 1987). Burial of caryopses occurs often between growing seasons. This accounts for the rare occurrence of marshhay cordgrass seedlings in forb-dominated communities (Tyndall *et al.*, 1987).

Bertness and Ellison (1987) and Crain, Albertson, and Bertness (2008) noted that *S. patens* has a phalanx growth form and advances slowly into wash overs by a dense production of rhizomes and adventitious tillers. Godfrey and Godfrey (1976) found that extant colonies of *S. patens* recovered from 20-cm sand coverage 2 years after simulated wash over sand accretion. Travis (1977) noted that marshhay cordgrass plants had shorter culms and fewer leaves but produced more flowering culms following burial, and Ehrenfeld (1990) reported that burial increases rhizome density and aerial growth at a burial depth of 15 cm. She further noted that recovery occurred at a burial depth of 30 cm and that erect forms had a higher success rate than decumbent types. Stallins (2002) indicated that *S. patens* and prostrate, stoloniferous *Hydrocotyle bonariensis* increased in areal coverage with increasing wash over exposure.

Similar results were obtained when dredged material was placed on stands of marshhay cordgrass. Dredged material leveled to equal the elevation of a marsh had a percentage cover of *S. patens* ranging from 60% to 90% at the end of the first growing season. The cover value was 100% at the end of the second growing season (Burger and Shisler, 1983). Sediments greater than 5.0 cm above the marsh elevation resulted in much slower recovery. Marshhay cordgrass represented only 5% of the vegetative cover at the end of the first year. All growth was initiated from germinating grains. Vegetative growth from rhizomes was not observed (Burger and Shisler, 1983).

Tolley and Christian (1999) found that *S. patens* and *D. spicata* populations recovered within one growing season after wrack deposition on a salt marsh community in Virginia. Similar results were reported by Stalter *et al.* (2006) in South Carolina. They studied the impact of hurricane wrack deposits of *S. alterniflora* on salt marsh vegetation. Populations of *S. patens* and *Borrichia frutescens* recovered 4–7 months after coverage at depths ranging from 2 to 20 cm. Contrasting results were reported for salt marsh communities in Rhode Island. Bertness and Ellison (1987) and Brewer, Levine, and Bertness (1998) found that high marsh dominants including *S. patens* and *J. gerardii* were decimated by experimental wrack burial. Wrack burial reduced shoot density and biomass. All *S. patens*

were killed after 5 weeks of coverage (Bertness and Ellison, 1987).

Role in Geomorphology

Spartina patens plays an important role in coastal geomorphology by stabilizing barrier flats. It is more luxuriant in moist sites but traps sand in drier locations (Craig, 1975). It rapidly colonizes open spaces following wash overs from tropical storms in North Carolina and Texas (Lonard and Judd, personal observations; Silander and Antonovics, 1979).

INTERACTION WITH OTHER SPECIES

Competition

Competition, disturbance, and the harsh environment are the parameters that define spatial patterns in salt marsh plant communities. Structure and composition of plant communities where *S. patens* is a dominant species is often determined by low levels of N, P, and K rather than competition with other species (Hester and Mendelssohn, 1990; van der Valk, 1975). However, Ehrenfeld (1990) noted that populations of *S. patens* increased after competing colonies of *Fimbristylis spadiacea* were removed from a wetland. Conversely, *F. spadiacea* populations increased after competing colonies of *S. patens* were removed. Bertness (1991a, 1991b) and Crain *et al.* (2004) reported that high intertidal borders where *S. patens* often is a dominant species appear to be influenced by competition, and lower intertidal boundaries are determined by physical factors. Salt marsh plants transplanted into freshwater thrived in the absence of adjacent species, but if marshhay cordgrass was adjacent to freshwater neighbors, *S. patens* populations were suppressed (Crain *et al.*, 2004).

Ewanchuk and Bertness (2004) reported similar results from salt marshes. They found that dicot dominated areas limit the expansion of marshhay cordgrass clones. LaPeyre *et al.* (2001) indicated that as abiotic stress increases, competition is less important in affecting species abundance.

Spartina patens has been identified as an important species in inhibiting the spread of aggressive rhizomatous species. By planting marshhay cordgrass in restored marshes in New Jersey, reinvasion of *Phragmites australis* was blocked (Wang *et al.*, 2006).

Spartina patens is a keystone species of East Coast and Gulf Coast salt marsh ecosystems, where it occurs in its native landscapes. However, it is recognized as an invasive species in California, Oregon, and Washington, where it is not an indigenous species (Anonymous, 1999; Anonymous-1, undated; Anonymous-2, undated). It was probably introduced in the late 1930s in packing material for oysters. Rapid asexual reproduction from an extensive rhizome system gives marshhay cordgrass a competitive advantage over native species (Anonymous, 1999). Possible allelopathic compounds that may impact native species have not been investigated.

The physical environment of the West Coast, United States, coastal salt marshes differs by being dominated by broad expanses of open sand and mudflats with smaller areas of high marsh. *Spartina patens* alters the ecological balance by converting mudflats to high marsh. Feeding areas and nursery

zones, migratory bird resting sites, and shellfish production sites are affected. The aggressive, invasive *S. patens* excludes native vegetation from the high marsh, which causes reductions in waterfowl food sources and a loss in plant species richness and diversity (Anonymous-2, undated).

In San Francisco Bay, California, *S. patens* has potential impacts on native marsh species including *Salicornia virginica* and *Distichlis spicata*, and may negatively affect the habitat of *Rallus longirostris* (California clapper rail) and *Reithrodontomys raviventris* (salt marsh harvest mouse). The rare root parasite *Cordylanthus mollis* (Scrophulariaceae) may be threatened in the high marsh (Anonymous-1, undated; Chuang and Heckard, 1993). *Sidalcea hendersonii* (Malvaceae) is threatened by the encroachment of *S. patens* in the high marsh in Oregon (Anonymous-2, undated). Control measures in Puget Sound, Washington, for a small population of marshhay cordgrass include mowing followed by covering clones with geotextile fabric (Anonymous, 1999).

Predation and Symbiosis

Spartina patens-dominated salt marshes support dense mosquito (*Aedes sollicitans*), larval green headfly (*Tabanus* sp.), and Eastern lubber grasshopper (*Romalia microptera*) populations (Daiber, 1974; White and Simmons, 1988). Larval stages of *Culex salinarius* mosquitoes, the putative vectors of West Nile Virus and Eastern Equine Encephalomyelitis in the northeastern United States, are found in salt marshes dominated by *S. patens* and *S. alterniflora* (Rochlin *et al.*, 2008).

In Rhode Island salt marshes, the grasshopper (*Conocephalus spartinae*) is a floral predator. Bertness, Wise, and Ellison (1987) found that in a given year ovule predation may vary from 35% to 70%, and pollen predation varies from 98% to 99% in the protogynous *S. patens*. Bertness and Shumway (1992) concluded that caryopsis production is essentially pollen-limited by grasshoppers.

Mammals, including the introduced nutria (*Myocaster coypus*) and muskrats (*Ondatra zibethicus*), feed on young shoots (White and Simmons, 1988). Bhattacharjee, Haukos, and Neaville (2007) found that muskrats eradicated 450 ha of intermediate coastal marsh on the upper Texas coast.

Snow geese (*Anser caerulescens atlantica*) may affect salt marsh plant communities by uprooting vegetation (Miller *et al.*, 2005; Smith, 1983). Miller *et al.* (2005) noted that extremes of annual rainfall, salinity values, and water levels had minor impacts on stands of marshhay cordgrass unless snow geese uprooted vegetation.

The toxic ascomycete ergot (*Claviceps purpurea*) parasitizes ovaries of *S. patens* in Mississippi marshes. Subsequently, the infection is transferred to *Spartina cynosuroides* and *S. alterniflora* (Eleuterius and Meyers, 1974).

Commensalism has been reported for *S. patens* and vesicular mycorrhizal fungi (VAM). Arbuscules are found at depths ranging from 5 to 37.5 cm below the soil surface (Cooke, Butler, and Madole, 1993).

RESPONSE TO WATER LEVELS

Spartina patens colonies are adversely affected by increased flooding depth (Bertness and Ellison, 1987; Spalding and

Hester, 2007). Baldwin and Mendelssohn (1998) found that *S. patens* was eliminated by flooding but was not adversely affected by higher salinity in Louisiana marshes. The lower border of *S. patens* colonies in the upper high marsh in South Carolina usually is flooded about 20 minutes per day (Stalter and Batson, 1969). Colonies transplanted into the lower high marsh where flooding occurs for 1 hour per day were limited to 10% survival success. Stalter and Batson (1969) suggested that *S. patens* cannot tolerate increasing inundation and/or increasing salinity. Burdick (1989) found that flooding increased mortality of existing roots and inhibits growth of new roots.

On the Connecticut coastline, marshhay cordgrass occurs in saturated soils 10 cm below mean high tide to 10 to 15 cm above mean high tide (Cooke, Butler, and Madole, 1993). Naidoo, McKee, and Mendelssohn (1992) found reduced growth rates under flooded but low salinity conditions in Louisiana marshes.

Sea level rise has affected New England salt marshes. Sites that once supported *J. gerardii* and *S. patens* have been replaced by a complex of stunted *S. alterniflora*, *D. spicata*, isolated stands of *S. patens*, and herbaceous dicots including *Triglochin maritima* (Warren and Niering, 1993).

ECONOMIC IMPORTANCE

Coastal Protection

Spartina patens is an important species for dissipating wave energy in low topography relief coastlines. It is not an efficient dune builder, but it has been used in dune restoration to repair more stable portions of damaged dunes (McKann *et al.*, 1991; Stallins 2002). Craig (1975) noted that *S. patens* shoots with rhizome segments planted 10.2 to 12.7 cm deep were successful in revegetating coastal sites in Florida. Hester, Spalding, and Franze (2005) found that plantings of *P. amarum*, *U. paniculata*, and *Croton punctatus* formed dunes up to 5.0 m high, but *S. patens* formed dunes less than 1.0 m high. In sites where *P. amarum*, *U. paniculata*, and *Paspalum vaginatum* were transplanted in Louisiana, naturally occurring populations of *S. patens* encroached on these sites and constituted 15% to 25% of the vegetative cover in 3 years (Mendelssohn *et al.*, 1991).

DeLaune *et al.* (2003) and Lin and Mendelssohn (2008) indicate that extant populations of *S. patens* may be important for remediating and restoring Louisiana marshes after oil spills. DeLaune *et al.* (2003) predict that *S. patens* dominated coastal wetlands will recover from oil spills without additional environmental intervention procedures.

Livestock and Wildlife Values

Spartina patens is good forage for livestock, and it provides cover for wildlife (Hatch, Schuster, and Drawe, 1999; Stutzenbaker, 1999). Stutzenbaker (1999) noted that it provides forage and cover for muskrats, nutria, rabbits, and mottled ducks in marshlands of southeastern Texas, and Abuzeineh *et al.* (2007) reported the importance of marshhay cordgrass as habitat for the marsh rice rat (*Oryzomys palustris*). Gedan, Crain, and Bertness (2009) noted that the high marsh in Rhode Island provides habitat for the meadow vole (*Microtus pennsylvanicus*) and white-footed mouse (*Peromyscus leucopus*). They indicated that these small mammals play an important role in

preventing establishment of aggressive populations of *P. australis* and *Typha angustifolia* in disturbed sites. Therefore these herbivores facilitated succession of the climax dominant marshhay cordgrass. In Canada, *S. patens* is the primary larval host of the endangered maritime ringlet butterfly (*Coenonympha nipisiquit*) (Sei, 2009). Seliskar (2003) reported that feral horses browse marshhay cordgrass and other dune grasses in Maryland and Virginia. Stalter (2003) stated that it is cut and dried for hay in New England and Newfoundland.

Medical Uses

No data are available about medicinal uses of this species.

Potential Biological Control Agents

No biological control agents have been isolated from marshhay cordgrass.

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