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REVIEW ARTICLES

Biological Flora of Coastal Wetlands: *Sporobolus cynosuroides* (L.) P.M. Peterson & Saarela

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ABSTRACT

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Sporobolus cynosuroides (L.) P.M. Peterson & Saarela = *Spartina cynosuroides* (L.) Roth is a temperate zone rhizomatous grass that often is a dominant species in coastal brackish marshes on the Gulf coast and Atlantic coasts of the United States where salinity ranges from 0 to 10 psu. *Sporobolus cynosuroides* (L.) P.M. Peterson & Saarela = *Spartina cynosuroides* (L.) Roth is usually absent where salinity values are >12 psu. *Sporobolus cynosuroides* occurs in coastal habitats characterized by infrequent tidal flooding and moderate nutrient levels. Also known as big cordgrass, it may account for net productivity in high marshes that rivals productivity of *Sporobolus alterniflorus* = *Spartina alterniflora* the dominant species in saline low marsh environments. *Sporobolus cynosuroides* and a limited number of cohorts are threatened by climate change and rising sea levels. This species provides important ecological services. In addition, *S. cynosurodes* provides cover and nutrition for wildlife, and has fair forage potential for livestock.

ADDITIONAL INDEX WORDS: *Big cordgrass, taxonomy, morphology, biogeography, habitats, reproduction, physiological ecology, coastal ecology, economic importance.*

INTRODUCTION

Spartina cynosuroides (L.) Roth is now included in the genus *Sporobolus* by Peterson *et al*. (2014). All species formerly included in the genus *Spartina* have been merged into the larger genus *Sporobolus*. Peterson *et al*. (2014) used molecular phylogenetic data to support the reclassification of all *Spartina* taxa at the subgeneric level. Therefore, a change in nomenclature is now in order, and the taxon is listed at *Sporobolus cynosuroides* (L.) P.M. Peterson & Saarla.

Coastal wetlands adjacent to the Gulf of Mexico and the Atlantic coast of the United States represent the most productive ecosystems in North America (Pezeshki and DeLaune, 1991). In estuarine environments below-and-above-ground standing crop biomass is greatest in brackish marshes where *S. cynosuroides* is often the dominant species and has a limited number of cohorts. Silberhorn (1992) stated that *S. cynosuroides* forms dense monotypic stands of 100 to 160 culms·m^{-2} in brackish marshes. He reported that productivity of *S. cynosuroides* nearly equals productivity of the salt marsh dominant *Sporobolus alterniflorus* = *Spartina alterniflora*.

Sporobolus cynosuroides provides numerous ecological services for coastal ecosystems and provides a number of potential economic benefits. Herein, the biology of this important native species is reviewed.

SYNONOMY AND TAXONOMY

Sporobolus cynosuroides (L.) P.M. Peterson & Saarela, family: Poaceae (Gramineae), subfamily: Chloridoideae, tribe: Zoysieae, subtribe: Sporobolinae, Synonyms: *Dactylis cynosuroides* L.; *Dactylis cynosuroides* (L.) Roth; *Trachynotia cynosuroides* (L.) Michx.; *Paspalum cynosuroides* (L.) Brot.; *Limnetis cynosuroides* (L.) Rich; *Spartina cynosuroides* (L.) Roth; *Cynodon cynosuroides* (L.) Raspail; *Spartina polystachya* var. *cynosuroides* (L.) Kuntze (Peterson *et al*., 2001; Peterson *et al*., 2014). Common names: big cordgrass, hog cane, giant cordgrass, salt-reedgrass.

Taxonomic Description

The following taxonomic description has been assembled (Allen, 1992; Barkworth, 2003; Correll and Correll, 1972; Gould, 1975; Kern, Guarise, and Vegetti, 2008; Mobberley, 1953; Radford, Ahles, and Bell, 1968; Shaw, 2012).

Roots, Rhizomes, and Shoots

Plants have a fibrous root system typical of grasses. Plants are perennial with deep seated, elongated rhizomes 7 to15 mm thick and are purplish, tan, or brown. Culms are erect and range from 2 to occasionally 4 m tall (Figure 1a). Culms are unbranched and leafy with internodes occasionally puberulent. The ligule is a ciliate membrane or a ring of hairs 1 to 3 mm

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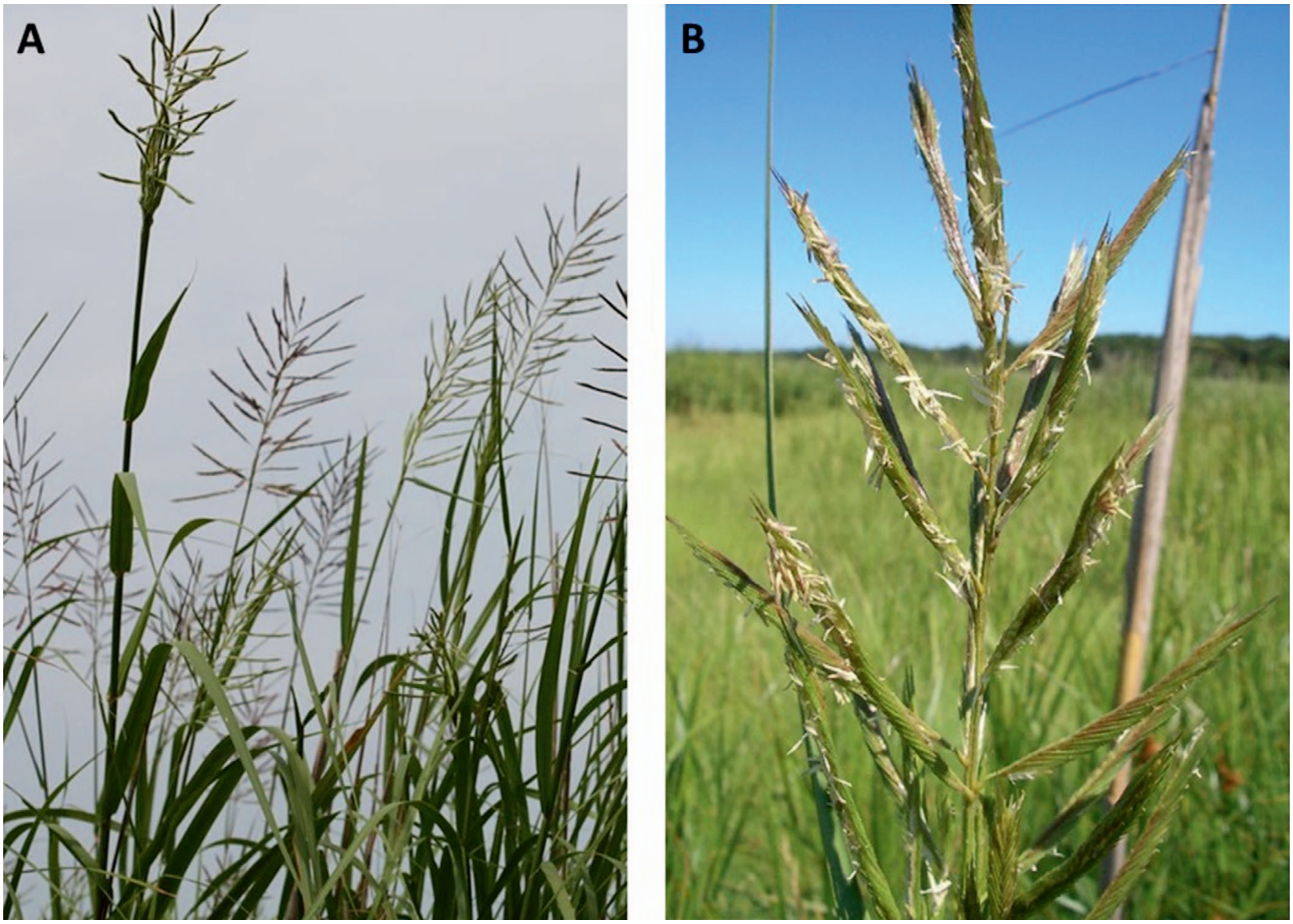

Figure 1. *Sporobolus cynosuroides* in a brackish marsh at Belle W. Baruch Institute for Marine Biology and Coastal Research, Georgetown, South Carolina: (a) monotypic stand, (b) panicle inflorescence.

long. Leaf blades are flat and are curved at the apex. The leaf sheath margins are scarious and pilose at the apex. Blade margins are usually serrulate and the epidermis is glabrous on both surfaces and pilose at the apex.

Inflorescence

The inflorescence is a terminal panicle with laterally compressed spikelets arranged on unilateral branches. Panicles are 15 to 30 cm long and 4 to 7 cm broad. The unilateral branches are 4 to 9 mm long and naked at the base with overlapping spikelets. Kern, Guarise, and Vegetti (2008) refer to the complex of lateral branches as long paracladia. The prolongation of the inflorescence has relatively few distal paracladia that contain a reduced number of spikelets. Therefore, the structure of the panicle is somewhat constricted. Paracladia (lateral branches) usually range from 25 to 45 per panicle, and the spikelets are overlapping (Figure 1b).

Spikelets, Caryopses, and Chromosome Number

Spikelets contain one floret, are 9 to 15 mm long, and are the basic units of the inflorescence. Disarticulation of the spikelet is below the glumes. Glumes are acute to acuminate and are scabrous on the keels. The lower glume is as long as the spikelet. The upper glume is 2 to 3 veined. The lemma is slightly shorter than the spikelet, and the lemma and palea are blunt at the apex and are of the same length. Both the lemma and palea are minutely pubescent or glabrous on the veins. Anthers are 4 to 6 mm long. The caryopsis (pericarp) is olivaceous and elliptical. Reproduction is almost entirely vegetative from rhizomes.

Sporobolus cynosuroides is a tetraploid and has a chromosome number of $2n=40$ (Ainouche *et al.,* 2007; Marchant, 1968; Peterson *et al*., 2014; Silander, 1979). The subgenus *Spartina* of the genus *Sporobolus* has a basic chromosome number of $x=10$. No diploids have been found.

GEOGRAPHIC DISTRIBUTION

Sporobolus cynosuroides has a wide geographic range in the United States. It occurs in northern Maine (47.1°N) on the Atlantic coast to the mouth of the Sabine River (29.1°N) near Port Arthur, Texas, on the coastline of the Gulf of Mexico

(Correll and Correll, 1972; Gould, 1975; Kern, Guarise, and Vegetti, 2008; Radford, Ahles, and Bell, 1968; Shaw, 2012). The herbarium voucher specimen from northern Maine requires verification. However, Potter *et al*. (1995) reported that big cordgrass could be successfully cultivated at 60°N latitude in northwest Europe and eastern England. Shaw (2012) noted that *S. cynosuroides* resembles *Arundo donax* and *Phragmites australis* in a vegetative condition in the estuary of the Sabine River on the Gulf of Mexico.

RANGE OF HABITATS AND ASSOCIATED SPECIES

Big cordgrass is an important species in brackish and intermediate marshes in estuarine sites that have a salinity range from 0 to 10 ppt (psu) and are subject to low tidal amplitudes (Stutzenbaker, 1999). Dense stands of *S. cynosuroides* are commonly found in a transition zone from freshwater upper marshes to seaward salt marshes, in brackish bays, and in river mouths (Correll and Correll, 1972). Habitats are usually slightly above mean high tide and include saturated soils of organic clays and sands (Stutzenbaker, 1999). Species commonly associated with *S. cynosuroides* are listed in Table 1.

Craft (2007) found that *S. cynosuroides* and *Juncus roemerianus* dominated estuarine sites near the mouth of the Altamaha River in Georgia where these species formed stands in intermediate and brackish marshes and salinities were 2 to 6 psu. *Zizaniopsis milacea* was found upstream in tidal freshwater where the salinity ranged from 0 to 0.3 psu. Mendelssohn and Marcellus (1976) found a similar situation in Virginia where *S. cynosuroides* stands were found where the salinity was 4 psu.

A narrow tidal range is an important topographic facet that provides an important ecological niche for big cordgrass on slightly elevated soils where tidal flooding is rare. *Sporobolus cynosuroides* occurs in coastal wetlands in Mississippi where the topographic relief is only 43 cm (Hackney and de la Cruz, 1978), and big cordgrass stands in brackish marshes are flooded only 2.2% of the time (Bishop and Hackney, 1987). In Alabama, the elevation span where big cordgrass typically occurs ranges from only –0.066 to 0.636 m above mean sea level (Constantin, Broussard, and Cherry, 2019). In Louisiana, Selman and Baccigalopi (2012) found a similar tidal range of –0.366 to 1.051 m above mean sea level.

Dense stands of *S. cynosuroides* develop in estuaries that are rich in organic matter and where well drained soils consist of clay, sand, and silt (Bishop and Hackney, 1987; Stutzenbaker, 1999). Stands of big cordgrass occur in environments where salinity typically ranges from 0 to 10 psu in the western Gulf of Mexico (Stutzenbaker, 1999). In Georgia, Craft (2007) reported that *S. cynosuroides* and *J. roemerianus* occur in intermediate and brackish marshes where salinities range from 2 to 6 psu. Mendelssohn and Marcellus (1976) found that optimal salinity condition in Virginia for stands of big cordgrass was 4 psu. However, they noted that big cordgrass can occur in sites that have a salinity range of 0.6 to 11 psu.

Hackney and de la Cruz (1978) and LaSalle and Bishop (1987) reported that pH values ranged from 4.0 to 7.5 in brackish marshes in Mississippi. In Georgia, Menon and Ghuman (1985) found that pH values ranged between 5.5 to 6.5.

PHYSIOLOGICAL ECOLOGY

Data are limited on the physiology of *S. cynosuroides*. Big cordgrass is a C_4 plant in its mode of carbon metabolism in the light reactions of photosynthesis (Beale and Long, 1997; Maricle, Cobos, and Campbell, 2007; Potter *et al*., 1995). Leaf anatomy features are consistent with Kranz anatomy and photosynthetic efficiency in a brackish marsh environment (Anderson, 1974; DeJong, Drake, and Pearcy, 1982). Vascular bundles are enclosed by a double bundle sheath with the outer sheath containing chloroplasts (Allen, 1974). Maricle *et al*. (2009) reported that *S. cynosuroides* leaves have flat surfaces with the epidermis similar on both blade surfaces. The upper epidermis has prickles on the surface and rounded and saddle-shaped silica bodies on both surfaces. Stomata are present on both surfaces. Subsidiary cells with papillae are adjacent to stomata on the upper epidermis. Carbon dioxide uptake is confined to the upper epidermis and water vapor loss is reduced by having furrows on the upper leaf epidermis (Maricle *et al*., 2009). Maricle, Cobos, and Campbell (2007) stated that the dark leaves of big cordgrass may intercept more solar radiation compared to other species in brackish marshes that are poorly adapted to high light levels.

McKee and Mendelssohn (1984) indicated that a close relationship of adenylate energy charge with growth in early spring and summer. They reported a decline in growth in late summer that is correlated with a decline in adenine nucleotide concentrations. Adenine nucleotide concentrations peaked during rapid vegetative growth.

Parrondo, Gosselink, and Hopkinson (1978) found that increasing salinity reduced shoot growth more than root and rhizome growth. Overall growth of *S. cynosuroides* was greater in well-drained rather than in flooded sites. Under drought conditions in Georgia as freshwater decreased in brackish sites, *S. cynosuroides* stands decreased in zones where high tide salinities exceeded 14 psu (White and Alber, 2009). *Sporobolus alterniflorus* migrated into the higher salinity environments formerly occupied by *S. cynosuroides* and *J. romerianus* in areas that formerly had brackish conditions. *Sporobolus alterniflorus* stands persisted after drought conditions eased and brackish conditions returned. Meanwhile dominance of *S. cynosuroides* shifted upstream 3 to 6 km from the mouth of the Altamaha River estuary (White and Alber, 2009).

Data on flowering and maturation of pericarps for this species are limited. Hopkinson, Gosselink, and Parrondo (1978) reported an annual flush of vegetative growth occurs in spring. Aerial shoots died to the ground in late fall and little or no aerial growth from rhizomes occurred in winter in Louisiana. Beale and Long (1997) stated that peak nutrient production occurs in late summer and at the end of the growing season in late autumn. Nutrients are translocated to deep seated rhizomes.

BIOMASS AND LITTER DECOMPOSITION

Productivity in coastal brackish marshes is influenced by the substrate with biomass usually greater in warm temperate climates in the United States. Aboveground biomass is most often recorded due to the relative ease of data collection. However, belowground biomass sampling is gaining favor as both above-and-belowground samplings produce a more accu-

Table 1. *Representative species associated with* Sporobolus cynosuroides *in intermediate and brackish marshes*.

Species	MISS	ALA	GEO	SCA	NCV	MAR	NEJ	MASS
Atriplex patula							x	
Batis maritima			x					
Bolboschoenus robustus			x	x			x	
Carex hyalinolepis					x			
Cladium jamicense		x						
Distichlis spicata			x			x	x	
Hibiscus moseheutos					x			
Iva frutescens			x				x	x
Juncus roemerianus	x	x	x	x	x	x		
Limonium carolinianum			x					
Phragmites australis				x			x	x
Sagittaria lancifolia	x							
Sarcocornia sp.			x					
Schoenoplectus americanus			x	x	x	x		
Schoenoplectus pungens				x				
Schoenoplectus			x	x				
tabernaemontani			x					
Solidago sempervirens								x
Sporobolus alterniflorus	x		x	x	x		x	
Sporobolus patens					x	x	x	
Sporobolus pectinata						x		
Trifolium sp.			x					
Typha angustifolia					x			
Zizania aquatica				x				
Zizaniopsis miliacea				x				

MISS = Mississippi (Bishop and Hackney, 1987; Rush et al.*, 2010); ALA = Alabama (Constantin, Broussard, and Cherry, 2019); GEO = Georgia (Craft, 2007; Capehart and Hackney, 1989; Hensel* et al.*, 2021; Wieski* et al.*, 2010); SCA = South Carolina (Baden, 1971; Stalter, 1973; Stalter, Rachlin, and Baden, 2021; Wilkinson* et al.*, 2016); NCV = North Carolina and Virginia (Hackney* et al.*, 1996; Perry and Hershner, 1999; Rheinhardt and Rheinhardt, 2004; Watts* et al.*, 2008); MAR = Maryland (Leonard, Ahn, and Birch, 2010; Woodland, Rowe, and Henry, 2017); NEJ = New Jersey (Artigas* et al.*, 2015; Elsey-Quirk* et al.*, 2019); MASS = Massachusetts (Massachusetts Natural Heritage & Endangered Species Program, 2015)*

rate estimate of total productivity. Osland *et al*. (2014), Stagg *et al*. (2017), and Wieski *et al*. (2010) stated that aboveground productivity is usually highest in brackish marshes than either in freshwater, intermediate or salt marshes.

Productivity in brackish and salt marshes may be inhibited by high sulfide concentrations (Bradley and Dunn, 1989). However, Stribling (1997) found that big cordgrass did not exhibit a significant growth response with an increasing concentration of sulfate. After a sufficient amount of sulfate enters the substrate sulfate reducing bacteria convert sulfate to hydrogen sulfide which is toxic to non-adapted species (Hackney and Avery, 2015). Hydrogen sulfide toxicity damages enzymes which catalyze the final reactions of aerobic respiration in the root system (Martin and Maricle, 2015).

In a review of the literature, a limited number of productivity investigations of *S. cynosuroides* have been conducted namely: Louisiana, Mississippi, Georgia, North Carolina, and Virginia.

Louisiana

Hopkinson, Gosselink, and Parrondo (1978) recorded high biomass estimates for big cordgrass in Louisiana. They found that *S. cynosuroides* had a high annual aboveground biomass of 1,355 $g \cdot m^{-2} \cdot yr^{-1}$ with peak productivity in June. They indicated that big cordgrass had a low biomass loss rate of only 4 $mg \cdot day^{-1}$.

Mississippi

Hackney and de la Cruz (1986) estimated both above-and-belowground biomass in Mississippi tidal marshes. Belowground productivity was estimated in the rhizome-root complex in the top 20 cm of the substrate. They said their estimate of underground biomass of 2.2 $kg \cdot m^{-2} \cdot yr^{-1}$ was an underestimate because the root-rhizome mass was more deeply anchored. About 1.9 $kg \cdot m^{-2} \cdot yr^{-1}$was produced in late spring and summer and 0.3 $kg \cdot m^{-2} \cdot yr^{-1}$ was produced in late autumn. Hackney and de la Cruz (1986) estimated net productivity of both above- and belowground biomass ranging from 4.4 to 6.2 $kg \cdot m^{-2} \cdot yr^{-1}$. They stated that belowground biomass was equal to or slightly greater than aboveground biomass.

Georgia

In a coastal marsh ecosystem in Georgia, Linthurst and Reimold (1978) reported aboveground productivity of *S. cynosuroides* as 6,040 $g \cdot m^{-2} \cdot yr^{-1}$. Gallagher and Plumley (1979) estimated aboveground biomass as 2,200 $g \cdot m^{-2} \cdot yr^{-1}$ and belowground biomass as 3,560 $g \cdot m^{-2} \cdot yr^{-1}$ for a total biomass of 5,760 $g \cdot m^{-2} \cdot yr^{-1}$. Schubauer and Hopkinson (1984) estimated belowground biomass of 4,628 $g \cdot m^{-2} \cdot yr^{-1}$and aboveground biomass of 3,080 $g \cdot m^{-2} \cdot yr^{-1}$ for a total biomass of 7,708 $g \cdot m^{-2} \cdot yr^{-1}$. Shubauer and Hopkinson (1984) reported that rhizomes account for 76 to 87% of live biomass belowground.

North Carolina

Sporobolus cynosuroides shows a single late summer or early autumn surge in North Carolina of aboveground biomass with annual increments ranging from 0.25 to 1 $kg \cdot m^{-2} \cdot yr^{-1}$ (Bellis and Gaither, 1985). Belowground estimates ranged from 1 to 8 times greater than aboveground annual increments. Bellis and Gaither (1985) estimated winter die-back of 0.8 to 0.9 $kg \cdot m^{-2} \cdot yr^{-1}$. Capehart and Hackney (1989) reported that big cordgrass roots and rhizomes form an extensive network that produced 6.3 $kg \cdot m^{-2} \cdot yr^{-1}$.

Virginia

Silberhorn (1992) indicated that *S. cynosuroides* forms dense monotypic stands of 100 to 160 culms·m^{-2}. He estimated total productivity of this species ranging from 2 to 6 tons·acre·yr^{-1} and that productivity in tidal marshes of big cordgrass rivals only *Sporobolus alterniflorus* in coastal wetlands in Virginia.

Tidal wetlands remove carbon by sequestering carbon in sediments that are rich in organic material. Artigas *et al*. (2015) stated that the high marsh with brackish, intermediate, and freshwater have greater carbon storage potential than low marsh zones dominated by *S. alterniflorus*. Artigas *et al*. (2015) estimated a net ecosystem exchange of 979 g·cm^{-2}·yr^{-1} with a carbon loss by respiration of 768 g·cm^{-2}·yr^{-1} resulting in a total uptake of carbon of 211 g·cm^{-2}·yr^{-1}.

Detritus and Decomposition

Tidal marsh vegetation in Georgia releases large amounts of detritus into adjacent estuaries and is primarily responsible for high productivity in the ecosystem. Menon and Ghuman (1985) stated that *S. cynosuroides* stands produce significant amounts of detritus and that detritus retains significant amounts of heavy metals. Zinc is retained in detritus at a rate of 1.21 g·m^{-3}·yr^{-1}. However, the heavy metal manganese is released into the Altamaha River at a rate of 17 g·m^{-3}·yr^{-1}. Substrate surface retention of big cordgrass detritus may be as high at 499 g·m^{-3}·yr^{-1} (Menon and Ghuman, 1985).

In Mississippi brackish marshes, Hackney and de la Cruz (1980) found that decomposition of *S. cynosuroides* and *J. roemerianus* was greatest in the upper 10 cm of marsh soil and no apparent decomposition occurred below a depth of 20 cm. Rhizome decomposition for big cordgrass was 16%·yr^{-1} whereas decomposition of *J. roemerianus* was 27%·yr^{-1}.

Available nitrogen increases in early stages of decomposition. However as much as 30% of the nitrogen content in detritus may exist in a form of non-protein compounds and may not be readily available for detritivores (Odum, Kirk, and Zieman, 1979).

FIRE AND POPULATION BIOLOGY

Populations of big cordgrass form dense, monotypic stands from an extensive rhizome complex. This robust perennial rarely produces from seed (Barkworth, 2003). Natural disturbance and anthropogenic perturbations are significant features of population dynamics in coastal vegetation (Judd and Lonard, 1987; Lonard, Judd, and Smith, 2003).

Prescribed burns and wildfires usually do not affect population dynamics in coastal areas. Lonard, Judd, and Smith (2003) reported that *Sporobolus patens* recovered from rhizomes 9 months after a wildfire on North Padre Island, Texas. In Maryland, prescribed burns are used to support waterfowl and to manage the invasive variety of *Phragmites australis* (Leonard, Ahn, and Birch, 2010). They found no consistent effects of fire on biomass production of *Distichlis spicata, S. alterniflorus*, *Schoenoplectus americanus, S. patens*, and *S. cynosuroides*. However, their results showed little effect of prescribed burns on increasing aboveground biomass.

In Mississippi, Faulkner and de la Cruz (1982) found that nutrient mobilization following a prescribed burn during winter produced minimal input of ash-borne nutrients. They estimated that the loss of nitrogen and potassium from the *S. cynosuroides* community exceeded 50%.

REPRODUCTION

Data related to pollen production, pollen viability, fertilization, caryopsis viability, caryopsis dispersal, seed bank, germination, and establishment of seedlings have not been found in a search of the literature. Caryopsis dispersal is most likely by water or by wind. Vegetative reproduction is more common than sexual reproduction (Barkworth, 2003). Barkworth (2003) indicated that mature caryopses were uncommon in herbarium specimens. Fragmentation and lateral spreading of the rhizome complex is a major factor in the limited species dispersal of this species.

Li and Gallagher (1996) used tissue culture techniques to produce viable big cordgrass caryopses in the greenhouse. They recommended that tissue culture techniques be used as a regenerative tool for the selection of ecotype varieties for revegetation efforts in brackish marsh restoration.

ROLE IN GEOMORPHOLOGY

A small number of species is adapted to the harsh conditions that prevail in tidal brackish, intermediate, and salt marshes (Table 1). *Sporobolus cynosuroides* plays an important role in trapping sediment in oligohaline (0.5 to 5.0 psu) marshes in Georgia and accounts for a net accretion of sediment of 15.2·mm·yr^{-1} (Ensign *et al*. 2014). Stutzenbaker (1999) stated that the deep-seated root-rhizome complex plays and important role in erosion protection.

CLIMATE CHANGE

Coastal marsh vegetation transition zones usually occur in freshwater, brackish, intermediate, and salt marshes in very narrow bands characterized by only a few centimeters in elevation (Constantin, Broussard, and Cherry, 2019). Hackney *et al*. (1996) found that a brackish marsh in North Carolina has six vegetation zones within an 18 cm portion of a 1.35 m tidal range. Therefore, *S. cynosuroides* populations are susceptible to flooding associated with sea level rise and barriers in the upper marsh that may halt a landward migration (Constantin, Broussard, and Cherry, 2019).

Stagg *et al*. (2017) stated that as sea level rises a shift to more salt tolerant communities is a result. Perry and Hershner (1999) found that big cordgrass was not included with dominant species in a freshwater tidal marsh in 1974. However, three years later it ranked fourth in importance value of all species that were formerly found in freshwater. The marsh reflected conditions associated with encroachment of seawater and a 4·mm·yr^{-1} rise in sea level.

INTERACTIONS WITH OTHER SPECIES

Competition within and among species in coastal marshes may be altered by indirect effects in these species-limited communities. Facilitation may buffer competitive effects (Callaway and Pennings, 2000). Dense monotypic stands of the perennial *S. cynosuroides* and brackish conditions eliminates most potential competitors.

White and Alber (2009) reported that drought conditions decreased freshwater input into the Altamah River estuary in

Georgia. *Sporobolus cynosuroides* stands decreased at the expense of the more salt tolerant *S. alterniflorus*. Once established *S. alterniflorus* inhibited big cordgrass from returning to previously occupied sites after the drought was lifted.

Mycorrhiza

Arbuscular mycorrhizal fungi, formerly referred to as vesicular arbuscular fungi, have an important symbiotic relationship at the plant-soil boundary. Arbuscular mycorrhizal fungi improve environmental stress tolerance, enhances nutrient uptake, and aids in water absorption in host plants (Alarcón and Cuenca, 2005). However, the mycorrhizal relationships with *S. cynosuroides* are largely unexplored. McHugh and Dighton (2004) reported that big cordgrass roots are moderately colonized by mycorrhiza after inoculation in the laboratory. They found that inoculation marginally enhanced growth and improved phosphorus and nitrogen content of host plants. McHugh and Dighton (2004) suggested that mycorrhiza may be beneficial in increasing tillering in *S. cynosuroides* in brackish marshes.

Herbivores, Predators, and Symbionts

LaSalle and Bishop (1990) reported that a larval fly (*Pelastoneurus abbreviatus*) feeds on rhizomes and roots of big cordgrass at a depth of 10 cm in Mississippi brackish marshes. However, they did not indicate appreciable damage in stands of big cordgrass. Wheeler (2010) reported that a rare lady beetle (*Hyperaspidius ventustilus*) is associated with stands of *S. cynosuroides* in South Carolina brackish marshes where the lady beetle is a predator on the mealybug *Dysmicoccus dennoi*. LaSalle and de la Cruz (1985) recorded the presence of 36 spider species in Mississippi marsh communities. Spiders were common in dense big cordgrass litter and wrack. Hollow dead culms provided additional habits for the spiders. Cromartie and Schweitzer (1993) reported that larvae of the rare skipper butterfly (*Problema bulenta*) in New Jersey occurs in big cordgrass stands. However, adults were collected at sites adjacent to nectar-bearing species. Conocephaline grasshopper immature nymphs feed on *S. cynosuroides* shoots. Parson and de la Cruz (1980) indicated that grasshoppers commonly fed on *J. roemerianus* and *S. cynosuroides*.

Gastropods and mollusks are common in the big cordgrass wetland community. Periwinkles (*Littoraia irrorata*) graze on microbiota on big cordgrass shoots and have greater survivorship on *S. cynosuroides* than on shorter and more exposed shoots of *S. alterniflorus* (Failon, Wittyngham, and Johnson, 2020). Snails have been found to account for a limited amount of grazing pressure on big cordgrass. Li and Pennings (2016) reported that about 3% of blade damage of *S. cynosuroides* and *J. roemerianus* stands was caused by snails.

The Carolina marsh clam's (*Polymesoda caroliniana*) habitats are the root-rhizome network of big cordgrass and *J. roemerianus* (Bishop and Hackney, 1987). However, in Mississippi clams were most abundant in the root-rhizome network of *J. roemerianus*.

Salt marsh topminnows (*Fundulus jenkinsii*) are abundant in shallow pools in stands of big cordgrass. Lopez *et al*., (2011) indicated that abundance is high in the *S. cynosuroides* habitat compared to other plant communities.

Invasive feral hogs do extensive damage to coastal plant communities in the southeastern United States by consuming shoots and rhizomes of native grasses, sedges, and rushes. In the coastal zone of Georgia, Hensel *et al*. (2021) reported that foraging and trampling impact dominant species leaving brackish marsh sites disturbed and subsequently inhibiting recovery of the plant community. They found that *S. cynosuroides* and *J. roemerianus* were eliminated by consumption of rhizomes and roots. Hensel *et al*. (2021) found a five-fold increase of weedy species due to increased solar radiation in these disturbed sites with a resulting doubling of species diversity. Overall, they reported a decline in aerial plant coverage of about 30%. Native plant communities did not recover after feral hogs were eliminated (Hensel *et al*., 2021).

ECONOMIC IMPORTANCE

Sporobolus cynosuroides has important ecological and economic values in the coastal zone. The existence of an extensive deep-seated rhizome-root network is important in halting erosion. This species serves as a habitat for a wide range of organisms in food webs as well as providing a sink for sequestering carbon. The species is a major source of wrack and detritus which supports a wide variety of organisms in the marine ecosystem.

Big cordgrass has been suggested as a potential biofuel for northwestern Europe. Potter *et al*. (1995), found that as a renewable resource, 96% of vegetative propagules survived the first year after transplanting, and seven years after establishment in the field produced 1.1 $kg{\cdot}m^{-2}{\cdot}yr^{-1}$ to 1.3 $kg{\cdot}m^{-2}{\cdot}yr^{-1}$ of biomass. They pointed out that as a fuel source the species is a renewable carbon-neutral energy source.

Sporobolus cynosuroides stands provide cover and nutrition for a wide variety of wildlife. Stutzenbaker (1999) reported that muskrats and invasive nutria feed extensively on rhizomes in the southwestern Gulf of Mexico, and Silberhorn (1992) indicated that muskrats use big cordgrass shoots for lodge construction in brackish marshes in Virginia. Selman and Baccigalopi (2012) and Woodland, Rowe, and Henry (2017) noted that hatchlings, juveniles, and adult diamondback terrapins (*Malaclemys terrapin*) frequent big cordgrass communities. Wilkinson *et al*. (2016) stated that alligators frequent tidal marshes in South Carolina dominated by dense stands of *S. cynosuroides*, *S. alterniflorus*, and the bulrush *Schoenoplectus robustus*.

Several species of sparrows, rails, and geese frequent big cordgrass communities. Silberhorn (1992) stated that migratory geese consume rhizomes. Watts *et al*. (2008) stated that the coastal swamp sparrow *Melospiza georgiana nigrescens* has extended its breeding range into brackish marshes in Virginia, and Greenburg and Maldonado (2006) reported that seaside sparrows (*Ammodramus maritimus*), salt marsh sharp-tailed sparrows (*Ammodramus caudacutus*), and the black rail (*Laterallus jamaicensis*) frequent tidal marshes. Clapper rails (*Raillus longirostis*) frequent brackish marshes in Mississippi where the dominant species are *S. cynosuroides, J. roemerianus,* and *Sagittaria lancifolia* (Rush, Woodrey, and Cooper, 2010).

Wild horses were introduced on isolated spit on the Currituck Banks in Virginia and North Carolina. Horses graze on young shoots of *S. cynosuroides*, *P. australis*, and *J. roemerianus* in the early growing season and feed on young shoots of big cordgrass, *S. patens*, and the bulrush *Schoenoplectus americanus* during summer (Rheinhardt and Rheinhardt, 2004).

Hatch, Schuster, and Drawe (1999) stated that *S. cynosuroides* provides some forage value to cattle in spring after brackish marshes are burned in late fall or early winter.

FUTURE RESEARCH

A number of pressing research needs should be addressed for *S. cynosuroides*. Competition investigations with the aggressive invasive *P. australis* haplotype M should be addressed in Atlantic coastal wetlands where *P. australis* has supplanted native species. Data could provide important information for resource managers.

This study was unable to locate literature related to sexual reproduction of big cordgrass. It would be useful to obtain data on pollen production and viability, viability of caryopses, and the establishment of seedlings.

Finally, data related to productivity for both below-and aboveground biomass should be collected. Productivity data are limited to studies completed three to four decades ago in a limited number of sites. Therefore, it would be beneficial to have productivity of *S. cynosuroides* in light of climate change and sea level rise.

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