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Biological Flora of Coastal Dunes and Wetlands: *Borrichia frutescens* (L.) DC.

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ABSTRACT

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Borrichia frutescens (L.) DC. is a New World warm-temperate, subtropical, and tropical zone, perennial subshrub that is an important species in hypersaline coastal sites. Also known as sea ox-eye, it tolerates salinities ranging from less than 20 ppt to 130 ppt. It occurs in substrates low in organic matter and deficient in nitrogen, phosphorus, and potassium. Nearly all reproduction is vegetative from an extensive rhizome system. Populations of this species recover quickly after coverage by wrack. Stands of *B. frutescens* often dominate the landward border of salt marshes.

ADDITIONAL INDEX WORDS: *Sea ox-eye, morphology, geographical distribution, habitats, plant communities, reproduction, physiological ecology*.

INTRODUCTION

Borrichia, in the family Asteraceae, is a warm-temperate, subtropical, and tropical genus that includes two species, *Borrichia frutescens* (L.) DC. and *Borrichia arborescens* (L.) DC., one hybrid complex, *Borrichia* × *cubana* Britton and Blake, and one doubtful species *Borrichia peruviana* DC., known only from a vegetative type collection (Semple, 1978; Semple and Semple, 1977). *Borrichia frutescens* and *B. arborescens* are sympatric in south Florida and Bermuda, where they hybridize and produce *B.* × *cubana* (Semple and Semple, 1977).

Borrichia frutescens is morphologically variable, and it occurs throughout a broad salinity gradient, ranging from less than 20 ppt to 130 ppt (Richards *et al.,* 2004, 2010; Semple, 1978). *Borrichia frutescens* is often a dominant species in high marsh sites that are only infrequently inundated. This species uses limited resources for sexual reproduction (Cattell and Karl, 2004). Vegetative reproduction by rhizomes is the primary mechanism of the lateral spread of this species into hypersaline salt pans. Herein, we review the biology of this important coastal-zone species.

TAXONOMY AND VARIATION

Borrichia frutescens (L.) DC. is a member of the family Asteraceae (Compositae) and is included in the tribe Heliantheae. The genus *Borrichia* was described by M. Adanson in 1763. Synonyms or rejected names for this species are *Buphthalmium incanum* Mill., *Diomedea bidentata* Cass. and *Borrichia frutescens* (L.) DC. var. *angustifolia* DC. Common names include sea ox-eye, ox-eye daisy, bush sea ox-eye, sea daisy, and bushy seaside tansy.

Taxonomic Description

The following taxonomic description has been derived from Correll and Johnson, 1970; Crespo, Ruiz de León, and Rios, 2002; Everitt, Drawe, and Lonard, 2002; Gandhi and Thomas, 1989; Lehman, 2013; Lehman, O'Brien, and White, 2005; Lonard, personal observations; Radford, Ahles, and Bell, 1968; Richardson and King, 2011; and Semple, 2006.

Seed Morphology

A single, nearly translucent seed about 2.0 mm long is borne in an indehiscent achene (cypsela).

Seedling Morphology

Sea ox-eye seedlings produce several pairs of glabrate, juvenile leaves with entire margins. Toothed margins are produced on more-typical blades during leaf expansion (Semple, 1978).

Root Morphology

Adventitious roots are formed at the nodes of the rhizomes.

Shoot Morphology

Borrichia frutescens is a rhizomatous, somewhat succulent, canescent or glabrate subshrub, which forms extensive colonies. Stems are erect or occasionally decumbent, are

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Figure 1. *Borrichia frutescens* on the margin of a salt marsh at Boca Chica State Park, Texas.

branched or unbranched, and are 0.1 to 1.5 m tall. Plant heights on Galveston Island, Texas, are usually less than 1.0 m tall. Petioles are united at their bases, up to 2 cm long, and often bearing lateral projections near the base of the blades. Leaves are simple, opposite, obovate to oblanceolate, obtuse, and apiculate. Blades are 2 to 10 cm long, 0.5 to 1.5 cm wide, and coriaceous. Epidermal surfaces are canescent. Blade margins are variable but are usually serrate-dentate or entire on the distal blades.

Inflorescence

The inflorescence consists of globose, mostly solitary, radiate, heads (capitula) on peduncles 2 to 6 cm long. The heads are 2.5 to 3.5 cm wide and terminate the shoots. Involucres are hemispheric, about 5 mm high and 2.2 cm wide, and becoming firm with age. Phyllaries are imbricated in three to five series with the outer phyllaries somewhat herbaceous, oblong, and reflexed at maturity. The inner series is obovate, with a spine-tipped apex to 12 mm long and about 4.5 mm wide at the base. The receptacle is slightly convex and densely covered with chaff, similar to the inner phyllaries. Chaff scales are oblanceolate, 5 to 9 mm long, folded, partially enclose the achenes, and have a distal woody, orange-yellowish spine 1 to 3 mm long. Ray florets are 15 to 30, pistillate, fertile, 5 to 12 mm long, yellow or orange-tinged, and 3-toothed distally. Disc florets are bisexual, 30 to 75 per head; corolla is cylindrical, 5 to 6.5 mm long, yellow, and 5-toothed apically. The pappus is a dentate crown 0.5 to 1.0 mm long and is present on both ray and disc florets (Figure 1).

Fruits

The achenes (cypselae) are dimorphic, glabrous, and black at maturity. Achenes of ray florets are three-angled and 2.5 to 3 mm long. Achenes of disc florets are four-angled, 3 to 5 mm long, and about 1 mm wide.

Variability

Borrichia frutescens is a phenotypically variable species (Richards *et al.,* 2004, 2010; Semple, 1978). The degree of leaf serration and the size of the inflorescence vary greatly (Semple, 1978). This species occurs along a broad range of salinities, ranging from less than 20 ppt to greater than 130 ppt. Richards *et al*. (2004) stated that the edaphic factor of salinity defines 20 to 50% of variation in plant height in naturally occurring populations. However, Richards *et al*. (2010) reported that phenotypic plasticity, not adaptation to salinity levels, determines variation along a salinity gradient in coastal wetlands.

Borrichia frutescens and *B. arborescens* (L.) DC. are sympatric in South Florida and Bermuda where hybridization occurs (Semple and Semple, 1977). The hybrid swarm has been designated as *Borrichia* × *cubana* Britton & Blake = *Borrichia cubana* Britton & Blake and is intermediate in leaf pubescence and in the morphology of spines on the phyllaries (Semple and Semple, 1977). The hybrids in south Florida are maintained by assortative mating and clonal reproduction (Cattell and Karl, 2004). Hybrids typically backcross with *B. frutescens,* and both species and F_1 hybrids occur in disturbed sites (Cattell and Karl, 2004; Semple and Semple, 1977).

Chromosome Number

Borrichia frutescens has a chromosome number of $2n = 28$ or rarely $2n = 42$ (Crespo, Ruiz de León, and Rios, 2002; Long and Lakela, 1971; Semple, 2006).

GEOGRAPHIC DISTRIBUTION

In the United States, *B. frutescens* is distributed along the Atlantic coastline from Maryland to Florida (Adams, 1963; Antlfinger, 1981; Blake, 1951; Cattell and Karl, 2004; Guo and Pennings, 2012; Harvill, 1965; Hill, 1986; Kelley, 2006; Long and Lakela, 1971; Luken, 2012; Radford, Ahles, and Bell, 1968; Semple, 1978, 2006; Semple and Semple, 1977; Smith, 1953; Stalter and Batson, 1973; Stalter and Lamont, 1990, 1993; Stalter *et al.,* 1999). Along the Gulf Coast of the United States, this species occurs from Florida to Texas (Alexander and Dunton, 2006; Anderson and Alexander, 1985; Correll and Johnston, 1970; Eleuterius, 1972; Heinsch *et al.,* 2004; Judd and Lonard, 2004; Lonard and Judd, 2002; Marquardt and Pennings, 2011; Proffitt *et al.,* 2005). In Texas, it occurs inland in the Rio Grande Delta and upstream along the Rio Grande about 200 km and has been reported in south-central Texas (Correll and Johnston, 1970; Judd and Lonard, 2002; Semple, 2006; Semple and Semple, 1977).

Borrichia frutescens occurs in coastal wetlands in Mexico, from Tamaulipas to Quintana Roo, and in inland, saline sites in San Luis Potosi and Coahuila (Correll and Johnston, 1970; Gómez-Pompa, 1973; Moreno-Casasola, 1988; Moreno-Casasola and Espejel, 1986; Sauer, 1967; Semple, 1978; Semple and Semple, 1977). Sea ox-eye has been introduced sparingly in Grand Bahamas, Cuba, and Bermuda (Semple, 1978, 2006; Semple and Semple, 1977; Thomas, 1993). Semple (1978) indicated that the occurrence of *B. frutescens* in Cuba and Grand Bahamas is documented by only a few voucher specimens. Recently, Crespo, Ruiz de León, and Rios (2002) reported the occurrence of sea ox-eye in a coastal site in southern Spain.

RANGE OF HABITATS

Borrichia frutescens is an important species of coastal zone vegetation in a wide variety of habitats in the United States. It

is common in high salt marsh habitats that are flooded infrequently (Adams, 1963; Antlfinger, 1981, 1982; Antlfinger and Dunn, 1979, 1983; Cleary, Hosier, and Wells, 1979; Feagin and Wu, 2006; Guo and Pennings, 2012; Oosting, 1954; Stalter, 1968, 1993; Stalter and Lamont, 1990, 1993, 1997). Colonies in the high marsh are often separated by extensive areas of salt flats (Antlfinger and Dunn, 1979). In the high marsh, it also occurs in an ecotone between the low marsh, typically dominated by *Spartina alterniflora,* and upland sites dominated by a variety of shrubs and/or herbaceous species (Luken, 2012; Pennings and Moore, 2001; Richards, Pennings, and Donovan, 2005). Sea ox-eye occurs along estuaries and occasionally inland in south Texas and northern Mexico (Semple, 1978, 2006; Semple and Semple, 1977).

Borrichia frutescens is also an important species in the vegetation of brackish marshes (Eleuterius and McDaniel, 1978; Judd and Lonard, 2004; Lehman, O'Brien, and White, 2005; Lonard *et al.,* 2005; Radford, Ahles, and Bell, 1968; Semple, 2006; Stutzenbaker, 1999). Bradley and Dunn (1989) found this species in disturbed sites in salt marshes in Georgia.

On Padre Island, Texas, *B. frutescens* occurs in nearly all topographic facets, excluding the backshore and the primary dune complex (Judd, Lonard, and Sides, 1977). It occurs in depressions in the vegetated flats and on the margins of wind–tidal flats adjacent to the Laguna Madre (Judd, Lonard, and Sides, 1977; Negrete *et al.,* 1999; Nelson *et al.,* 2000). In the lower Rio Grande Delta, adjacent to the Laguna Madre, *B. frutescens* is found in resaca (abandoned oxbows of the Rio Grande) basins, on salt flats, and in disturbed saline sites, including roadsides (Judd and Lonard, 2002; Lonard, Richardson, and Richard, 2004).

In Mexico, sea ox-eye occurs in salt marshes in the lee of primary dune complexes, in moist depressions among secondary dune complexes, and on stabilized dunes about 60 m from the high tide mark (Castillo, Popma, and Moreno-Casasola, 1991; Espejel, 1986; Gómez-Pompa, 1973; Moreno-Casasola and Espejel, 1986; Sauer, 1967).

Substrate Characteristics

Borrichia frutescens typically occurs in soils deficient in nitrogen, potassium, and phosphorous and in soils that are low in organic matter (Drawe *et al.,* 1981; Profitt *et al.,* 2005). Most of the organic matter is in the upper 15 cm of the substrate (Hanson, 1983). Hanson (1983) reported annual nitrogen fixation rates as low as 0.36 g N m^{-2} y^{-1}. Substrates range from heavy clays to silty sands (Hanson, 1983; Lonard and Judd, 1981; Proffitt *et al.,* 2005; Stiling *et al.,* 1999; Stutzenbaker, 1999). Clay substrates in south Texas are often waterlogged (Johnston, 1952, 1955).

In Tamaulipas, Mexico, Sauer (1967) noted that sea ox-eye occurred on white sand, clay and shell, quartz sand and shell, and calcareous sand. Semple (2006) indicated that *B. frutescens* could occur on limestone and rocky shorelines 0 to 10 m above mean high tide.

Richards *et al.* (2010) found that the salinity in brackish and salt marsh habitats in Georgia ranged from 4 to 127 ppt. Antlfinger and Dunn (1979) noted that salinity in other high marshes where *B. frutescens* is a dominant species ranged from 20 to 50 ppt. In salt flats where growth is stunted, the salinity ranges from 100 to 130 ppt (Antlfinger and Dunn, 1979). Stalter (1968) reported salinity values in the high salt marsh in South Carolina that ranged from 10 to 50 ppt. In lower areas of the high marsh, salinity ranged from 10 to 30 ppt (Stalter, 1968).

Judd, Lonard, and Sides (1977) found that 80% of the sand particle sizes ranged from 0.18 to 0.25 mm on the margins of the wind-tidal flats on South Padre Island, Texas. Depth to the water table is only 14 cm in isolated stands of *B. frutescens* (Judd, Lonard, and Sides, 1977).

Stalter (1968) found that the pH of salt marsh habitats in South Carolina ranged from 4.8 to 7.5 and 6.0 to 7.5 in the high marsh. Adams (1963) noted pH values ranging from 4.19 to 7.62 in high marshes in North Carolina. Drawe *et al.* (1981) reported pH values ranging from 7.7 to 8.4 on North Padre Island, Texas.

Climatic Requirements

The natural geographical distribution of *B. frutescens* extends from 38°05′ N latitude on the Maryland side of Assateague Island National Seashore (Virginia and Maryland), in the temperate zone to about 20° N latitude in Quintana Roo, Mexico, in the New World tropics (Sauer, 1967; Smith, 1953; Stalter and Lamont, 1990). *Borrichia frutescens* overwinters in the temperate zone by producing rhizomes 15 to 20 cm below the surface (Lonard, personal observations). *Borrichia frutescens* maintains a typical subshrub growth form and survives during mild winters in the subtropics. Individual woody shoots may live for up to 5 years (Cattell and Karl, 2004). The northern distribution appears to be limited by the severity and duration of freezing temperatures. No freeze-tolerance studies have been reported, to our knowledge, for this species.

PLANT COMMUNITIES

Plant communities on coastlines where *B. frutescens* occurs are typically referred to by terminology used to describe habitats and topographic zones. Communities are designated as salt marshes, brackish marshes, salt pans, salt flats, salt prairies, or estuary communities (Eleuterius, 1972; Harvill, 1965; Judd and Lonard, 2002; Kelley, 2006; Johnston 1952, 1955; Oosting, 1954; Stalter and Lamont, 1990, 1993). On South Padre Island, Texas, Judd, Lonard, and Sides (1977) associated plant communities with topographic facets. *Borrichia frutescens* occurs in depressions in the secondary dunes and vegetated flats, on the margins of wind–tidal flats, on the margins of hurricane washover sites, and in disturbed sites, including roadsides (Judd, Lonard, and Sides, 1977).

Johnston (1952, 1955); Castillo, Popma, and Moreno-Casasola (1991); and Moreno-Casasola and Espejel (1986) designated plant communities in coastal wetlands with species-specific nomenclature. In the Rio Grande Delta of Texas, Johnston (1952, 1955) referred to poorly drained flats that support a plant community dominated by halophytic shrubs and cacti as a *Borrichia* flats community. This community usually occurs on waterlogged clays 0 to 3 m above sea level. Species associated with the dominant *B. frutescens* include *Batis maritima, Salicornia virginica, Suaeda* spp., and *Distichlis littoralis*. In Tamaulipas,

Table 1. *Representative species associated with* Borrichia frutescens *in Bermuda and from Virginia to Florida.*

Species	BE	VA	NC	SC	GA
Asparagus sprengeri	X				
Avicennia germinans	X				
Baccharis halimifolia		X		X	
Batis maritima				X	X
Borrichia arborescens	X				
Carex albolutescens			X		
Centella erecta			X		
Conocarpus arborescens	X				
Cyperus grayi		X			
Cyperus strigosus			X		
Distichlis spicata		X	X	X	X
Eleocharis albida			X		
Erechtites hieraciifolia			X		
Eupatorium capillifolium			X		
Fimbristylis castanea		X	X	X	
Heliotropium curassavicum	X				
Iva frutescens		X		X	
Juncus dichotomus			X		
Juncus marginatus			X		
Juncus maritimus	X				
Juncus megacephalus			X		
Juncus roemerianus		X	X	X	X
Limonium carolinianum		X	X	X	X
Lythrum lineare			X		
Paspalum vaginatum	X				
Pluchea purpurascens		X			
Rhizophora mangle	X				
Sabatia stellaris			X	X	
Salicornia bigelovii		X			X
Salicornia europaea		X			
Salicornia virginica			X	X	X
Samolus valerandi ssp. *parviflorus*			X		
Sarcocornia perennis	X		X		
Schinus terebenthifolius	X				
Sesuvium portulacastrum	X				
Spartina alterniflora		X	X	X	X
Spartina patens		X		X	
Sporobolus virginicus				X	X
Suaeda linearis				X	X
Symphyotrichum tenuifolium				X	

BE = Bermuda (Anonymous, 2013b; Thomas, 1993); VA = Virginia (Harvill, 1965; Stalter and Lamont, 1990); NC = North Carolina (Cleary, Hosier, and Wells, 1979; Kelley, 2006; Wright, Edwards, and van de Plassche, 2011); SC = South Carolina (Luken, 2012; Stalter and Lamont, 1993; Stalter *et al.,* 2006); GA = Georgia (Antlfinger, 1981, 1982; Antlfinger and Dunn, 1983; Guo and Pennings, 2012; Hanson, 1983; Pennings and Callaway, 2000; Richards, Pennings, and Donovan, 2005).

Tabasco, and Campeche, Mexico, Castillo, Popma, and Moreno-Casasola (1991) and Moreno-Casasola and Espejel (1986) identified a *Borrichia frutescens–Fimbristylis spadicea* = *F. puberula* community that occurred in wet depressions in sheltered sites on the leeward margins of foredunes. In coastal wetlands in Tabasco and Campeche, these authors identified a *Borrichia frutescens* community that occurred in protected and stabilized dunes about 60 m from the high tide mark, and in Campeche, they identified an *Ernodea littoralis–Borrichia frutescens* community in stabilized, vegetated flats. Shrubs including *Coccoloba uvifera, Randia laetevirens*, and *Lantana involucrata* characterized that assemblage. In Veracruz, Gómez-Pompa (1973) indicated that *B. frutescens* was an important species in "espartal" (*Spartina*) grasslands that are periodically inundated. Tables 1 and 2 contain representative species associated with *B. frutescens* throughout its range in North America and Bermuda.

Table 2. *Representative species associated with* Borrichia frutescens *from Florida to Texas and on the coastline of Veracruz, Mexico.*

Species	FL	MS	LA	TX	MV
Agalinis maritima	X				
Amaranthus hybridus			X		
Andropogon glomeratus	X				X
Avicennia germinans	X		X	X	
Baccharis halimifolia	X	X	X	X	
Batis maritima	X		X	X	X
Blutaparon vermiculare				X	
Bolboschoenus maritimus				X	
Borrichia arborescens	X				
Borrichia cubana	X				
Batis maritima	X	X	X		
Conocarpus erectus	X				
Cuscuta indecora				X	
Distichlis littoralis				X	
Distichlis spicata	X		X		
Eleocharis austrotexanus				X	
Eryngium integrifolium		X			
Fimbristylis castanea					X
Fimbristylis spathacea	X				X
Heliotropium curassavicum				X	
Hydrocotyle bonariensis				X	
Ipomoea purpurascens		X			
Iva angustifolia			X		
Iva frutescens	X	X	X	X	
Juncus roemerianus	X	X	X	X	
Laguncularia racemosa	X				
Limonium carolinianum	X		X	X	
Machaeranthera phyllocephala				X	
Prosopis reptans				X	
Rhizophora mangle	X				
Salicornia bigelovii			X	X	
Salicornia perennis					X
Salicornia virginica	X			X	
Sesuvium portulacastrum	X				
Samolus valerandi				X	
Schoenoplectus americanus		X			
Schoenoplectus pungens				X	
Schoenoplectus robustus			X		
Solidago sempervirens		X			
Spartina alterniflora	X	X	X	X	
Spartina bakeri	X				
Spartina patens	X	X	X	X	
Spartina spartinae	X			X	X
Sporobolus virginicus	X			X	
Suaeda linearis	X			X	
Symphyotrichum divaricatum			X		
Symphyotrichum tenuifolium		X			
Typha domingensis				X	

FL = Florida (Anderson and Alexander, 1985; Schmidt *et al.,* 2010; Stalter and Lynch, unpublished data; Stiling *et al.,* 1992); MS = Mississippi (Eleuterius, 1972; Elsey-Quirk, Middleton, and Proffitt, 2009; McCall and Pennings, 2012; Proffitt *et al.,* 2005); LA = Louisiana (Elsey-Quirk, Middleton, and Proffitt, 2009; McCall and Pennings, 2012; Proffitt *et al.,* 2005); TX = Texas (Abuzeineh *et al.,* 2007; Alexander and Dunton, 2006; Feagin and Wu, 2006; Heinsch *et al.,* 2004; Johnston, 1955; Lonard and Judd, 2002; Lonard *et al.,* 2005; Marquardt and Pennings, 2011; Nelson *et al.,* 2000; Stutzenbaker, 1999; Tunnell, Withers, and Hardegree, 1997); MV = Mexico, Veracruz (Gómez-Pompa, 1973).

PHYSIOLOGICAL ECOLOGY

Borrichia frutescens is a C_3 halophyte in carbon fixation with its light-independent reactions to photosynthesis (Antl-

finger and Dunn, 1979). In the tropics and subtropics, photosynthesis occurs throughout the year, but winter rates of CO_2 exchange are reduced (Antlfinger and Dunn, 1979). Respiration rates are similar in summer and winter (Antlfinger and Dunn, 1979).

Infrequent flooding in the high salt marsh and evaporation results in concentration of salts. *Borrichia frutescens* in sites of highest salinity is stunted (Antlfinger and Dunn, 1983). Salinity typically varies from 20 to 50 ppt in the high marsh and from 100 to 130 ppt in adjacent salt flats in Georgia (Antlfinger, 1981). Sea ox-eye exhibits salt-induced succulence in leaves, and the root system removes salt. The relative water content attributed to leaf succulence is 73%. Salts are sequestered within cellular vacuoles (Antlfinger, 1981).

Salinity tolerance is associated with sodium accumulation and dilution through succulence and the synthesis of nitrogen-rich compatible solutes proline and glycine–betaine (Richards *et al.,* 2010). Ash content is high in plant tissues, which is indicative of NaCl accumulation (Lanning and Eleuterius, 1985). However, Cavalieri and Huang (1979) found that the osmoregulatory function of proline occurs only in soil salinities exceeding sea water. Cavalieri and Huang (1977) reported that *B. frutescens* has a salt tolerant enzyme, NAD–malate dehydrogenase, which represents a possible adaptation to a salt marsh environment.

Alexander and Dunton (2006) and Dunton, Hardegree, and Whiteledge (2001) noted that *B. frutescens* responds by producing greater biomass and plant cover following the reduction of salinity. Heinsch *et al*. (2004) found that high salinity values that occur during extended periods of tidal inundation or extended drought conditions cause this species to lose its leaves.

High sulfide concentrations in salt marshes are metabolic toxins. Both plant size and biomass are reduced by increasing concentrations of this toxin, and rhizomes are particularly sensitive (Bradley and Dunn, 1989). Clonal integration of *B. frutescens* stands allows rhizomatous parental clones in low-salinity sites to supply water to lateral growth, salt-stressed shoots on the high-salinity margins of the stand (Pennings and Callaway, 2000). Antlfinger (1982) found that salinity in the center of *B. frutescens* stands was about 15 ppt, whereas salinity was about 45 ppt on the margins of clones.

Phenology

Flowering and fruiting in sea ox-eye is expected at any time of the year because of its distribution in warm–temperate, subtropical, and tropical environments (Correll and Johnston, 1970; Lonard and Judd, 1989; Rossi *et al.,* 1999. In Maryland and Virginia, flowering occurs from July to September (Hill, 1986). Peak flowering in Mississippi is from June to August (Eleuterius and Caldwell, 1984), and in Florida, it is from May to July (Rossi *et al*., 1999). Gandhi and Thomas (1989) and Lehman, O'Brien, and White (2005) noted that peak flowering occurred from April to December in Louisiana and Texas. *Borrichia frutescens* has been introduced in coastal sites in southern Spain, where flowering has been reported from February to April, and seedlings are common after rainfall in autumn (Crespo, Ruiz de León, and Rios, 2002).

PRODUCTIVITY

Net aerial primary productivity is often used to elucidate the growth potential of salt marsh plants. Linthurst and Reimold (1978) estimated living biomass for *B. frutescens* in Georgia salt marshes ranged from a minimum value of 648 g m^{-2} to a maximum of 1860 g m^{-2}. They noted a fairly high litter base of dead biomass, ranging from a minimum of 184 g m^{-2} to as high as 291 g m^{-2}. Stem density was high and varied from 213 m^2 to 380 m^2 (Linthurst and Reimold, 1978). Pennings, Stanton, and Brewer (2002) fertilized the ecotone between *Spartina alterniflora* and *B. frutescens* in salt marshes in Georgia. They found much higher productivity in *S. alterniflora* but a reduction in biomass and plant height of *B. frutescens*. They concluded that fertilization favored the low marsh-dominant species *S. alterniflora* (Pennings, Stanton, and Brewer, 2002).

POPULATION BIOLOGY

Borrichia frutescens is a long-lived, rhizomatous subshrub that has individual stems that typically live for 5 years. Aerial shoots usually arise singly from laterally spreading rhizomes (Cattell and Karl, 2004). Elongated rhizomes enable populations to colonize barren, hypersaline salt pans (Pennings and Callaway, 2000). Rhizome lengths of plants in the saline wetlands of Galveston, Texas, are 50 cm or longer.

Population Dynamics

Population dynamics in coastal habitats is controlled by physical factors and naturally occurring and anthropocentric disturbances. Salinization influences highly clonal populations of *B. frutescens* to form dense stands with intense competition in crowded niches. Vegetative reproduction is enhanced.

Only a few offspring are produced by sexual reproduction (K-selection) (Blits and Gallagher, 1991; Semple and Semple, 1977). Antlfinger (1982) found that random mating and complete outcrossing occurred in *B. frutescens* populations. Pollen flow is only effective where 20 to 30 individuals occur within 1 m^{-2}.

Tunnell, Withers, and Hardegree (1997) followed the recovery of *B. frutescens* populations in a Texas bay system following an oil spill. The site was burned to remove the oil. They found that the site, formerly dominated by *B. frutescens,* was dominated by *Distichlis spicata* several years after the fire. Lonard, Judd, and Smith (2003) noted that *B. frutescens* populations recovered quickly after a wild fire on the margins of the wind-tidal flats on North Padre Island, Texas. They found that *B. frutescens* was the only species in flower 108 days after the fire.

REPRODUCTION

Borrichia frutescens is self-incompatible and depends on insects to transfer spinulose, tricolporate pollen to receptive stigmatic surfaces (Crespo, Ruiz de León, and Rios, 2002; Gandhi and Thomas, 1989). Sea ox-eye is visited by generalist pollinators, including bees, butterflies, moths, wasps, and beetles (Antlfinger, 1982; Crespo, Ruiz de León, and Rios, 2002). Bees and butterflies are the most important pollinators, and pollen exchange is weighted toward a few individuals (Antlfinger, 1982). Mean pollinator flight distance is only 40 cm between inflorescences (Antlfinger, 1982).

Achene Production

Achene production, equated with seed production, is great in *B. frutescens*. Each inflorescence contains 15 to 30 pistillate florets and 20 to 75 disc florets (Antlfinger, 1981; Semple, 2006).

Dispersal

Borrichia frutescens is a widely distributed, New World temperate, subtropical, and tropical maritime species. Animals, including invertebrates and vertebrates, are the most likely vectors of the achenes. The firm, crown-like pappus of both ray and disc achenes may serve to aid in dispersal. Achenes may be carried on the external surfaces of birds and mammals or ingested and dispersed in feces. Tidal action may serve to move achenes over wide distances.

No data are available for seed viability after exposure to sea water.

Seed Banks

Ungar (2001) stated that seed banks may have an important role in temporal and spatial distributions of halophytes. However, seed bank data have not been reported for this species.

Germination Ecology and Establishment of Seedlings

Crespo, Ruiz de León, and Rios (2002) noted that seedlings were abundant on sandy, saline substrates in Spain after autumn rainfall. However, Antlfinger (1981) indicated that seedling establishment was a rare event in saline wetlands in Georgia.

Vegetative Reproduction

Salt marsh vegetation depends almost entirely on vegetative reproduction. *Borrichia frutescens* is a perennial clonal species that provides small amounts of resources into sexual reproduction (Cattell and Karl, 2004). Vegetative reproduction by rhizomes is the primary mechanism for the lateral spread of this species into bare patches in saline coastal wetlands and salt pans.

GEOMORPHOLOGICAL INTERACTIONS

Stands of *B. frutescens* and other species in coastal wetlands are often buried by wrack deposition by abnormally high tides. Stalter *et al*. (2006) found that virtually all salt marsh vegetation, with the exception of *Spartina patens* and *B. frutescens,* disappeared after 2 months of coverage by wrack. Stalter *et al*. (2006) reported that *B. frutescens* was resilient even after 7 months of coverage by 15 to 25 cm of wrack.

Role in Geomorphology

Borrichia frutescens is often the climax species in saline coastal wetlands where few halophytes are adapted to that harsh environment (Tunnell, Withers, and Hardegree, 1997). The primary role in geomorphology is the stabilization of the substrate, particularly in the high marsh.

INTERACTIONS WITH OTHER SPECIES

Competition in natural plant communities is more important in communities that have favorable conditions than it is in those communities exposed to harsh physical circumstances (Bertness and Shumway, 1993). Positive or facilitation interactions among species are more often a feature of unfavorable physical parameters. Neighboring individuals or adjacent species may serve as buffers from physical stress factors (Bertness and Shumway, 1993).

In Georgia, *B. frutescens* dominates the landward border of most salt marshes (Pennings and Moore, 2001). The lower border of salt marshes is influenced more by physical stress than by competition, whereas the upper border of the herbaceous or grassy zone is set mostly by competition with shrubs (Pennings and Moore, 2001). Plant height and the number of leaves of sea ox-eye increase with higher elevations, and improved soil drainage promotes growth (Pennings and Moore, 2001).

Guo and Pennings (2012) found that localized oyster shell deposits altered the dynamics of salt marsh populations. The annual succulent *Suaeda linearis* is usually excluded by waterlogging and by perennial community dominants, including *B. frutescens, Juncus roemerianus*, and *S. alterniflora*. The physical condition of slightly elevated topography provided by oyster shell deposits produces a physical niche that provides a unique habitat for *S. linearis*. The niche does not allow the usual perennial dominants to colonize those sites (Guo and Pennings, 2012).

Herbivores, Predators, Parasites, and Parasitoids

Borrichia frutescens is often subjected to a wide variety of nematode infestations, insect herbivores, parasites, parasitoids, and commensalistic imperfect fungi. The nematode *Tylenchulus palustris,* which is closely related to roundworm infestations of commercial citrus trees, parasitizes the root system of *B. frutescens* (Dow *et al.,* 1990; Tanha Maafi *et al.,* 2012).

The gall-forming midge (*Asphondylia borrichiae*) may transmit the imperfect fungi *Alternaria* sp. and *Fusarium* sp. when the midge parasitizes *B. frutescens* (Strake, Keagy, and Stiling, 2006). Midges initiate solitary galls adjacent to the apical meristem of sea ox-eye shoots and can assume the role of a parasitoid and kill the sea ox-eye host (Stiling *et al.,* 1992). Galls, in turn, are affected by several species of parasitoid wasps that lay eggs in the galls. Developing wasp larvae then consume the midge larvae (Strake, Keagy, and Stiling, 2006). A specialized plant hopper (*Pissonotus quadripustulatus*) feeds only on *B. frutescens* and the gall-forming midge. (Stiling *et al.,* 1999; Stiling and Moon, 2005). Thrips (Order: Thysanoptera) have been collected from *B. frutescens* shoots in south Texas, but Cole and McDaniel (1964) did not indicate how those insects affect sea ox-eye populations. The angiosperm hemiparasite *Cuscuta indecora* (dodder) infects *B. frutescens* early in the growing season, but dodder usually does not kill host plants (Marquardt and Pennings, 2011).

RESPONSE TO WATER LEVELS

Borrichia frutescens is periodically inundated by high tides or less frequently by storm surges. Populations on the margins of wind–tidal flats on South Padre Island, Texas, occur where the water table is only 14 cm below the substrate surface (Judd, Lonard, and Sides, 1977). In South Carolina salt marshes, Stalter (1968) noted that sea ox-eye occurs in the high marsh and the low high marsh, in sites 1.43 to 1.81 m above mean sea level and where submergence averages 58 min d^{-1}.

ECONOMIC IMPORTANCE

Borrichia frutescens populations may have some value in stabilization of substrates in salt marshes and brackish marshes, but its potential has not been explored. Stutzenbaker (1999) stated that sea ox-eye is not a candidate for propagation and transplantation, but the best method for propagation is to plant rhizomes in wet sites in late winter. Stutzenbaker (1999) further indicated that this perennial species does not require resource management actions.

Wildlife and Ornamental Values

Borrichia frutescens provides cover and nutrition for wildlife. Sand fiddler crabs (*Uca pugilator*) forage on sparsely vegetated stands of *B. frutescens* and *S. alterniflora* in South Carolina (Viscido and Wethey, 2002). In Georgia, Buck *et al*. (2003) found that salt marsh crabs (*Armases cinereum*) foraged on fresh leaves and leaf litter of sea ox-eye. In Texas wetlands, *B. frutescens* provides nectar for butterflies and bees and achenes for granivorous birds (Anonymous, 2013a).

On the Texas coastline, laughing gulls (*Laurus atricilla*), American white pelicans (*Pelecanus erythrorhynchos*), and roseate spoonbills (*Ajaia ajaja*) build nests with *B. frutescens* or seek cover in stands of this species (Texas Colonial Waterbird Society, 1982; Thebeau and Chapman, 1984; White, Mitchell, and Cromartie, 1982). The endangered whooping crane (*Grus americana*) overwinters in Texas salt marshes in plant communities dominated by *B. frutescens*, *Batis maritima, S. alterniflora,* and *Salicornia* spp. (Lewis, 1995). The habitat of the endangered Lower Keys marsh rabbit (*Sylvilagus palustris hefneri*) is coastal salt marsh prairies and buttonwood ecotones where sea ox-eye is an important species. *Borrichia frutescens* makes up 25% of the diet of that species (Forys, 1999).

An overlooked value for the attractive inflorescences of this species is its potential value as an ornamental. Richardson and King (2011) stated that sea ox-eye is a candidate for landscaping in saline soils that would otherwise inhibit growth of glycophytes.

Medicinal Uses

No information, to our knowledge, is available about medical uses of *B. frutescens*.

Potential Biological Control Agents

No biological control agents have been isolated from this species.

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