The Biology of *Limonium carolinianum* (Walt.) Britt. (Plumbaginaceae) in Coastal Wetlands

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ABSTRACT

Limonium carolinianum (Walt.) Britt. is a New World humid continental, temperate, subtropical, and tropical maritime taxon. It is a long-lived perennial that is found in wet sand and clay mineral soils. This species is a salt tolerant halophyte where salinity values approach 30 parts per thousand. Reproduction is primarily vegetative. However, seed production is estimated at 1,000 to 10,000 per individual plant. Also known as sea lavender, it has been suggested as a species that can be used for re-vegetation efforts. Inflorescences of this species are often harvested for dried floral arrangements.

Keywords: Sea lavender, morphology, habitats, communities, population ecology, physiological ecology, economic values.

INTRODUCTION

The genus *Limonium* (Plumbaginaceae) includes about 300 to 350 species, and is primarily represented in maritime or in arid environments in the northern hemisphere (Correll and Correll 1972; Mabberley 1997). Eight species have been reported in North America including four species that have escaped from cultivation in California (Flora of North America Editorial Committee 2005; Luteyn 1990). *Limonium carolinianum* typically occurs in brackish marshes, salt marshes, salt meadows, in irregularly flooded tidal wetlands, and on barrier island beaches (Duncan 1974; Stutzenbaker 1999). It tolerates salinity conditions ranging from freshwater to 30 parts per thousand(ppt) (Stalter 1968). Inflorescenes are often harvested for dried flower arrangements (Baltzer et al. 2002a; Baltzer et al., 2002b; Richardson and King 2011). Herein, we summarize important aspects of this species.

1.0 TAXONOMY AND VARIATION

Limonium carolinianum (T. Walter) N. Britton is a member of the family Plumbaginaceae P. Miller. The taxon was published under the name *Statice caroliniana* Walt.in 1788. A partial list of synonyms or rejected names includes *Limonium angustatum* (A. Gray) Small, *L. carolinianum* var. *angustatum* (A. Gray) S.F. Blake, *L. carolinianum* var. *compactum* Shinners, *L. carolinianum* var. *nashii* (Small) B. Boivin, *L. carolinianum* var. *obtusilobum* (S.F. Blake) H.E. Ahles, *L. carolinianum* var. *trichogonum* (S.F. Blake) B. Boivin, *L. nashii* Small, *L. nashii* var. *angustatum* (A. Gray) H.E. Ahles, *L. obtusilobum* S.F. Blake, *L. trichogonum* S.F. Blake (Flora of North America Editorial Committee 2005; Luteyn, 1976). Common names include sea lavender, Carolina sea lavender, marsh rosemary, American thrift, marsh root, canker root, seaside thrift, lavender thrift, ink root, and statice. The following taxonomic description has been derived from Correll and Correll 1972; Flora of North America Editorial Committee 2005; Hamilton 1997; Lehman 2013; Luteyn 1976, 1990; and Radford et al. 1968.

Limonium carolinianum has a woody taproot typical of dicots that extend up to 30.5 cm below the soil surface (R. Stalter, personal observation). Plants are long-lived perennials. Stems are acaulescent. Primary leaves are in a basal rosette. Petioles are glabrous, 2.5 to 15 cm long, and narrowly winged at the base. Blades are 5 to 30 cm long and 0.5 to 7.5 cm wide, glabrous and leathery, and are spatulate-elliptic, lance-elliptic, oblanceolate, or obovate. The blade margins are entire.

The inflorescence is a diffuse panicle that extends up to 90 cm above the basal rosette. One to 3 flowers are borne on one side of the inflorescence axis, and are subtended by papery, secund bracts. The bracts are 2 to 6 mm long. The funnel-form calyx consists of 5 united, pale white sepals, 4 to 6 mm long. The calyx is persistent, dry, membranous, and glabrous, but pilose along the veins. The corolla consists of 5 slightly united petals with elongated claws. The petals are lavender to purple or occasionally white, and are 1 to 2 mm longer than the calyx. Five stamens are present, and the filaments are adnate at the base of the corolla. The pistils have 5 styles, and are free at the base (Figure 1). The fruit is a one-seeded, indehiscent utricle 3 to 7 mm long. Seeds are brown, lustrous, reticulate, spindle-shaped, and 3 to 4 mm long.

The genus *Limonium* is characterized by having significant biodiversity, and is taxonomically complex (Cortinhas et al. 2015). Luteyn (1976) concluded that *L. carolinianum* is a complex of 6 to 7 taxa formerly recognized as varieties or separate

species. He noted that morphological variation is almost continuous across the geographical range of the taxon. Hamilton (1997) reported that genetically isolated populations occur within 5 km of each other on the coastline of Rhode Island. He recognized the role of isolation by distance in influencing ecological variation. Sea lavender has a chromosome number of 2*n* = 36 (Flora of North America Editorial Committee 2005).

2.0 GEOGRAPHIC DISTRIBUTION and RANGE of HABITATS

Limonium carolinianum is distributed from about 47.5°N latitude in Newfoundland and Labrador, Canada, to Florida, and from the Gulf coast of Florida to about 24.5°N in Tamaulipas, Mexico (Lehman, 2013; Luteyn, 1976, 1990; Rachlin et al. 2012; Stalter 1994; Stalter et al. 1986, 1990). This species is also reported from Bermuda (Luteyn 1976).

Sea lavender typically occurs in regularly or irregularly flooded saline habitats 1.4 to 1.7m above mean sea level at Georgetown, South Carolina (Stalter 1968). It is primarily found in saturated soil conditions in brackish marshes, salt marshes, and on the margins of salt pans or salt flats. It is rarely a dominant species. In Rhode Island and New Hampshire, *L. carolinianum* occurs in regularly inundated upper middle and high marsh habitats, in saturated depressions in the secondary dune complex, and occasionally on rocky beaches (Dunlop and Crow 1985; Hacker and Bertness 1999).

In the mid-Atlantic states of Virginia and Maryland to subtropical sites in Florida, *L. carolinianum* occurs in similar habitats listed above, but it is also found in irregularly flooded higher elevations in the salt marsh, on the margins of tidal flats, and on the margins of hurricane washover channels (Duncan 1974; Hill1986; Radford et al. 1968; Richards et al. 2005; Stalter, 1974; Stalter et al. 1999a, 1999b).

In Mississippi, sea lavender also occurs in brackish, saline, and hypersaline coastal sites (Eleuterius and McDaniel 1978). In Texas coastal wetlands, it occurs on the margins of mostly bare wind tidal flats, in irregularly flooded salt marshes, on beaches, in wet depressions in the secondary dune topographic zone, and on the margins of hurricane washover channels (Judd et al. 1977; Lehman 2013; Nelson et al. 2000).

2.1 SUBSTRATE CHARACTERISTICS and CLIMATIC REQUIREMENTS

Limonium carolinianum is found in highly stressful physical environments in coastal wetlands. Substrate conditions include wet, tidal-influenced, sandy and clay mineral soils that are deficient in organic material, and in nitrogen, phosphorus, and potassium (Drawe et al. 1981; Proffitt et al. 2005; Stutzenbaker 1999). In South Carolina tidal marshes, Stalter (1968) found that sites where *L. carolinianum* occurs are flooded for one hour daily by spring tides. Under more xeric conditions in irregularly flooded sites on South Padre Island, Texas, the water table on the margins of the wind-tidal flats is 13 to 15 cm below the soil surface (Judd et al. 1977). The pH typically ranges between 6.0 to 8.5, and the salinity ranges from 0 to 30 ppt on North Padre Island, Texas, and in South Carolina in saline wetlands (Drawe et al. 1981; Stalter 1968). Soil temperatures can reach 52.8 °C in North Carolina sites (Oosting 1954).

This species occurs over broad climatic conditions ranging from a humid continental climate in Newfoundland and Labrador to a subtropical climate in Tamaulipas, Mexico. In the broad continuum of climatic zones for this species, plants survive unfavorable

temperatures by producing a basal rosette, and by having a perennial caudex. Cold tolerance studies have not been conducted.

2.2 PLANT COMMUNITIES

Plant communities in saline coastal wetlands where sea lavender is present are referred to by a variety of inconsistently used terminology. Most workers name plant communities according to topographic zones in which they occur or by listing a habitat. For example, Judd et al. (1977) associated plant communities of South Padre Island, Texas, with topographic facets including backshore, primary dunes, secondary dunes and vegetated flats, and tidal flats. They also identified washovers as a site for a plant community. Judd et al. (1977) reported *L. carolinianum* on the margins of washover channels and in the mostly barren wind tidal flats associated with *Salicornia bigelovii, Sarcocornia utahensis = Salicornia virginica, Blutaparon vermiculare, Sporobolus tharpii,* and *Sesuvium portulacastrum*. Lonard (personal observation) found *L. carolinianum* on the margins of a salt marsh on the Texas mainland adjacent to Galveston Bay dominated by low-growing *Spartina alterniflora*. *Limoniumcarolinianum* is associated with *Batis maritima, S. bigelovii, S. utahensis, Distichlis spicata, Borrichia frutescens,* and *Bolboschoenusmaritimus*subsp. *paludosus.*

Other workers have named plant communities on the basis of the dominant species in the community. Harvill (1965) referred to a *Salicornia - Sarcocornia - Distichlis* tidal flat community in Virginia where *L. carolinianum* is associated with *S. utahensis* and *D. spicata* as the most important species. He also identified a *Spartina alterniflora-Spartina patens-Distichlis-Juncus roemerianus* marsh community. However, *L. carolinianum* was a minor species in the community (Harvill 1965).

Dunlop and Crow (1985) and Stalter and Lamont, (1990, 2000, 2002) recognized plant communities associated with habitats; namely tidal marshes and salt marshes. All communities are in saline and hypersaline sites and are subject to periodic flooding. Table 1 includes common species associated with *L. carolinianum* throughout its range.

3.0 PHYSIOLOGICAL ECOLOGY

Limonium carolinianum is a salt tolerant halophyte that occurs where salinity values approach 30ppt (Stalter 1968). Little is known about the physiology of this species. Anatomical features include highly developed aerenchyma tissue in the root system and petioles (Lehman 2013). Aerenchyma tissue aids in diffusion of oxygen to tissues that are otherwise subjected to anaerobic conditions. Salt glands are present on leaves and stems. Aerosol salt spray and salt crystals are often found on leaves and stems.

The non-essential protein proline plays an essential role in the response of sea lavender to high salinities. Proline acts as an osmoprotectant that does not affect the functions of most enzymes at high concentrations (Cavalieri and Huang 1979). Therefore, water-soluble proline allows for osmotic adjustments to high salinity conditions in a salt marsh (Cavalieri and Huang 1979).

4.0 PHENOLOGY

In Rhode Island, *L. carolinianum* has flowering and fruiting phenophases from late July to October (Hamilton, 1997). In Virginia and Maryland flowering and fruiting phases are slightly later in August and extend through October (Hill 1986). In Gulf Coast sites in Florida, Anderson and Alexander (1985) reported that this species

flowers and fruits from July to September. However, they noted an ecotype that they referred to as *L. angustatum* that has a sexual reproductive phase that extends from late September to November. In Mississippi, flowering and fruiting occur from August to October (Eleuterius and Caldwell 1984). Sexual reproductive phases in Texas are reported from May to November (Correll and Correll 1972; Lehman2013; Lonard and Judd 1989; Stutzenbaker 1999).

5.0 PRODUCTIVITY

Limited data are available for the productivity of *L. carolinianum*. However, Rietsma et al. (2011) found low plant cover values (0.3 ± 0.3%) and low biomass values (12.3 ± 0.7 g/m^2) for *L. carolinianum* in salt marshes in Massachusetts. Lonard et al. (2003) noted that *L. carolinianum* had relative plant cover values that did not exceed 1.3% on burned wind-tidal flats on Padre Island National Seashore, Texas.

6.0 POPULATION BIOLOGY

Limonium carolinianum is a perennial that takes 9 years to reach sexual maturity (Baltzer et al. 2002b). Populations are often subjected to disturbance. Inflorescences are harvested for floral arrangements. Harvesting pressure can reduce population stands 25% within 6 to 8 years of harvesting pressure, and population recovery could take from 34 to 103 years to recover (Baltzer et al. 2002b).

Populations are resistant to oil pollution. Booker et al. (1989) reported that sea lavender survived 8 to 12 oilings of Kuwait crude oil. They indicated that tolerance was related to the secondary growth of the root cambium and to suberization of the pellem (cork layer) in the woody roots (Booker et al. 1989).

6.1 REPRODUCTION

Fertility is low in this species. Plants are typically self-compatible, but individuals produce both self-pollinated and out-crossed flowers (Hamilton 1997). Hamilton (1997) noted that pollinators are unknown, but bees and unidentified wasps are suggested as pollen vectors. Pollen is tricolpate, and the pollen surface is finely to coarsely reticulate (Mabberley 1997).

Seed dispersal is usually limited to short distances from parent plants (Hamilton 1997). Baltzer (2002b) found that 50% of seedlings were within 34 cm of the parent, and 90% were within 61 cm. Birds and ocean currents are vectors for seed dispersal, and detached inflorescences are often found in wrack (Hamilton 1997; Lonard and Judd 1980; Luteyn 1990). Seeds float about 1.5 to 7 hours before sinking (Baltzer et al. 2002a). Vivian-Smith and Stiles (1994) noted that brants (*Branta bernicla*) and red-breasted mergansers (*Mergus serrator*) disperse adhesive bracts containing seeds.

6.2 SEED BANK, GERMINATION ECOLOGY and ESTABLISHMEBNT OF SEEDLINGS

Seed production in this species is estimated at 1,000 to 10,000 seeds per individual (Smith et al. 2013). *Limonium carolinianum* lacks a persistent seed bank because seeds survive only one year (Baltzer et al. 2002a). Seedlings in Nova Scotia populations emerge in mid - May until early June (Baltzer et al. 2002a). Seeds buried 2.5 cm below the soil surface have the highest viability, but seeds remaining on the inflorescence do not germinate in the second year (Baltzer et al. 2002a). Shumway and Bertness (1992) found that freshwater additions in a salt marsh reduced soil salinity and subsequently increased germination for sea lavender as well as for other halophytes. Seeds treated

with freshwater and direct sunlight and freshwater and shaded conditions have nearly 100% germination (Shumway and Bertness 1992). Shumway and Bertness (1992) noted that only 56% ± 5.5% of seeds germinate at a salinity of 30 ppt.

6.3 VEGETATIVE REPRODUCTION

Seedlings generated by sexual reproduction are rare. Asexual reproduction in sea lavender is from rhizomes and lateral branches from the woody caudex (Luteyn 1990). Luteyn (1990) reported that adjacent clones with different morphological features may spread laterally and coalesce.

7.0 INTERACTION WITH OTHER SPECIES

Competition and the harsh physical environment in salt marshes contribute to the zonation of the limited number of species that occur in this habitat. In the upper middle and higher elevations of salt marshes in Rhode Island, *L. carolinianum* is shaded by the taller and more robust *Iva frutescens* that result in 100% mortality of sea lavender (Hacker and Bertness 1999).

Physical conditions in the lower middle intertidal marsh are so harsh that competition plays a small role. Only the stress-tolerant *L. carolinianum* occurs in this zone (Hacker and Bertness 1999). In the upper middle intertidal zone, *L. carolinianum* survives equally well with or without the adjacent cohort *Juncus gerardii* (Hacker and Bertness 1999).

Stalter (1973) transplanted sea lavender and several other species into different microhabitats in a South Carolina salt marsh. He found 100% mortality of this species when it was transplanted into lower elevations of the high marsh and into the upper regions of the low marsh. After 6 months, Stalter et al. (2006) found that *L. carolinianum* covered with 15 to 20 cm of wrack died after 1 to 2 months of coverage.

7.1 FUNGI

Limonium carolinianum is virtually free of fungal pathogens. Rust lesions (*Uromyces limonii-caroliniani*) are often noted on older leaves, but the infection does not appear to be severe (Savile and Conners 1951). An alternate host has not been reported for this species.

8.0 RESPONSE TO WATER LEVELS

Sea lavender occurs in saturated soils. In South Carolina tidal marshes it is present in sites that are regularly inundated for up to 64 minutes during spring tides (Stalter 1968). Data are not available for the effects of depth and duration of flooding.

9.0 ECONOMIC IMPORTANCE

Imonium carolinianum has been suggested as a candidate species for re-vegetation efforts in dieback areas where crabs have denuded the vegetation (Smith et al. 2013). Stalter (1968) reported that sea lavender transplanted at the highest levels of a salt marsh had a 30% survival rate, but when clones were transplanted into the high low marsh survival rates are 100%. Hacker and Bertness (1999) found that sea lavender was the only halophyte species that naturally occurs in the lower middle intertidal zone in Rhode Island salt marshes.

9.1 WILDLIFE VALUES

Sea lavender is a major nectar source for rare maritime ringlet butterflies (*Coenonympha tullia nipisiquit*) in New Brunswick, Canada. The insects survive periodic tidal submergence and use the associated *Spartina patens* as a larval host (Sei and Porter, 2003).

Gedan et al. (2009) found that upland margins of the high marsh in Rhode Island where *Phragmites australis, I. frutescens, D. spicata, Salicornia europaea*, and *L. carolinianum* occur provide a habitat for meadow voles (*Microtus pennyslvanicus*) and white-footed mice (*Peromyscus leucopus*).

9.2 ORNAMENTAL VALUES

Inflorescences of the species are harvested for dried floral arrangements and crafts (Baltzer et al. 2002a; Richardson and King 2011). Baltzer et al. (2002a) noted that over-harvesting can seriously deplete populations.

9.3 MEDICINAL VALUES

Root extracts of sea lavender contain astringent tannins that have been used in folk medicine remedies. Dried and powdered roots have been used to treat diarrhea, dysentery, ulcers, hemorrhoids, and mouth ulcers (Anonymous 2015).

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Figure 1. *Limonium carolinianum* on the margin of a brackish marsh on South Padre Island, Texas.

Table 1. Species associated with *Limonium carolinianum* in Canada and U.S.A.

Species	NB	MA	RI	NY	NJ	VA	NC	GA	LA	TX
Atriplex patula			X							
Baccharis halimifolia					X	X				
Batis maritima								X		X
Blutaparon vermiculare										X
Borrichia frutescens						X	X	X	X	X
Cyperus grayii						X				
Distichlis littoralis										X
Distichlis spicata		X	X	X		X	X	X		X
Fimbristylis castanea						X				
Glaux maritima	X									
Iva frutescens		X	X	X		X			X	
Juncus gerardii		X	X	X	X					
Juncus roemerianus						X	X	X		
Kosteletskya virginica							X			
Lycium carolinianum										X
Morella cerifera						X				
Plantago juncoides		X								
Plantago maritima	X									
Pluchea purpurascens						X				
Sabatia stellaris						X				
Salicornia bigelovii		X						X	X	
Salicornia europaea		X	X	X		X				
Salicornia sp.					X					
Sarcocornia perennis							X			
Sarcocornia utahensis		X				X	X	X		X
Schoenoplectus robustus						X				
Solidago sempervirens	X		X		X					
Spartina alterniflora	X	X		X	X	X	X			
Spartina patens	X	X		X	X	X				
Spergularia marina							X			
Sporobolus virginicus										X
Suaeda linearis		X					X			X
Suaeda maritima				X						
Symphyotrichum tenuifolium			X	X		X	X		X	
Triglochin maritima	X									

NB = New Brunswick, Canada (Sei and Porter 2003); MA = Massachusetts (Rietsma, Monteiro, and Valiela 2011; Smith, Tyrrell, and Congretel 2013), RI = Rhode Island (Hacker and Bertness 1999), NY = New York (Stalter and Lamont 2002), NJ = New Jersey (Vivian-Smith and Stiles 1994), VA = Virginia (Harvill, 1965; Perry and Atkinson 1997), NC = North Carolina (Adams 1963; Oosting 1954; Wright, Edwards, and van de Plassche 2011), GA = Georgia (Antlfinger and Dunn 1983), LA = Louisiana (Proffitt et al. 2005), TX = Texas (Alexander and Dunton 2006; Drawe et al. 1981; Heinsch et al. 2004).

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