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Source: Journal of Coastal Research, 31(6) : 1512-1520

Published By: Coastal Education and Research Foundation

URL: https://doi.org/10.2112/JCOASTRES-D-14-00261.1

Journal of Coastal Research	31	6	1512–1520	Coconut Creek, Florida	November 2015

REVIEW ARTICLES

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The Biological Flora of Coastal Dunes and Wetlands: *Solidago sempervirens* L. and *Solidago sempervirens* L. subsp. *mexicana* (L.) Semple

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ABSTRACT

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Lonard, R.I.; Judd, F.W., and Stalter, R., 2015. The biological flora of coastal dunes and wetlands: *Solidago sempervirens* L. and *Solidago sempervirens* L. subsp. *mexicana* (L.) Semple. *Journal of Coastal Research,* 31(6), 1512–1520. Coconut Creek (Florida), ISSN 0749-0208.

Solidago sempervirens L. and *Solidago sempervirens* L. subsp. *mexicana* (L.) Semple are New World humid continental, temperate, subtropical, and tropical maritime taxa. Both taxa are long-lived perennials that occur in wet mineral sands and clay soils. Reproduction is primarily vegetative in stable sites. However, achene/seed production is prolific, and seed viability is high in either stable or disturbed sites. Also known as seaside goldenrod, both taxa occur in conditions ranging from freshwater to salinity conditions of 40 parts per thousand. Seeds and seedlings do not tolerate excessive burial, but high levels of sand deposition are associated with plant vigor in mature clones. Optimal growth for both taxa occurs in habitats with increasing distance from the water table.

ADDITIONAL INDEX WORDS: *Seaside goldenrod, morphology, population biology, habitats, communities, competition, reproduction.*

INTRODUCTION

The perennial genus *Solidago* (Asteraceae) includes about 80 species in North America and several additional species in South America, the Azores, and Eurasia (Mabberley, 1997; Semple *et al*., 1984). The genus is represented in a wide variety of habitats including grasslands and disturbed sites. Some species have been introduced into Europe as ornamentals. *Solidago sempervirens* (seaside goldenrod) is a long-lived perennial that occurs on dunes, in brackish marshes, in grasslands, and in disturbed sites in the coastal landscape. Seaside goldenrod is occasionally a codominant species associated with a perennial grass *Ammophila breviligulata* in dunes in the coastal landscape of the northeastern Atlantic coast of North America. Herein, we review the biology of this important coastal species.

TAXONOMY AND VARIATION

Solidago sempervirens L. is a member of the family Asteraceae (Compositae), and is included in the tribe Astereae. A synonym and rejected name for *S. sempervirens* subsp. *sempervirens* is *Aster sempervirens* (L.) Kuntze. Common names include seaside goldenrod and verge d'or toujours verte. Synonyms for *S. sempervirens* L. subsp. *mexicana* (L.) Semple are *A. mexicanus* (L.) Kuntze, *S. sempervirens* var. *mexicana* (L.) Fern., *S. limonifolia* Pers., *S. laevigata* Ait., and *S. mexicana* L. Seaside goldenrod, saltmarsh goldenrod, and small-headed seaside goldenrod are common names for the taxon.

Taxonomic Description

The following taxonomic description has been derived from Correll and Correll (1972), Fernald (1950), Flora of North America Editorial Committee (2006), Gandhi and Thomas, (1989), Gleason and Cronquist (1963), Lehman, O'Brien, and White (2005), and Radford, Ahles, and Bell (1968).

Seeds

A single seed lacking endosperm is borne in an indehiscent cypsela (achene). Many authors use the term "seed" to designate the seed and the enveloping mature ovary wall.

Seedling Morphology

Seaside goldenrod seeds often germinate in late fall and winter (Orava and Drake, 1997). Seedling recruitment is rare and is limited to open spaces or blowout gaps (Lee, 1993). Leaves, 55 days after germination, are simple, alternately arranged, and gradually tapered and winged to the petiole (Goodwin, 1937). Blades are linear, mostly glabrous, and have a net venation pattern with inconspicuous venation (Goodwin, 1937).

DOI: 10.2112/JCOASTRES-D-14-00261.1 received 24 December 2014; accepted in revision 19 January 2015; corrected proofs received 19 February 2015; published pre-print online 23 March 2015.

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Figure 1. *Solidago sempervirens* subsp. *mexicana* in cultivation with monarch butterflies in Brownsville, Texas. *Solidago sempervirens* subsp. *sempervirens* (not shown) is morphologically similar at maturity. It has larger heads and broader lower leaves.

Shoot Morphology

Plants are perennial, 0.4 to 2.5 m tall with short, persistent woody bases (caudices). Stems are 1 to 20, unbranched, erect or ascending, and are usually glabrous. Leaves are simple, alternate, somewhat succulent and glabrous, and the margins are entire. Blades are narrowly ovate to oblanceolate, 10 to 40 cm long and 1 to 7 cm wide, tapered to elongate, and with winged petioles. Blades near the stem apex are numerous and sessile. A basal rosette of leaves is conspicuous.

Inflorescence

The inflorescence consists of a series of heads (capitula). Heads are arranged in paniculate, corymbiform, or recurved-secund branching patterns. Peduncles are glabrous or slightly pubescent and 2 to 3 mm long. Involucres are 3 to 7 mm long, the phyllaries are imbricate, acute, or acuminate, and ciliate on the margins. The heads are radiate. Ray florets are pistillate, yellow, 8 to 17 in number, 5 to 6.5 mm long, and about 0.5 mm wide. Disc florets are bisexual, yellow, 10 to 22 in number, and are 3 to 5.5 mm long, and the lobes are 0.5 to 1.0 mm long. The receptacle is naked.

Fruits

The achenes are obconic, 1 to 3.5 mm long, and strigose pubescent. The pappus is about 3.5 to 5.5 mm long and club shaped.

Variability

Two closely related subspecies of *S. sempervirens* are recognized in North America, subsp. *sempervirens* and subsp. *mexicana* (Semple, 2003). Subspecies *sempervirens* is a robust plant with lower leaves 2 to 7 cm wide. The involucre is 4 to 7 mm long. The receptacle has 12 to 17 ray florets and 17 to 22 disc florets. Subspecies *mexicana* is a more slender plant with lower leaves 1 to 3 cm wide. The involucre is 3 to 4.5 mm long. The receptacle contains 7 to 11 ray florets and 10 to 16 disc florets (Figure 1).

Semple *et al*. (1984) recognized *S. sempervirens* var. *azorica* (Hochstetter *ex* Seubert) H. St. John, which is naturalized or adventive in the Azores. A cultivated variety has been identified as *S. sempervirens* var. *viminea* (Ait.) Gray.

Solidago sempervirens is known to hybridize in North America as follows: *S. sempervirens* × *S. rugosa* Mill. = *Solidago* × *asperula* Desf.), and *S. sempervirens* × *S. canadensis* L. = *Solidago* × *erskinei* Boivín (Goodwin, 1937; NYFA, 2014). A rare pale yellow color form was described by Harris (1958).

Chromosome Number

Solidago sempervirens has a chromosome number of $2n = 18$ with no variation in chromosome numbers across the range of the species and its varieties or subspecies (Goodwin, 1944; Innes and Hermanutz, 1988; Radford, Ahles, and Bell, 1968; Semple *et al*., 1984).

GEOGRAPHIC DISTRIBUTION

Solidago sempervirens has a broad distributional range from Newfoundland and Labrador in Canada, through the Atlantic coastal states of the United States, to the West Indies and Central America (Flora of North America Editorial Committee, 2006).The species has been introduced inland adjacent to saline sites in the last 60 years along the shorelines of the Great Lakes including Ontario, Canada, Michigan, Ohio, Illinois, and Indiana (Flora North America Editorial Committee, 2006; Wieczorek and Geber, 2002).

Subspecies *sempervirens* has a northern distributional range from the Canadian provinces southward to New York, southeastern Massachusetts, and locally to northern Virginia (Lamont, 1994). Subspecies *mexicana* has a southern distributional pattern that ranges from Central America, southern Mexico, the northern West Indies, and from Texas to Florida. It also occurs in Delaware and locally from southern New York and southeastern Massachusetts (Flora of North America Editorial Committee, 2006; Lamont, 1994). Therefore, the distributional range of the two subspecies overlaps in coastal sites of Virginia to New York and southeastern Massachusetts. Subspecies *mexicana* has been reported inland in south-central Texas (Fleenor and Taber, 2009). Table 1 includes a summary of the geographical distribution patterns and morphological variability of the closely related subspecies *sempervirens* and subspecies *mexicana*.

RANGE OF HABITATS

Solidago sempervirens subsp. *sempervirens* and *S. sempervirens* subsp. *mexicana* occur in similar habitats in the broad geographical distribution of the species. Oosting and Billings (1942) reported that this species is found with greater cover values with increasing distance from the water table.

Table 1. *Comparison of* Solidago sempervirens *subsp.* sempervirens *and* Solidago sempervirens *subsp.* mexicana *(adapted from Flora of North America, 2006 and Lamont, 1994).*

	subsp. *sempervirens*	subsp. *mexicana*
Distribution	Canadian maritime provinces; locally to northern Virginia	Mostly southern, but locally in New York and Massachusetts, mid-Atlantic, SE United States, West Indies, Mexico, Central America, Florida to Texas
Seedlings	Leaves linear (see Goodwin, 1937). Abundant in blowouts	Leaves linear, but seldom observed in dense vegetation
Growth Habit	Robust	Usually slender, not as robust
Lower Leaves	2 to 7 cm wide	1 to 3 cm wide
Involucre Height	4 to 7 mm	3 to 4.5 mm
Ray Florets	12 to 17	7 to 11
Disc Florets	17 to 22	10 to 16.

Subspecies *sempervirens* is reported on embryo dunes, foredunes, dune ridges, in slightly accreting sites close to the beach, in swales, in coastal grasslands, on margins of estuaries, on upper margins of salt marshes, in brackish marshes, and in freshwater wetlands (Buchsbaum *et al.*, 2006; Clampitt, 1991; Crain, Albertson, and Bertness, 2008; Crain *et al.*, 2004; Disraeli, 1984; Dunlop and Crow, 1985; Godfrey and Wooten, 1981; Innes and Hermanutz, 1988; Klotz, 1986; Lamont and Stalter, 1991; Lee, 1993, 1995; McAvoy and Bennett, 2001; Stalter, 1974; Wunderlin and Hansen, 2001). It also occurs in disturbed sites including drift lines, overwashes, blowouts, roadside margins that have been treated with deicing agents, sites adjacent to inland brine wells, and even on an abandoned elevated rail line in New York City (Hill, 1986; Innes and Hermanutz, 1988; Rhoads and Block, 2007; Stalter, 2004; Swink and Wilhelm, 1994).

Habitats and topographic facets where subspecies *mexicana* occurs in more temperate, subtropical, and tropical regions include upper beaches; dunes; swales; upper, rarely flooded salt marshes; brackish marshes; freshwater marshes; and disturbed sites (Anderson and Alexander, 1985; Eleuterius, 1972; Eleuterius and McDaniel, 1978; Fleenor and Taber, 2009; Lehman, O'Brien, and White, 2005; Lonard *et al.*, 1991, 1999; McAvoy and Bennett, 2001; Oosting and Billings, 1942; Radford, Ahles, and Bell, 1968; Stalter, 1974, 1993; Stalter and Lamont, 1993, 1997; Stutzenbaker, 1999).

Substrate Characteristics

Subspecies *mexicana* typically occurs in low-mineral wet sands and clay soils, and salinity values usually range from 0 to 10 parts per thousand (ppt) in the Upper Gulf of Mexico coastal zone (Stutzenbaker, 1999). In South Carolina, Stalter (1968) reported that this subspecies usually occurs about 1.7 m above mean sea level, and salinity values range from 10 to 40 ppt. He noted that pH values range from 6.0 to 7.5. In southern Florida, Stalter *et al.* (1999) indicated that soil salinities ranged from 25.4 to 39.9 ppt. On South Padre Island, Texas, Judd, Lonard, and Sides (1977) noted that the depth to the water table in dune depressions where subspecies *mexicana* occurs is 14 to 56 cm, and 85.9% of sand particles range from 0.18 to 0.25 mm.

Climatic Requirements

Solidago sempervirens, including its two subspecies, occurs over climatic conditions ranging from a tropical to a humid continental (temperate oceanic) climate in Newfoundland where winter-extreme low temperatures may range from –19°C to –32°C (Brown and Cooprider, 2010; Stalter and Lamont, 2006). The species extends from about 18°N latitude in southern Tabasco, Mexico, to about 47°N latitude in southern Newfoundland. In the broad spectrum of climatic zones where this species occurs, plants survive unfavorable conditions through a compact rhizome system and by the production of freeze-resistant achenes. In more temperate, subtropical, and tropical regions plants overwinter as basal rosettes (Cartica and Quinn, 1982; Lee, 1995).

PLANT COMMUNITIES

Plant communities on sandy coastlines where this species occurs are referred to by inconsistently used terminology. Most workers identify plant communities according to the topographic facets in which *S. sempervirens* occurs. For example, Judd, Lonard, and Sides (1977) associated plant communities on South Padre Island, Texas with topographic facets. They noted that subspecies *mexicana* typically occurs in swales in the secondary dunes and vegetated flats zone. Lee (1995) indicated that subspecies *sempervirens* is an important taxon in the primary dunes in New Jersey where the perennial grass *Ammophila breviligulata* is the dominant species.

Stalter (1993) and Sutton, Meyer, and Stalter (1990) placed seaside goldenrod in dune plant communities in New Hampshire and New Jersey, and Lamont and Stalter (1991) and Stalter and Lamont (2000, 2002) stated that *S. sempervirens* occurs in maritime beach and swale communities in New York and Virginia.

A few workers have named plant communities according to the dominant species in the community. A marram (*A. breviligulata*)–forb grassland community has been described in Nova Scotia (Catling, Freedman, and Lucas, 1984), and Martin (1959) described a dune grass (*A. breviligulata*)–beach heather (*Hudsonia tomentosa*)–low thicket mixture in New Jersey where *S. sempervirens* is a conspicuous species. Table 2 includes species associated with *S. sempervirens* in selected sites without designations of topographic zones, habitats, or plant communities.

PHYSIOLOGICAL ECOLOGY

Limited physiological data are available for *S. sempervirens*. It is a somewhat succulent C_3 plant in its manner of carbon fixation in the light-independent reactions of photosynthesis (Wozniak *et al.*, 2006). Plants are salt tolerant in the harsh coastal environment where salt spray is usually deposited

Table 2. *Representative species associated with* Solidago sempervirens *in the New World*.

Species	NFL	NSO	MAS	RHI	NHS	NYK	NJY	VIR	TEX
Achillea lanulosa		X							
Agrostis stolonifera				X					
Ammophila breviligulata	X	X	X		X	X	X	X	
Andropogon glomeratus									X
Arenaria peploides			X						
Argentina anseria			X	X					
Aristida tuberculosa					X				
Artemisia stelleriana	X					X	X		
Atriplex arenaria					X				
Atriplex patula var. *hastata*			X	X		X			
Baccharis halimifolia						X	X		X
Bacopa monnieri									X
Cakile edentula			X			X	X	X	
Carex kobomugi							X		
Carex silicea						X			
Cenchrus tribuloides						X		X	
Chamaesyce polygonifolia			X			X	X	X	
Chrysopsis falcata			X						
Cyperus filiculmis					X				
Cyperus grayi					X		X		
Cyperus lupulinus					X				
Danthonia spicata					X				
Digitaria sanguinalis						X			
Distichlis spicata			X	X					
Eleocharis sp.				X					
Euthamia graminifolia						X			
Festuca rubra	X			X					
Fuirena simplex									X
Heterotheca subaxillaris									X
Honkenya peploides subsp. *robusta*							X		
Hudsonia tomentosa	X		X		X		X		
Hydrocotyle bonariensis									X
Ilex opaca							X		
Iva frutescens			X			X			
Juncus gerardii			X	X		X			
Juniperus virginiana							X		
Lathyrus japonicus	X	X	X		X	X	X		
Lechea maritima					X		X	X	
Leymus mollis	X								
Mollugo verticillata						X			
Monarda punctata								X	
Morella pensylvanica			X			X	X		
Panicum amarum var. *amarulum*									X
Panicum amarum var. *amarum*									X
Panicum virgatum				X		X			
Parthenocissus quinquefolia							X		
Phragmites australis			X	X		X			
Pinus rigida							X		
Pluchea purpurascens				X					
Polygonella articulata					X				
Prunus serotina							X		
Rosa rugosa			X						
Rumex crispus				X					
Rhynchospora colorata									X
Salsola kali						X	X	X	
Sanguisorba canadensis						X			
Schizachyrium scoparium					X				
Schoenoplectus pungens						X			X
Schoenoplectus robustus				X					
Smilax rotundifolia							X		
Spartina patens			X	X		X		X	X
Symphyotrichum tenuifolius				X					
Toxicodendron radicans			X			X	X		
Triglochin maritimum			X						
Triplasis purpurea						X			
Typha angustifolia			X	X					
Uniola paniculata								X	

Table 2. *Continued.*

Species	NFL	NSO	MAS	RHI	NHS	NYK	NJY	VIR	TEX
Xanthium echinatum			X				X		
Xanthium strumarium var. *canadense*						X			

NFL = Newfoundland (Thannheiser, 1984); NSO = Nova Scotia (Catling, Freedman, and Lucas, 1984); MAS = Massachusetts (Arnold, Nisbet, and Veit, 2011; Disraeli, 1984; Minchinton, Simpson, and Bertness, 2006; Shumway, 2000; Shumway and Banks, 2001); RHI = Rhode Island (Gedan, Crain, and Bertness, 2009; Crain *et al*., 2004); NHS = New Hampshire (Dunlop and Crow, 1985); NYK = New York (Cheplick and Aliotta, 2009; Lamont, 1994; Stalter and Lamont, 2002); NJY = New Jersey (Cartica and Quinn, 1982; Lee, 1995; Martin, 1959; Stalter, 1993; Sutton, Meyer, and Stalter, 1990); VIR = Virginia (Klotz, 1986; Stalter and Lamont, 2000); TEX = Texas (Lonard, personal observations at Galveston Island, 2014; Lonard *et al*., 1999).

within 500 m of the high-tide mark (Ehrenfeld, 1990). Martin (1959) found no foliar damage of mature plants after 15 consecutive days of watering with undiluted seawater. Brauer and Geber (2002) indicated that this species does not have a physiological dependence on salt. Cartica and Quinn (1980) found that leaf thickness of dune colonies is significantly greater than in populations protected in the lee of the dune complex. No significant differences were noted in stomatal and foliar pubescence in either population. Salts are apparently sequestered in vacuoles (Cartica and Quinn, 1980). Leaves and stems have a low silica content ranging from 0.06% to 0.22%, and ash contents range from about 6.8% to 9.6% in leaves and stems (Lanning and Eleuterius, 1983).

Phenology

Flowering phenophases for both subspecies vary along a N-S geographical gradient (Goodwin, 1944). In New Jersey, Cartica and Quinn (1982) noted that aerial shoots of subspecies *sempervirens* die in the fall and survive winter conditions in a basal rosette. Fernald (1950), Hill (1986), Lee (1995), and Rhoads and Block (2007) stated that flowering occurs from late July to November. Achenes are mature in late November, and the aerodynamic achenes are dispersed through late April. Peak flowering phenophases correspond to short-day photoperiods (Brauer and Geber, 2002).

Flowering phenophases for subspecies *mexicana* in warm temperate and subtropical regions are usually later in season. Anderson and Alexander (1985) and Eleuterius and Caldwell (1984) reported flowering in October and November in Florida and Mississippi, respectively, and Lonard and Judd (1989) noted that this subspecies is in flower and fruit throughout the calendar year on South Padre Island, Texas.

POPULATION BIOLOGY

Solidago sempervirens is a long-lived perennial with short clustered rhizomes. It survives harsh winter conditions as a basal rosette throughout most of its range. Older clones usually produce 5 to 20 densely arranged rosettes, but up to 100 rosettes have been recorded for long-lived clones (Lee, 1995).

Population Dynamics

Natural disturbance is an important factor affecting population dynamics in coastal ecosystems. Seaside goldenrod is referred to as a gap species in blowouts in the dune complex of New Jersey, but it also occurs in immature grasslands and as well as in well-established grassland zones (Lee, 1993). Blowouts and transition zones are sites where seed (achene) rain produces an extensive achene shadow in exposed gaps in the plant cover. Lee (1993) noted that achenes fall to the ground within 10 m outside blowouts. Lower cover values of plants were found in undisturbed sites due to lack of achene dispersal from blowouts.

REPRODUCTION

Solidago sempervirens reproduces sexually, is self-incompatible, and depends on insects for pollination (Brauer and Geber, 2002; Cartica and Quinn, 1980). Cartica and Quinn (1982) reported that 3.9% to 28.3% of aboveground biomass is directed toward sexual reproduction. Pollinators include honeybees and butterflies (Richardson and King, 2011; Stutzenbaker, 1999).

Achene (Seed) Production and Viability

Achene production, equated with seed production, is extraordinary. Lee (1993) reported a seed rain in blowouts on dunes in New Jersey as 30,700 ±1000 seeds/m^2. Lee (1995) found that 76% to 98% of subspecies *sempervirens* seeds germinated from populations sampled in New Jersey. Stalter (1968) and Stalter and Batson (1973) estimated that 67% are viable in populations of subspecies *mexicana* in South Carolina.

Dispersal

Solidago sempervirens is a widely distributed New World humid continental, temperate, subtropical, and tropical maritime species. Ridley (1930) estimated that the plumed pappus of the achenes allows aerodynamic propagules to travel an estimated 2200 km to oceanic islands. Orava and Drake (1997) also indicated that this species is adapted to oceanic dispersal with subsequent establishment in saline sites.

Minchinton, Simpson, and Bertness (2006) reported that achenes float. Ehrenfeld (1990) stated that subspecies *mexicana* achenes may be dispersed by ghost crabs (*Ocypode albicans*) and buried in their burrows. Dispersal by birds is also possible (Lonard and Judd, 1980).

Achene Size and Seed Bank

Achene lengths of subspecies *mexicana* range from 2.2 to 3.5 mm (Orava and Drake, 1997), and achenes weigh 0.79 mg for subspecies *sempervirens* (Goodwin, 1937). Lee (1993) reported that the seed bank for subspecies *sempervirens* is negligible and 0 to 57 seeds/m^2 were found in sample plots. Most achenes fell from inflorescences between late November and late April on New Jersey coastal dunes (Lee, 1993). Crain, Albertson, and Bertness (2008) found 26 to 38 achenes/m^2 but found no germinating seeds in the substrate from 0.25-m^2 plots in Rhode Island brackish marshes.

Germination Ecology and Establishment of Seedlings

Optimal germination of subspecies *sempervirens* seeds is promoted by freshwater and sunlight and is inhibited by high salinities and shading (Shumway and Bertness, 1992). Complex dormancy mechanisms promote germination in subspecies *mexicana* after cold stratification and exposure to light (van der Valk, 1974). van der Valk (1974) noted that few seedlings of subspecies *mexicana* were found on the foredunes of the North Carolina shoreline.

Seeds of subspecies *sempervirens* exposed to seawater at 30 ppt for 1 to 10 days, washed, and placed in freshwater had 45% to 60% germination success, but seeds exposed to seawater 6 to 10 days germinated more rapidly than seeds exposed for shorter periods and subsequently placed in freshwater (Orava and Drake, 1997). Seeds exposed only to a freshwater treatment germinated at a rate eight times higher than those exposed to seawater (Orava and Drake, 1997).

Vegetative Reproduction

Reproduction in subspecies *mexicana* in relatively stable sites on North Carolina foredunes is primarily vegetative (van der Valk, 1974). However, Lee (1995) stated that perennial clones of subspecies *sempervirens* produce numerous compact rosettes on dunes in New Jersey, but vegetative reproduction by compact rhizomes is limited.

GEOMORPHOLOGICAL INTERACTIONS

Solidago sempervirens plays a minor role in coastal geomorphology. Sheahan (2012) suggested that this species could play a role in erosion control and dune stabilization. Courtmanche, Hester, and Mendelssohn (1999) found that subspecies *mexicana* was eliminated by overwash of a hurricane. Plants were absent 1 year after the storm but were found in low frequency the following year.

Response to Burial

Solidago sempervirens seeds and seedlings do not tolerate excessive burial (Baptista and Shumway, 1998). van der Valk (1974) indicated that seedlings are unable to survive under more than 5 cm of sand. However, high levels of sand deposition are associated with plant vigor in mature clones (Lee, 1995). van der Valk (1974) reported that mature plants survived 56 cm of sand deposition.

INTERACTION WITH OTHER SPECIES

A symbiotic relationship exists between arbuscular mycorrhizal fungi (AMF) and *S. sempervirens*. AMF promote absorption of water and minerals from the substrate. At least six species of AMF are found in the rhizosphere of seaside goldenrod on the coastal dune complex of Rhode Island (Koske and Halvorson, 1981). AMF were noted only on small lateral roots and ranged from 10% to 80% for individual plants (Koske and Halvorson, 1981).

Predation

Rabbits and white-tailed deer occasionally browse on juvenile *S. sempervirens* plants (Sheahan, 2012). Insect predators may cause extensive defoliation and include beetles (*Trirhabda borealis*) and seed moths (*Coleophora triplicus*) (Ancheta, Heard, and Lyons, 2010). Ho and Pennings (2013) and Salgado and Pennings (2005) studied the food habits of grasshoppers (*Paroxya clavuliger*) and aphids (*Uroleucon pielou*) that feed on *S. sempervirens* populations in northern and southern latitudes. High-latitude populations of seaside goldenrod have a higher nitrogen content and are more palatable to grasshoppers than plants native to southern latitudes (Salgado and Pennings, 2005). Ho and Pennings (2013) reached a similar conclusion in a feeding study of aphids. High-latitude plants have higher food quality than lower-latitude plants, and insect predators are larger at high altitudes.

Competition and Facilitation

Solidago sempervirens is often regarded as a gap specialist because it occurs in blowouts in dune systems dominated by the perennial grass *A. breviligulata* (Lee, 1995). Blowouts may bury *A. breviligulata* clones and this enhances cover and aboveground biomass of *S. sempervirens* (Lee, 1995). Lee (1995) stated that *S. sempervirens*, an inferior competitor with *A. breviligulata*, can coexist in an environment dominated by the superior competitor.

Brauer and Geber (2002) found that seaside goldenrod has low competitive ability in a nonsaline landscape. Physical factors including human-induced changes in soil salinity are correlated with an increase in abundance of seaside goldenrod (Frankowski *et al*., 1977).

In Massachusetts, Minchinton, Simpson, and Bertness (2006) found that the aggressive dominant, *Phragmites australis,* excluded *S. sempervirens* and other species by competitive interactions at the highest elevations of brackish marshes. They noted that the presence of *P. australis* litter has a negative impact on the colonization of seaside goldenrod and other species.

In a pioneer zone of blowouts and other disturbed sites, the perennial *S. sempervirens* has negative impacts on smaller annuals (Cheplick and Aliotta, 2009). Weedy grasses including *Cenchrus tribuloides*, *Digitaria sanguinalis*, *Triplasis purpurea*, and the mat-forming forb *Mollugo verticillata* show significant reductions in vegetative cover in sites adjacent to established populations of *S. sempervirens*. A taller species, *C. tribuloides*, is significantly reduced when it occurs in proximity to seaside goldenrod (Cheplick and Aliotta, 2009).

Facilitation or positive interactions occur between the nitrogen-fixing shrub *Morella pensylvanica* and *S. sempervirens* and *A. breviligulata* on the Massachusetts coastline (Shumway, 2000). *Solidago sempervirens* plants growing under the canopy of *M. pensylvanica* are more robust, are more likely to flower, have a higher photosynthetic efficiency, and have a higher concentration of nitrates than plants outside the canopy (Shumway, 2000). The environment below the canopy has lower soil temperatures and higher soil nitrogen levels. Therefore, growth, reproduction, and recruitment of *S. sempervirens* are facilitated.

In a study of the interactions of competition and physical environmental factors, Hacker and Bertness (1999) found that physical conditions in the lower middle salt marshes of Rhode Island are so harsh as to eliminate interactions of *S. sempervirens* with other species. All *S. sempervirens* clones transplanted into this habitat died with or without the co-occurrence of the dominant species *Juncus gerardii*. In the upper middle marsh *J. gerardii* facilitates the growth and reproduction of *S. sempervirens*. Therefore, *S. sempervirens* is capable of competitive tolerance in the higher elevations of a salt marsh (Hacker and Bertness, 1999).

RESPONSE TO WATER LEVELS

Oosting and Billings (1942) indicated that optimal growth of *S. sempervirens* occurs in habitats with increasing distance from the water table. *Solidago sempervirens* is a dune species in Massachusetts and grows poorly in inundated conditions (Shumway and Banks, 2001). Plants are abundant in dunes and are rare in *J. gerardii* depressions and in cranberry swales (Shumway and Banks, 2001).

ECOMONIC IMPORTANCE

Solidago sempervirens has limited value in coastal protection. It is common in protective foredunes in New Jersey, but cover values only range from 1.4% to 2.3% of total foliar cover (Nordstrom *et al.*, 2007). Seaside goldenrod is subject to moderate damage due to pedestrian traffic in coastal dune habitats in Massachusetts (McDonnell, 1981).

Wildlife Values

Seaside goldenrod has several wildlife values. It serves as a source of nectar for bees and migrating butterflies (Stutzenbaker, 1999), and has been recommended for cultivation in butterfly gardens (Richardson and King, 2011).

Plant communities where *S. sempervirens* occurs are important concealment and nesting sites for birds. Craik and Titman (2009) found that red-breasted mergansers (*Mergus serrator*) and the common tern (*Sterna hirundo*) nest in this habitat in New Brunswick, Canada. In New York, Safina and Burger (1983) found that *Solidago sempervirens* and other species provide nesting habitat for willets (*Catoptrophorus semipalmatus*), killdeer (*Chradrus vociferous*), piping plovers (*C. melodus*), black skimmers *(Rynchops niger*), common terns, and roseate terns (*Sterna dougalli*).

Medicinal Uses

Folk literature has some reports of medicinal uses for various species of *Solidago*, but none is listed for *S. sempervirens* and its subspecies. All species of *Solidago* are insect pollinated. Pollen of the genus *Solidago* does not cause respiratory allergies.

Potential Biological Control Agents

Cheplick and Aliota (2009) found that densities and plant heights of weedy, annual pioneer grasses shaded by *S. sempervirens* were significantly reduced. *Triplasis purpurea, Cenchrus tribuloides,* and *D. sanguinalis* were affected, but the annual, prostrate, broad-leaved dicot, *Mollugo verticillata*, was not. A diterpene, sempervirenic acid, has been isolated from *S. sempervirens* (Purushothaman *et al.*, 1983). Terpenes are unsaturated hydrocarbons in most oleoresins and essential oils in plants. Exudates of sempervirenic acid from shoots, roots, and rhizomes of *S. sempervirens* clones may be involved in allelopathic effects on low-growing annual grasses. However, this hypothesis has not been tested.

ACKNOWLEDGMENTS

We thank Glennis and David Lonard for assistance in the preparation of the manuscript. Dr. Alfred Richardson and Ken King provided digital images of *Solidago sempervirens* subsp. *mexicanus*. Dr. Eric Lamont kindly verified our identification of *S. semperivirens*. We are grateful to the anonymous reviewers who helped improve the manuscript.

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