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The Biological Flora of Coastal Dunes and Wetlands. *Sesuvium portulacastrum* (L.) L.

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ABSTRACT

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Sesuvium portulacastrum (L.) L. (sea purslane, cenicilla) is a pantropical, perennial, trailing herb (Aizoaceae) with pink-purple or occasionally white flowers that grows on coastal beaches of five continents and many islands. Herein we present a review of the biology of *S. portulacastrum.* It is an important pioneer species on sandy beaches in the subtropics and tropics, where its stoloniferous, mat-forming growth habit promotes embryonic dune formation in belts parallel to the shoreline. Colonies act as barriers to intercept and hold water and wind transported sand. *Sesuvium portulacastrum*'s success as a colonizing species is related, in large part, to its ability to be propagated by vegetative fragments and the tolerance of these fragments to salt water. Indeed, it has apparently reached nearly all locations in which it occurs by drifting segments in the sea. Other factors contributing to its success as a pioneer species include its tolerance of salt spray, sand scouring and burial, high substrate temperatures and low levels of soil nutrients. Its northern and southern distribution limits appear to be limited by the frequency, duration and severity of freezing temperatures.

ADDITIONAL INDEX WORDS: *Sea purslane, variation, morphology, habitats, communities, physiology, population ecology, reproduction, geomorphological interactions, economic importance.*

I. INTRODUCTION

Sesuvium portulacastrum (L.) L. (sea purslane) is a pantropical, perennial, succulent, trailing herb with apetalous, pink-purple flowers. It is frequently a pioneer species in the backshore zone of coastal beaches where sand movements are influenced by prevailing winds near the berm crest (Judd *et al.,* 1977; Johnson, 1977). However, *S. portulacastrum* has also been reported on rocky shores, shell beaches and coral cays as well as on the margins of salt marshes, tidal flats, mangrove swamps, and estuaries (Lloyd and Tracy, 1901; Whistler, 1980; Lacerda, 1982; Joshi and Bhosale, 1982; Allaway *et al.,* 1984). The species typically traps sand and initiates the formation of small, widely-spaced, embryonic dunes that are parallel to the shoreline (Judd *et al.,* 1977; Johnson, 1977). Many aspects of the biology of *S. portulacastrum* remain unknown. Herein, we review the biology of this important pioneer species.

II. TAXONOMY AND VARIATION

(a) Name:

Sesuvium portulacastrum (L.) L., family Aizoaceae. Synonyms: *Portulaca portulacastrum* L., *S. revolutifolium* Ortega, *S. ortegae* Spreng., *S. pedunculatum* Pers., *S. sessile* Pers., *S. sessiliflorum* Domb. *ex* Rohrb., *Halimus portulacastrum* O. Kuntze (Nevling, 1961; Bogle, 1970; Rico-Gray, 1990), sea purslane, cenicilla, cenicienta, ts'a'ay, káan, ts'in kaan, xaw tsikin, xukul, pico real, verdolaga xukul, verdolaga de costa, verdolaga de la playa, kihikihimaka, 'akulikuli, chara, pourpier bord de mer.

(b) Taxonomic Description

The following account has been assembled from Nevling, 1961; Radford *et al.,* 1968; Bogle, 1970; Correll and Johnston, 1970; Correll and Correll, 1972; Rico-Gray, 1990.

(i) Seed Morphology

The numerous stalked seeds (ca. 50 per capsule) are black, smooth and lustrous, 1.2–1.5 mm long.

(ii) Seedling Morphology

Each of the pair of cotyledons is fleshy and oblong. Seedlings and juveniles strongly resemble mature plants. The foliage leaves are opposite, oblong, or oblanceolate, entire, and rounded or acute at the apex.

(iii) Shoot Morphology

Trailing or suberect glabrous herbs with terete, succulent, green, pink or reddish stems diffusely branched, often forming mats or patches 2 m or more in diameter. Petioles nearly ensheathing stems, 8–12 mm long with a winged hyaline margin, $\frac{1}{2}$–$\frac{2}{3}$ its length, exstipulate. Leaves simple, opposite, blades glabrous, succulent, 2–6 cm long with minute epidermal papillae, 3–10 mm wide, oblong-oblanceolate, elliptic-

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ovate, or spatulate, often vertically oriented, obtuse or acute at the apex; midrib and lateral vascular bundles not visible (Figure 1).

(iv) Root Morphology

Sesuvium portulacastrum has a tap root that extends 15–30 cm into the soil. Numerous smaller adventitious roots develop from the nodes, but typically extend only 2–6 cm into the soil (LACERDA *et al.*, 1983; LONARD and JUDD, *personal observations*).

(v) Inflorescence

Sesuvium portulacastrum flowers are solitary and axillary; pedicels 0.5–2 cm long, firm, terete, glabrous. Calyx tube turbinate, adnate below the ovary. Sepals 5, actinomorphic, petaloid, pink-purple or white within, green externally, 7–10 mm long and up to 6 mm wide, margins hyaline, hooded and bearing a horn-like appendage up to 2 mm long dorsally near the apex. Petals absent. Stamens numerous (ca. 50), perigynous; filaments pink or reddish-purple, 4–7 mm long; anthers reddish-purple to brown at maturity, oblong-elliptic up to 1 mm long. Pollen 20–40 μm long, tricolpate, stenopalynous (LUDLOW-WIECHERS, 1982). Ovary semi-superior, glabrous, ovoid-globose, greenish-red, 3–5 mm long; stigmas 3–5, styles numerous, 6–7 mm long, distinct above, but connate near the base.

(vi) Fruits

The circumscissile capsule is firmly enclosed by the calyx until maturity. It is red, membranous below and cartilaginous above, glabrous, conic, 7–10 mm long, and 5–6 mm in diameter; locules 3–5; placentation axile.

(c) Variability

(i) Varieties

Sesuvium portulacastrum (L.) L. var. *tawandanum* Nakajima, endemic to Okinawa, has been described (NAKAJIMA, 1970). It differs from the typical variety by having slightly shorter leaves (1.5–4.0 cm long), and flowers 8–10 mm in diameter.

(ii) Ecotypes

In the Bay of Bengal (India) an ecotype of *S. portulacastrum* with a "globular elongate" leaf type has been reported that has a chromosome number of $2n = 36$ (SUBRAMANIAN, 1988). An ecotype from the Western Pacific has white flowers and smaller sepals, 5–7 mm long (WHISTLER, 1980). Only pink or pinkish-purple sepals have been observed from the Gulf of Mexico and Atlantic coast.

(iii) Chromosome Number

A chromosome number of $2n = 40$ was reported for the "oblong-oblanceolate" leaved ecotype (SUBRAMANIAN, 1988), but RAGHAVAN and SRINIVASHAN (1940) and SHARMA and BHATTACHARRYA (1956) reported chromosome numbers of $2n = 48$ and $2n = 36$, respectively, for "globular elongate" leaved plants. Conversely, DI FULVIO (1967) and BOGLE (1970) found a chromosome number of $2n = 16$ from plants in the Southeastern U.S.A. Apparently, a polyploid and/or aneuploid series occurs in *S. portulacastrum* with base numbers of 8 and 9.

III. GEOGRAPHICAL DISTRIBUTION

Sesuvium portulacastrum occurs on the coastlines of five continents (Figure 2). It is present on many tropical islands as well as on subtropical shores (FOSBERG, 1953; BRITTON and MILLSPAUGH, 1962; JOHNSON, 1977; WICKENS, 1979; SAUER, 1982; DOING, 1985; DE SLOOVER, 1992; TAYLOR, 1992; THOMAS, 1993). CORRELL and JOHNSTON (1970) and CORRELL and CORRELL (1972) report that the species is rarely found inland in Texas.

IV. RANGE OF HABITATS

(a) Zone of Occurrence

Sesuvium portulacastrum is widely distributed as a pioneer strand species on tropical and subtropical beaches throughout the world. It frequently grows in the backshore topographic zone on sandy beaches as the initial pioneer species just above the high tide line on barrier islands (JUDD *et al.*, 1977; JOHNSON, 1977; MORENO-CASASOLA and ESPEJEL, 1986; BARBOUR *et al.*, 1987). It is also a common species on the margins of hurricane washover channels, disturbed roadsides, and tidal flats (JUDD *et al.*, 1977; LONARD *et al.*, 1978; LONARD *et al.*, 1991). In the tropics, the species occurs on estuarine mudflats adjacent to mangrove swamps (NAVALKAR, 1973; JOSHI and BHOSALE, 1982), in salt marshes and on calcareous shorelines (WHISTLER, 1980; DOING, 1985), on the margins of lagoons (MARTYN, 1934), and on coral sand and rubble shorelines (SAUER, 1982; ALLAWAY *et al.*, 1984).

The seaward extent of *S. portulacastrum* is restricted by the stranding of vegetative fragments at the high tide line. It does not naturally invade inland habitats (CORRELL and JOHNSTON, 1970). The landward extent is limited by competition and shading by taller plants.

JUDD *et al.* (1977) found *S. portulacastrum* on South Padre Island, Texas, in the backshore topographic zone. This zone extends from the high tide line to the seaward base of the primary dunes and is inundated only during spring tides and storms. *Sesuvium portulacastrum* is typically the only species to occupy the tops of small embryonic or coppice dunes nearest the berm crest on the southern Texas Gulf Coast, the tropical Gulf of Mexico and Caribbean coastlines of Mexico, and the arid shoreline of Baja California, Mexico (JUDD *et al.*, 1977; JOHNSON, 1977; BLUM and JONES, 1985; MORENO-CASASOLA and ESPEJEL, 1986). The species occurs on coastlines where sand movements are influenced by prevailing winds. The shoots, particularly the stems, remain fleshy after burial. Buried stems develop adventitious roots at the nodes.

Sesuvium portulacastrum traps sand and tolerates salt spray deposition and burial by accreting sand. During storms embryonic dunes are obliterated by overwash and highwinds. Sea purslane colonies are either uprooted and washed away

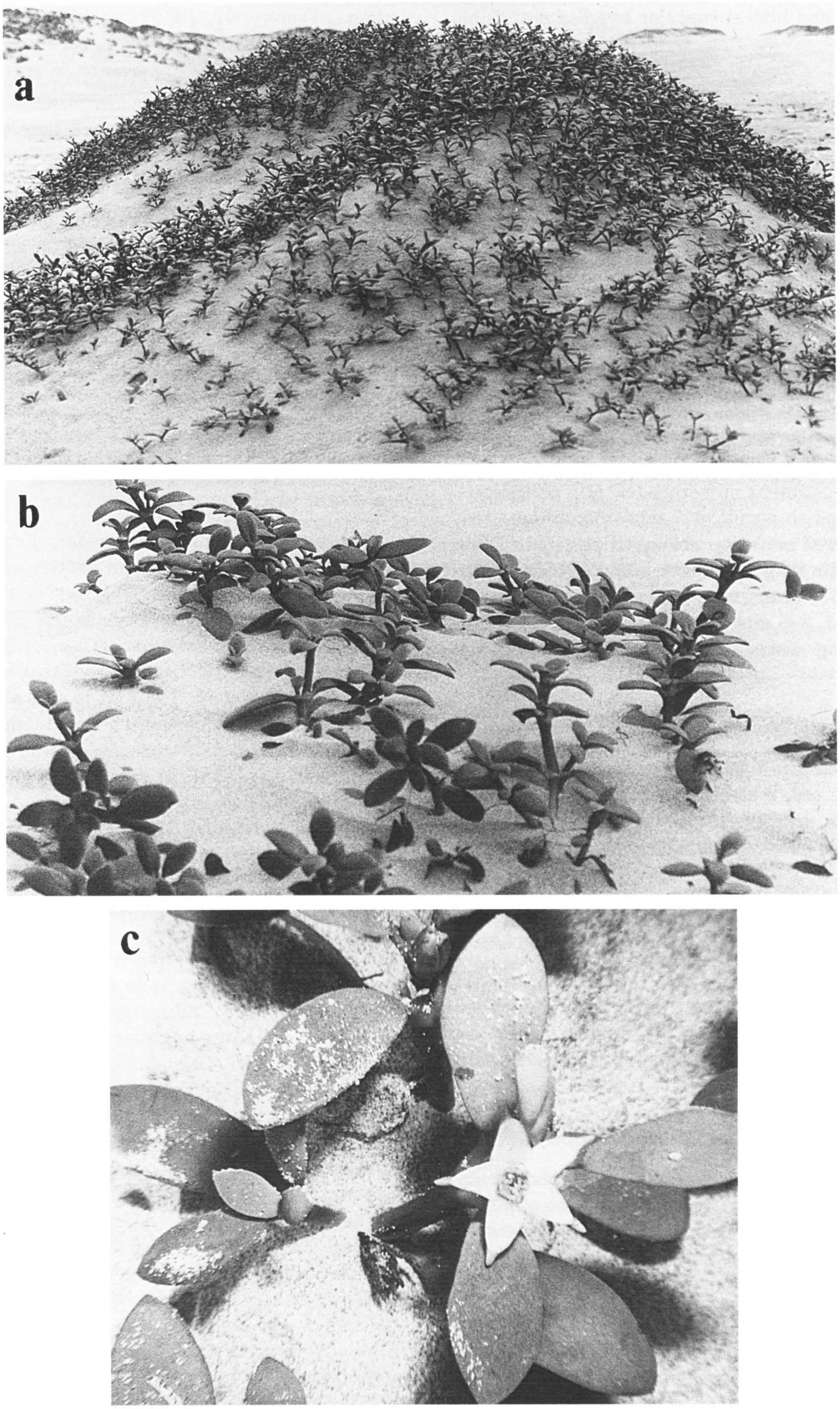

Figure 1. *Sesuvium portulacastrum*: colony forming a foredune (a), stems and leaves (b), inflorescence (c).

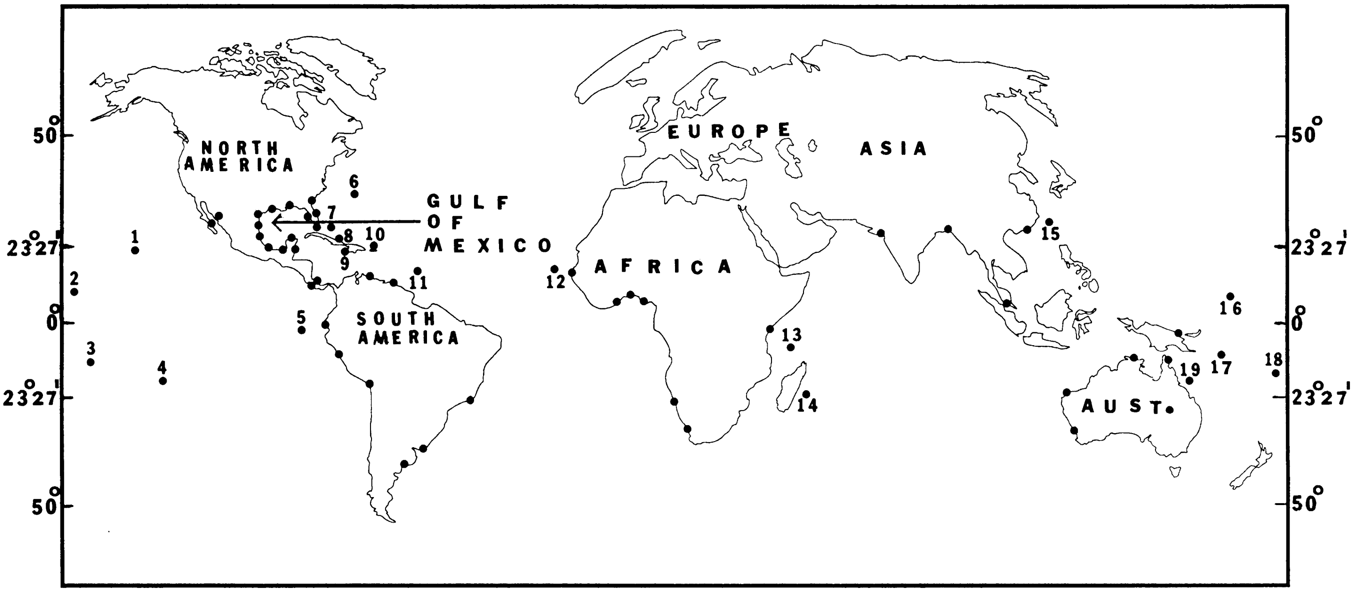

Figure 2. The distribution of *Sesuvium portulacastrum*. Numbers indicate island locations: (1) Hawaiian Islands, (2) Marshall Islands, (3) Samoa Islands, (4) Society Islands, (5) Galapagos Islands, (6) Bermuda Islands, (7) Bahamas, (8) Cuba, (9) Haiti, (10) Puerto Rico, (11) Guadeloupe, (12) Cape Verde, (13) Aldabra Island, (14) Mascarene Islands, (15) Ryukyu Islands, (16) Federated States of Micronesia, (17) Solomon Islands, (18) Fiji, (19) Great Barrier Reef.

or covered by transported sand. JUDD and SIDES (1983) reported that *S. portulacastrum* was absent in the backshore zone of South Padre Island after Hurricane Allen in 1980 and JUDD and LONARD (*unpublished data*) noted a reduction of cover from 1.3% to 0.066% after Hurricane Gilbert in 1988. Subsequent to hurricanes, increased vehicular traffic in the backshore zone severely impacts the recovery of *S. portulacastrum* (JUDD and LONARD, 1987).

Sesuvium portulacastrum is occasionally the first colonizing species along barrier island roadsides on South Padre Island, Texas (LONARD *et al.,* 1991), and it is present in disturbed sites in the secondary dunes and vegetated flats on North Padre Island, Texas (CARLS *et al.,* 1991).

(b) Substrate Characteristics

Sesuvium portulacastrum is common on a great variety of substrates including limestone-shell, coral, pyroclastic sand shingle, and unconsolidated beaches (JUDD *et al.,* 1977; SAUER, 1982; DOING, 1985). POGGIE (1963) reported *S. portulacastrum* from sandy beaches south of Tampico, Mexico, and SAUER (1967) found sea purslane at all sampling sites from northern Tamaulipas to northern Quintana Roo, Mexico. JUDD *et al.* found *S. portulacastrum* in the sandy backshore topographic zone on South Padre Island, Texas, where 77.4% of the sand particles were between 0.18 and 0.25 mm diameter. At a depth of 25 cm, the mean water content was 8.9%, but the mean depth to the water table at this site was only 68 cm.

Sesuvium portulacastrum is an important sand binding species on heavy siliceous sand derived from volcanic rocks in Veracruz and Tobasco, Mexico (MORENO-CASASOLA, 1988), and on limestone beaches and in mangrove sites in the Yucatan Peninsula, Mexico (MORENO-CASASOLA and ESPEJEL, 1986). The species has also been reported from the Great Barrier Reef, Australia, on calcareous coral, rubble and coral sand where the subsoil is a gravelly mixture of coral fragments and coral sand (ALLAWAY *et al.,* 1984). However, STONE (1970) stated that the species does not occur on pure coral sand on Guam.

(c) Climatic Requirements

The geographical distribution of *S. portulacastrum* extends from the equator to about 34° north latitude and 42° south latitude. Its northern and southern distribution limits appear to be directly limited by the frequency, duration and severity of freezing temperatures. Occasional freezes of short duration on South Padre Island, Texas, damage exposed stems and leaves, but shoots buried in sand appear undamaged and recovery of colonies is rapid (LONARD and JUDD, *personal observations*).

Sesuvium portulacastrum occurs on the arid Baja California, Mexico, coastline where annual rainfall is as little as 50 mm per year (JOHNSON, 1977), and it also occurs on Merritt Island, Florida, where mean annual rainfall is 150 cm (LEENHOUTS and BAKER, 1982). It remains green in areas with long dry seasons, even in habitats subject to salt spray. Many of the locations where *S. portulacastrum* occurs are subject to severe storms including hurricanes and typhoons. Populations on the sand beaches of South Padre Island, Texas, recover slowly after hurricanes (JUDD and LONARD, 1987).

V. PLANT COMMUNITIES

DOING (1985) referred to the pioneer plant communities on sandy and rocky, calcareous tropical and subtropical shores as ephemeral tidemark communities. Other terms for this entity include: strand vegetation (GATES, 1915), coastal strand (BEARD, 1944), vegetación de dunas costeras (ESPEJEL, 1986), cordón litoral (MIRANDA, 1942), and embryo dune vegetation (MORENO-CASASOLA and ESPEJEL, 1986). In the Cayman Islands, SAUER (1982) referred to the harsh environment occupied by *S. portulacastrum* as supratidal outpost vegetation.

Common backshore plants associated with *S. portulacastrum* on South Padre Island, Texas, include: *Uniola paniculata, Ipomoea imperati* (=*I. stolonifera*), *I. pes-caprae, Panicum amarum, Fimbristylis castanea, Schizachyrium scoparium, Croton punctatus,* and *Sporobolus virginicus* (JUDD *et al.,* 1977). Along the Pacific and Gulf of California coastlines in Baja California, *S. portulacastrum* is associated with strand species such as *Abronia maritima, Astragalus magalenae,* and *Atriplex barclayana.* However, *S. portulacastrum* and *A. maritima* constitute almost 90% of the plant cover (JOHNSON, 1977).

In Taiwan, species associated with *Sesuvium portulacastrum* include *Ipomoea pes-caprae, Spinifex littoreus* and *Canavalia lineata* (KAN, 1988). On the Ivory Coast of East Africa and on the coastlines of Brazil and Guadeloupe (French Antilles) *S. portulacastrum* is typically associated with *Blutaparon (Philoxerus) vermicularis*; in Senegal it occurs with *Sporobolus virginicus* (VANDEN BERGHEN, 1979; PARADIS, 1981; PFEIFFER *et al.,* 1982; DE FOUCAULT, 1987).

VI. PHYSIOLOGICAL ECOLOGY

(a) Physiology

Sesuvium portulacastrum is tolerant of nearly continuous exposure to salt spray deposition. In the Cayman Islands it grows in spray-drenched limestone pockets within 10 m of the sea. SAUER (1982) observed the species in rock pools where it was constantly submerged in seawater like a "sea anemone". It tolerates high substrate temperatures, wind scouring, and low levels of soil nutrients. JUDD (*personal observation*) has recorded a summer sand temperature of 60 °C in the backshore where the species occurs on South Padre Island, Texas.

In Venezuela, LÜTTGE *et al.* (1989) reported high leaf sap osmotic pressures, xylem tensions, and sodium and chloride levels and confirmed that *S. portulacastrum* is a salt accumulating halophyte. In Brazil, LACERDA *et al.* (1983) found that leaves and stems had high water and ash contents. The water content of leaves was 90.7%. Stems had a water content of 86.8%. Ash content of leaves and stems was 37.6% and 24.6%, respectively.

Sesuvium portulacastrum has been categorized as a C_3 plant in its manner of carbon fixation in the light-independent reactions of photosynthesis. BOHSALE and SHINDE (1983) found that the species synthesizes aspartate and alanine as major products of short-time photosynthesis and that the enzyme aspartate amino transferase influenced the formation of aspartate. The low highly negative carbon isotope ratios ($S^{13}C = -25.8‰$) demonstrates that *S. portulacastrum* is a C_3 plant (LÜTTGE *et al.,* 1989).

An analysis of the mineral constituents of *S. portulacastrum* indicates that Na accounts for 18% of the dry weight. The highest concentrations are in the leaves. The Cl ion accounts for the succulent texture of the leaves (JOSHI, 1981). SINGH and JOSHI (1966) found that Ca and K uptake are hampered in this species under conditions of high salinity.

Salt stress conditions associated with NaCl concentrations of 200 to 900 mM enhance net photosynthetic rates in whole leaves and in isolated mesophyll cells of *S. portulacastrum* (VENKATESALU and CHELLAPPAN, 1993). They found that a maximum net photosynthetic rate occurred at a concentration of 600 mM NaCl. This was correlated with increased succulence, *i.e.* increased salt concentration resulted in increased succulence. Total sugar accumulation declined while starch content increased up to 600 mM NaCl concentrations (VENKATESALU *et al.,* 1994).

Common free amino acids in the succulent stems and leaves of *S. portulacastrum* include proline, aspartic acid, glutamic acid, alanine, serine, and glycine (JOSHI, 1981; VENKATESALU *et al.,* 1994). The accumulation of these compounds is the result of disturbed nitrogen metabolism due to high salinity. The free amino acids apparently are not used for protein synthesis (STROGONOV, 1973). High levels of proline help to maintain intracellular osmotic potential (STEWART and LEE, 1974). Therefore, proline acts as a protective amino acid against the adverse effects of salinity.

Sesuvium portulacastrum has been suggested for use as a biological indicator of heavy metal pollution in tropical areas. It is a dominant species on the margins of a polluted estuary in Brazil where the soil pH is neutral (7.2) and the organic material is about seven times higher than the organic content (1.0%) of geographically similar areas. In this heavily polluted area, living tissues of *S. portulacastrum* show a high degree of resistance to metal pollution and support levels of 67, 17, 16, 5, and 3 times higher than normal for Cr, Zn, Cu, Ni, and Mn, respectively (LACERDA, 1982).

(b) Phenogy

No detailed information is available on flowering and fruiting cycles for *S. portulacastrum.* However, LONARD and JUDD (1989) noted that *S. portulacastrum* populations on South Padre Island, Texas, have a continuous flowering and fruiting cycle. Plants are in reproductive phases in all months except February. Flowers open at sunrise and close during late afternoon (LONARD and JUDD, *personal observations*).

VII. POPULATION BIOLOGY

(a) Perennation

Sesuvium portulacastrum is a stoloniferous perennial that may be long-lived. Its stems remain succulent after burial by sand, and it typically produces adventitious roots at the nodes (JOHNSON, 1977). In beachfront populations on South Padre Island, Texas, above-ground stems and leaves are occasionally frost damaged, but buried plant parts and plants in protected locations survive the mild winters.

(b) Population Dynamics

JUDD and SIDES (1983) reported that Hurricane Allen (1980) washed away or covered the *Sesuvium portulacastrum* zone of the backshore on South Padre Island, Texas. To assess recovery of *S. portulacastrum* after tropical storms, JUDD and LONARD (1987) established vegetation removal experiments in the *S. portulacastrum* belt to simulate storm effects. They found that neither species richness nor percent cover was restored to pre-hurricane status six years after Hurricane Allen in 1980. *Sesuvium portulacastrum* was present, but there was no well-developed belt of sea purslane that dominated embryonic dunes.

VIII. REPRODUCTION

(a) Sexual Reproduction

(i) Pollination and Fertilization

No pollination experiments have been conducted on *S. portulacastrum* populations. The numerous stamens that nearly match the length of the style and the anthers that dehisce inwardly near the stigmatic surfaces suggest that the species is autogamous or self-compatible. However, LONARD (*personal observations*) has noted small, brown lepidopterans and small bees visiting the flowers. No floral odor is noticeable.

(ii) Seed Production

Fifty or more seeds per capsule are usually produced, but occasionally a fruit contains less than 10 seeds. After pollination, the fleshy perianth encloses the developing circumscissle capsule and supports it in an erect position. When the capsule is mature the perianth and enclosed capsule turn downward; the perianth opens, the capsule dehisces, and the seeds are released.

(iii) Dispersal

Sesuvium portulacastrum is one of the most widely distributed seashore plants. It has apparently reached nearly all locations in which it occurs by drifting of vegetative segments in the sea. POGGIE (1963) observed stranded fragments in the backshore zone of Cabo Rojo south of Tampico, Mexico, after a tropical storm. The vegetative fragments were stranded 25 to 45 m above the high tide line and were soon covered by wind-blown sand. CARLQUIST (1974) reported that vegetative fragments are not only buoyant, but are not damaged by seawater. Vegetative fragments root in a manner similar to cuttings. Fragments placed in tap water produce adventitious roots within several days.

Seeds and fruits of *S. portulacastrum* are not buoyant (CARLQUIST, 1974). GUPPY (1917) suggested that seeds of this species may lodge in crevices in logs and pumice that are washed into the sea, and SAUER (1982) inferred that the small seeds may be carried externally by shore birds. WICKENS (1979) noted that boobies construct nests in the Aldabra Archipelago with vegetative fragments of sea purslane.

(iv) Seed Bank and Seed Size

No information is available on *S. portulacastrum* seed banks nor is there any information available on variation in seed sizes over the geographical range of the species.

(v) Germination Ecology and Establishment of Seedlings

Germination of *Sesuvium portulacastrum* seeds requires temperature fluctuations and the exposure of seeds to light. Germination can occur under a variety of salinity concentrations (MARTINEZ *et al.*, 1992). Seeds are capable of germination after 56 days of immersion in seawater (HUNATIUK, 1979). Seeds germinate 11–40 days after exposure and planting. Over 50% of the seeds germinate within 13 days. However, the final level of germination of the seed lot was only 20% (HUNATIUK, 1979). LONARD (*personal observation*), in a preliminary investigation, noted a 5% germination success (N = 20 seeds) 20 days after the addition of tap water for seeds collected on South Padre Island, Texas. The seeds had not been previously soaked in seawater. JOHNSON (1977) indicated that the species germinates only in moist depressions and not on dry ridges on sandy beaches in Baja California. Seedlings that germinate close to the high tide mark are uprooted and accreting sand in the backshore buries small seedlings. Seeds that germinate near parent plants or under taller plants may not receive sufficient light or nutrients to survive.

(b) Vegetative Reproduction

Sesuvium portulacastrum roots easily from shoot fragments and stem cuttings (see section on Dispersal). No information is available on the viability of cuttings after long term exposure to seawater.

IX. GEOMORPHOLOGICAL INTERACTIONS

(a) Response to Burial

Portions of the elongated mat forming shoots, flowers, and fruits are frequently covered by blowing sand. However, sand rarely covers the entire plant. Exposed portions generate new stolons. In less exposed sites, shoots are nearly prostrate. In sites where sand movements are more pronounced, stem apices and leaves are usually vertically oriented.

(b) Role in Geomorphology

Vegetation in a typical pioneer zone on a sandy beach is limited to a few vigorous, salt tolerant species. Plants such as the mat-forming *S. portulacastrum* play a significant role in coastal geomorphology as a dune initiator (WOODHOUSE, 1982). In *S. portulacastrum,* lateral growth is by means of short stolons which produce adventitious roots. Low embryonic coppice dunes form around the slowly advancing stolons.

X. INTERACTION WITH OTHER SPECIES

(a) Competition

On the southern Gulf of Mexico barrier island beaches, *S. portulacastrum* and *Uniola paniculata,* a rhizomatous, perennial grass, are the dominant species in the backshore zone. Percent cover values in the zone are typically below 5.0% (JUDD *et al.*, 1977). The two species characteristically occur in two distinct belts. Immediately leeward of the high tide line is a belt of low dunes that support *S. portulacastrum.* Leeward of this, a belt of taller dunes in the backshore support *Uniola paniculata* as the dominant species. *Sesuvium portulacastrum* colonies are inconspicuous or absent where taller plants are established and the sand is shaded. At more xeric sites on the coastline of Baja California, *S. portulacastrum* replaces *Abronia maritima* (Nyctaginaceae) as the dominant species (JOHNSON, 1977). Succulent halophytes with similar growth patterns as *S. portulacastrum, i.e. Bluetaparon (Philoxerus) vermicularis* and *Batis maritima* tend to form discrete patches and rarely overlap colonies of *S. portulacastrum* (LACERDA, 1982).

(b) Predation and Symbiosis

Sesuvium portulacastrum leaves are apparently protected from most insect and vertebrate herbivores by a high concentration of NaCl. The soluble tannin content (0.6% w/w) for the species is well within the range (0.3–3.0% w/w) for terrestrial vascular plants (KUTHUBUTHEEN, 1981). Therefore, tannins are apparently not a deterrent to herbivory or to many fungal parasites. STEFFNER (*unpublished data*) has observed jack rabbits feeding on *S. portulacastrum* on South Padre Island, Texas. ABHAYKUMAR and DUBE (1991) noted large populations of epiphytic bacteria on leaves and stems including *Flavobacterium, Pseudomonas,* and *Vibrio* species. It is not clear whether these bacteria have deleterious effects or if they promote growth.

LONARD (*personal observations*) has noted small black areas of localized necrosis in the subepidermal-mesophyll zones of both upper and lower leaf surfaces of plants on South Padre Island, Texas. However, leaf-damaging insects were not observed on *S. portulacastrum* nor were there insect eggs present in the leaf mesophyll. No information is available on seed predation.

In the United States, disease organisms affecting *S. portulacastrum* include *Albugo trianthemae* (white blister), *Phymatatrichum omnivorum* (root rot), *Puccinia aristidae* (rust), and *Meloidogyne marioni* (root-rot nematodes) (ANONYMOUS, 1960). In Malaysia, genera of Fungi Imperfecti associated with *S. portulacastrum* include *Aspergillus, Fusarium, Nigrospora, Trichoderma, Penicillium, Pestalotiopsis, Curvularia, Cephalosporium,* and *Cladosporium* (KUTHUBUTHEEN, 1981).

XI. RESPONSE TO WATER LEVELS

Sesuvium portulacastrum is a terrestrial species. It is, however, subjected to occasional flooding. In addition, storm surges are responsible for either the washing away of small dunes dominated by the species or for the coverage of plants by the deposition of sand. Colonies are tolerant of sand accretion (if coverage is not too great) and recover slowly.

XII. ECONOMIC IMPORTANCE

(a) Coastal Protection

Sesuvium portulacastrum is an important pioneer, colonizing species on sandy beaches in the subtropics and tropics. Its stoloniferous mat-forming growth habit promotes embryonic dune formation. Colonies act as barriers to deflect and hold shifting sand. Small drift lines form on the lee of the colonies. As a colony grows laterally and adventitious roots develop, some substrate stability is attained. Propagules of other rhizomatous or stoloniferous perennials are trapped around small dunes. Dunes are further stabilized subsequent to germination and growth of less tolerant species.

(b) Medicinal Uses

No information is availble about medicinal uses of the species. However, STONE (1970) indicated that the stems and leaves are salty but edible. The species has little or no use in Polynesia, Micronesia, or Melanesia, although it is widespread in these islands. It is usually unnoticed and unnamed by islanders (WHISTLER, 1980).

(c) Potential Biological Control Agents

High concentrations of ecdysterone (3.5 g/kg) have been isolated from *Sesuvium portulacastrum* (BANERJI *et al.*, 1971). The steroid hormone stimulates protein synthesis involved in the metamorphosis of insects. Therefore, extracts from the plants may have a possible role as a chemosterilant in the biological control of insect pests.

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