The Biological Flora of Coastal Dunes and Wetlands.

Ipomoea imperati (Vahl) Griseb.

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ABSTRACT

Beach morning glory, Ipomoea imperati (Vahl) Griseb. = I. stolonifera (Cirillo) Gmelin is a pantropical, prostrate, stoloniferous herb with large, tubular, white flowers. It is an important species in the backshore zone of coastal beaches where drifting sand movements are influenced by prevailing winds (Judd et al., 1977). Ipomoea imperati is common in the primary dune system where it may be a dominant species on windward and leeward slopes (Judd et al., 1977; Judd and Sides, 1983). Many aspects of the biology of I. imperati have not been investigated. Herein, we review the biology of this important coastal species.

INTRODUCTION


Taxonomic Description

The following account has been assembled from Radford et al., 1968; Correll and Johnston, 1970; Austin, 1975b; Walker, 1976; Wagner et al., 1990.

Seed Morphology

The 1–4 light brown seeds are short-tomentose with longer comose trichomes on the margins, 0.7–1.2 cm long. The mean seed length and mean seed weight at Veracruz, Mexico, are 7.18 mm and 119.7 mg, respectively (Martinez et al., 1992).

Seedling Morphology

Each of the pair of cotyledons is fleshy and slightly notched at the apex. The foliage leaves are simple, alternate, oblong, and the apex is usually notched. Juvenile leaves closely resemble those present on mature plants. Seedlings develop an extensive network of adventitious roots.

Shoot Morphology

Stoloniferous, prostrate, herbaceous vines; stems somewhat succulent, brown or reddish-brown, glabrous, mostly unbranched, 5–8 m in length, containing a viscous, milky latex (Lonard and Judd, personal observations). Petioles 0.5–8 cm long, glabrous, exstipulate. Leaves coriaceous, simple, alternate, 1–10 cm long, 1.0–4.5 cm wide, highly variable, occasionally secund, often vertically oriented, flat, or somewhat conduplicate, oblong-ovate, broadly short-oblong, or pandurate; margins entire, but usually 3–7 lobed; lobes may

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extend to the midrib; apex obtuse or emarginate; the base cordate, truncate, auriculate, or auriculate-hastate; lateral veins 5–9 on either side of the midrib; extrafloral nectaries absent from the base of the blade (KEELER and KAUL, 1979) (Figure 1).

**Root Morphology**

*Ipomoea imperati* has a tap root that extends vertically 0.4–1.8 m into the soil. Smaller adventitious roots at the nodes may extend up to 15 cm below the soil surface. In rapidly
Figure 2. The distribution of *Ipomoea imperati*. Numbers indicate island locations: (1) Hawaiian Islands, (2) Cuba, (3) Jamaica, (4) Haiti and Dominican Republic, (5) Puerto Rico, (6) Guadeloupe, (7) Trinidad and Tobago, (8) Ryukyu Islands, (9) Hainan (China), (10) Babuyan Islands (Philippines), (11) Calayan Island (Philippines), (12) Madura Island (Indonesia), and (13) Wellesley Islands (Australia).

Growing plants, adventitious roots develop approximately 2.0 m distally from the apical meristem (LONARD and JUDD, personal observations).

**Inflorescence**

*Ipomoea imperati* flowers are usually solitary or occasionally several-flowered cymes from the leaf axils; pedicels 1.5–4.5 cm long, terete, curved and holding the flower erect, glabrous. Sepals 5, actinomorphic, distinct nearly to the base, unequal, imbricate, yellowish-green, 1.5–2.5 cm long, glabrous, acute or mucronate at the apex, persistent; corolla buds induplicate-valvate; corolla 6.0–7.5 cm long, petals 5, sympetalous, actinomorphic, the tube up to 3.5 cm long, entire, funnelform, 5.0–7.5 cm in diameter, creamy-white, the throat yellow, somewhat purplish at the base of the throat. Stamens 5, included within the corolla tube, epipetalous near the base of the corolla tube; filaments unequal 1–2 cm long, densely glandular-pubescent at the base; anthers dorsifixed, 5.5–6.0 mm long, creamy-white. Pistil 1, included within the corolla tube; stigma capitulate, attached laterally to the style; style unbranched, about the same length as the longest stamens; ovary superior, glabrous, appearing 4-locular due to false septa, included within a nectariferous disc that contains a copious amount of milky latex.

**Fruits**

The capsule is 4-valved, subglobular, glabrous, with a persistent style, and 1.0–1.5 cm in diameter.

**Variability**

No varieties nor ecotypes of *I. imperati* have been recognized.

**Chromosome Number**

JONES (1964) reported a chromosome number of $2n = 30$ for *I. imperati* taken from a seed source in Florida.

**GEOGRAPHIC DISTRIBUTION**

*Ipomoea imperati* occurs on the coastlines of six continents (Figure 2). It is present on some tropical islands as well as on subtropical shores (HOUSE, 1908; BARKER and DARDEAU, 1930; VAN OOSTSTROOM, 1953; BOUGHEY, 1957; O’DONELL, 1960; SAUER, 1967, 1982; RADFORD et al., 1968; CORRELL and JOHNSTON, 1970; ADAMS, 1972; WAISEL, 1972; AUSTIN, 1975 b; AUSTIN and HUÁMAN, 1996; DE A. FAÇAÇO and DE A. FAÇAÇO, 1976; WALKER, 1976; JUDD et al., 1977; JOHN­SON, 1977; VANDEN BERGEN, 1979; DOING, 1985; DE­FOUCALD, 1987; DUNCAN, 1987; MORENO-CASASOLA, 1988; WAGNER et al., 1990; NODA et al., 1994). It is apparently extinct from the lectotype locality near Naples, Italy, as well as from other Italian coastal sites (LA VALVA and SABATO, 1983). Its distribution pattern is similar to that of *Ipomoea pes-caprae*, but it is less frequently encountered on remote oceanic islands (DEVALL, 1992).

**RANGE OF HABITATS**

**Zone of Occurrence**

*Ipomoea imperati* occurs as a pioneer strand species on tropical and subtropical shorelines. It frequently grows in the backshore and primary dune topographic zones on barrier islands (DAHL et al., 1975; JUDD et al., 1977; MORENO-CASASOLA et al., 1982; ANDERSON and ALEXANDER, 1985; MORENO-CASASOLA, 1988; WAGNER et al., 1990; STALTER and LAMONT, 1993). In Brazil, the species is common in the "res-
tinga", a sandy plain near the sea covered with woody vegetation (DE A. FALCAO and DE A. FALCAO, 1976). It is also a common species on disturbed roadsides and on the margins of hurricane washover channels on South Padre Island, Texas (LONARD et al., 1991).

The landward extent of *I. imperati* is influenced by dispersal and competition from taller plants. It does not naturally invade inland sites. The seaward extent is regulated by the physical environment through the movement of seeds away from the water and high seedling mortality in the backshore.

**JUDD** et al. (1977) report *I. imperati* on South Padre Island, Texas, in the backshore and primary dune topographic zones. It is occasionally a dominant species in the taller foredunes seaward of the primary dune system and is the dominant species on both the windward and leeward slopes of the primary dunes prior to hurricane perturbations (JUDD et al., 1977; JUDD and SIDES, 1983). The species occurs on coastlines where sand movements are influenced by prevailing winds. The succulent shoots remain fleshy after moderate burial. Mortality may occur along segments of buried stolons. PLATT and PLATT (unpublished data) note that juvenile plants are unable to survive on coastlines where rates of horizontal sand accretion are greater than 10 m/yr. However, exposed segments develop adventitious roots, and ramets may be formed (LONARD and JUDD, personal observations).

*Ipomoea imperati* traps sand and tolerates salt deposition and moderate burial by accreting sand. Beach morning glory stolons are either uprooted, washed away, or covered by transported sand during tropical storms. JUDD and SIDES (1983) report that *I. imperati* was absent in the backshore topographic zone of South Padre Island, Texas, after Hurricane Allen in 1980, and it was no longer the dominant on the windward and leeward slopes of the primary dune system. JUDD and LONARD (unpublished data) noted a reduction of plant cover from 0.4% to 0.15% in the backshore after Hurricane Gilbert in 1988. Subsequent to hurricanes, increased vehicular traffic in the backshore and primary dune zones severely impacts the recovery of *I. imperati* populations on South Padre Island, Texas (JUDD and SIDES, 1983).

*Ipomoea imperati* is occasionally a colonizing species that advances into disturbed patches along barrier island roadsides on South Padre Island, Texas (JUDD and LONARD, 1987). It is present in disturbed sites and blow-out areas in the secondary dunes and vegetated flats on North Padre Island, Texas (CARLS et al., 1991).

**Substrate Characteristics**

*Ipomoea imperati* is common on sandy as well as some calcareous beaches (JUDD et al., 1977; SAUER, 1982; DOING, 1985). POGGIE (1963) reports *I. imperati* from sandy beaches south of Tampico, Mexico, and SAUER (1967), MORENO-CASASOLA (1988), LOERA and MORENO-CASASOLA (1982), ESPEJEL (1986) found beach morning glory at nearly all sampling sites from northern Tamaulipas to Quintana Roo, Mexico. JUDD et al. (1977) found *I. imperati* in the sandy backshore and windward and leeward topographic zones on South Padre Island, Texas where 77.4%, 95.0%, and 86.9% of the sand particles were between 0.25 and 0.18 mm diameter, respectively. At a depth of 25 cm, the mean water content in the backshore and at the base of the primary dunes was 8.9% and 4.1%, but the mean depth to the water table was only 68 cm and 91 cm, respectively.

**Climatic Requirements**

The geographical distribution of *I. imperati* extends from the equator to 31° North latitude. The species is apparently extinct from the lectotype locality near Naples, Italy (40.5° North latitude). In the southern hemisphere, the species occurs as far south as 23° (Figure 2). Both the northern and southern distribution limits appear to be influenced by the severity, duration, and frequency of freezing temperatures. Episodic freezes of short duration on South Padre Island, Texas, damage exposed leaves, but recovery of ramets is rapid (LONARD and JUDD, personal observations).

*Ipomoea imperati* occurs on the arid peninsula of Baja California, Mexico, where annual precipitation is 50 mm (JOHNSON, 1977). It also occurs on Dog Island, Florida, where mean annual rainfall is 142 cm (ANDERSON and ALEXANDER, 1983). Many sites where beach morning glory occurs are subject to severe tropical storms. Populations on the sandy beaches of South Padre Island, Texas, recover slowly after hurricanes (JUDD and LONARD, 1987).

**PLANT COMMUNITIES**

Plant communities on sandy and calcareous tropical and subtropical shores where *I. imperati* occurs are referred to as perennial, tidemark communities (DOING, 1985), beach/dune communities (ANDERSON and ALEXANDER, 1985), and cenicilla-beach morning glory (Sesuvium portulacastrum-Ipomoea stolonifera-*I. imperati*) communities (DIAMOND et al., 1987). Other terms for this plant community type include: strand vegetation (BEARD, 1944), vegetation de dunas costeras (ESPEJEL, 1986), cordón litoral (MIRANDA, 1942), and embryo dune and foredune vegetation (MORENO-CASASOLA and ESPEJEL, 1986). In Brazil, *I. imperati* occurs with woody vegetation in a sandy plain near the sea in a community referred to as a “restinga”.

From the literature related to coastal vegetation, it is difficult to ascertain the position of *I. imperati* in various topographic facets or plant communities. Table 1 includes species associated with *I. imperati* in selected tropical and subtropical sites without designations of topographic zones or plant communities.

On South Padre Island, Texas, common backshore plants associated with *I. imperati* include: *Uniola paniculata*, *Sesuvium portulacastrum*, *Panicum amarum*, *Ipomoea pes-caprae*, *Fimbristylis castanea*, *Schizachyrium scoparium*, and *Croton punctatus*. *Ipomoea imperati* is the dominant species on the windward slopes of the primary dunes and is associated with *U. paniculata*, *C. punctatus*, *S. scoparium*, *Heterotheca subaxillaris*, and *P. amarum*. The protected leeward slopes of the primary dunes include *I. imperati* as the dominant species. Other species include: *U. paniculata*, *S. scoparium*, *C. punctatus*, *Chamaecrista fasciculata*, *H. subaxillaris*, *Oenothera*
Table 1. Sandy beach species associated with Ipomoea imperati. SCA = South Carolina (Stalter and Lamont, 1993); FLA = Florida (Anderson and Alexander, 1985); GFA = Guadeloupe, French Antilles (DePauw, 1987); TNP = Texas, North Padre Island (Dahl et al., 1975); TSP = Texas, South Padre Island (Judd et al., 1977); MVC = Mexico, Veracruz (Moreno-Casasola, 1988); MBC = Mexico, Baja California (Johnson, 1977); SEN = Senegal (Vanden Berghen, 1979); GHA = Ghana (Boughey, 1957); ZAI = Zaire (Boughey, 1957).

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Physiology

Information is limited related to metabolic processes in *I. imperati*. *Ipomoea imperati* is tolerant of exposure from salt spray deposition. In Hawaii, beach morning glory occurs within 0–20 m of the sea (WAGNER et al., 1990), and at Veracruz, Mexico, it typically grows within 25–35 m of the Gulf of Mexico (MORENO-CASASOLA et al., 1982). It tolerates low levels of soil nutrients, wind scouring, and high substrate temperatures. JUDD (personal observations) has recorded a sand surface temperature of 60°C in the backshore topographic zone adjacent to *I. imperati* populations on South Padre Island, Texas.

BARBOUR et al. (1987) categorized *I. imperati* as a C3 plant in its manner of carbon fixation in the light-independent reactions of photosynthesis. The palisade parenchyma is bifacial, and both epidermal surfaces are glabrous (BARBOUR et al., 1987).

Resin glycosides, called stoloniferins, have been isolated from beach morning glory plants in China. Some of the seven isolated compounds identified as stoloniferins I–VII are soluble in ether (NODA et al., 1994). A copious amount of viscous, white latex is present in the receptacle, presumably containing stoloniferins (LONARD and JUDD, personal observations).

Phenology

*Ipomoea imperati* flowers typically open at 6:00 am and close by 2:00 pm on the coast of Israel (WAISEL, 1972). On South Padre Island, Texas, corollas open at sunrise. The corollas lose turgor pressure in the early afternoon on sunny days, but some corollas are usually open until late afternoon (LONARD and JUDD, personal observations). The flowering period for *I. imperati* is from 1 April–1 November on the coastline of Israel (WAISEL, 1972) and from April to December on South Padre Island, Texas (LONARD and JUDD, 1989). Fewer flowers tend to form on rapidly growing stolons (LONARD and JUDD, personal observations). Fruits ripen from March–September on the coastline of Veracruz, Mexico (MARTINEZ et al., 1992), and dehiscent capsules are noted on South Padre Island, Texas, in early December (LONARD and JUDD, personal observations).

Population Biology

Perennation

*Ipomoea imperati* is a prostrate, stoloniferous perennial that may be long-lived. Shoots tolerate moderate burial by sand, and it typically produces superficial, adventitious roots at the nodes. Populations of *I. imperati* are occasionally frost-damaged on South Padre Island, Texas. Plants in protected locations survive mild winters in the subtropics and tropics.

Population Dynamics

PLATT and PLATT (unpublished data) note that genets of *I. imperati* may be long-lived due to the growth of clones. Life-spans of beachfront populations of *I. imperati* are finite, however. JUDD and SIDES (1983) report that Hurricane Allen (1980) washed away or covered beach morning glory plants in the backshore zone on South Padre Island, Texas, and reduced its plant cover values in both windward and leeward sites of the primary dunes. The decline of *I. imperati* as a dominant species is attributed to its susceptibility to sand coverage, its prostrate growth form, and its susceptibility to damage by off-road vehicular traffic (JUDD and LONARD, 1987). LOERA and MORENO-CASASOLA (1982) report that *I. imperati* invades the pioneer beach zone at Veracruz, Mexico, but does not produce adventitious roots in the zone.

Reproduction

Sexual Reproduction

Pollination and Fertilization

MARTIN (1970) notes that *I. imperati* is self-incompatible. The five epipetalous stamens are unequal in length and have anthers that dehisce extrorsely. Self-specific incompatibility occurs due to failure of the echinate pollen grains to germinate. If germination occurs occasionally, pollen tubes rarely grow longer than two pollen diameters (MARTIN, 1970). No floral odor is detectable. The primary pollinators of *I. imperati* on South Padre Island, Texas, appear to be lepidopterans. Ants are usually present on shoots and flowers (LONARD and JUDD, personal observations).

Seed Production

Four seeds per capsule are usually produced. However, fruits may contain one, two, or three seeds. Fruit production appears to be low on South Padre Island, Texas. DEVALL and THEIN (1989) report that fruit production of *I. pes-caprae* is sporadic. Fruit production in this related species appears to be limited by a lack of pollinators.

Dispersal

*Ipomoea imperati* is a widely distributed tropical, maritime species (LONARD and JUDD, 1980). Seeds, fruits and vegetative fragments are buoyant in seawater. However, it is not known how long seeds remain viable after immersion in seawater.

Seed Bank and Seed Size

No information is available on *I. imperati* seed banks. However, persistent seed banks of perennial coastal dune species may not be present (Zhang and MAUN, 1994). Mean seed weight at Veracruz, Mexico, is 119.7 mg, and mean seed length is 7.18 mm (MARTINEZ et al., 1992). Mean seed length on South Padre Island, Texas, was 9.9 mm (N = 50 seeds) (LONARD and JUDD, personal observations).

Germination Ecology and Establishment of Seedlings

MARTINEZ et al. (1992) report high germination rates for *I. imperati* seeds collected from beaches in Veracruz, Mexico. At least 90% of stored seeds germinated at a constant temper-
ature of 35°C, and germination was 60%–85% successful under fluctuating temperature regimes ranging from 20–40°C. Stored seeds germinated equally well in darkness and light. Only 40% of Ipomoea imperati seeds germinated when buried at a depth of 0.5 cm, and 52% germinated when they were planted 2.0 cm below the soil surface. No appreciable enhancement of germination rates was noted when nitrates were added as a fertilizer. Martínez et al. (1992) note low germination rates in nonscarified seeds.

Seeds that germinate near the high tide mark are up-rooted, and accreting sand buries small seedlings. Seeds that germinate under taller plants may not receive sufficient light or nutrients to survive. Few germinating seedlings have been observed on South Padre Island, Texas (Lonnard and Judd, personal observations).

Vegetative Reproduction

No information is available on vegetative reproduction of Ipomoea imperati. Viable shoot ramets have not been observed in the flotsam on South Padre Island, Texas, after storms. Stolons grow rapidly and produce superficial, adventitious roots at the nodes. Burial by accreting sand may kill a segment of a plant, but accretion seldom buries an entire plant.

GEOMORPHOLOGICAL INTERACTIONS

Response to Burial

Portions of the elongated, prostrate stolons are often covered by blowing sand. However, sand rarely covers an entire plant.

Role in Geomorphology

Vegetation on sandy, tropical and subtropical backshore zones and primary dune systems is limited to a small number of salt tolerant species. Ipomoea imperati, in conjunction with the mat-forming Sesuvium portulacastrum, play an important role as initiators of embryonic dunes (Woodhouse, 1982) and as stabilizers of vegetated primary dune systems (Judd et al., 1977).

INTERACTION WITH OTHER SPECIES

Competition

Devall et al. (1990) and Devall (1992) report that Ipomoea pes-caprae and Ipomoea imperati often co-occur on tropical shorelines. They indicated that basic patterns of growth and reproduction are similar for both species. However, densities of recently emerged seedlings of Ipomoea imperati decreased progressively as sand accretion rates increased. Ipomoea imperati seeds are smaller than Ipomoea pes-caprae seeds, and the latter emerge successfully from greater sand depths (15 cm for Ipomoea pes-caprae vs 5 cm for Ipomoea imperati).

Ipomoea pes-caprae occurs more abundantly on unstable substrates than Ipomoea imperati. On South Padre Island, Texas, Ipomoea pes-caprae is the dominant species on bulldozed waste sites containing rafted Sargassum debris in the backshore zone adjacent to resort hotels. Conversely, Ipomoea imperati is more abundant in the taller foredunes and is a dominant species in primary dune sites (Judd et al., 1977).

Predation

Lonnard and Judd (personal observations) have observed areas of localized necrosis in the subepidermal-mesophyll zones of both upper and lower surfaces of Ipomoea imperati plants on South Padre Island, Texas. No leaf-damaging insects were observed nor were there insect eggs or larvae in the leaf mesophyll. The large, tubular corollas are apparently rarely consumed by predators. On Merritt Island, Florida, Peromyscus polionotus niveiventris (beach mouse) is a common resident in habitats dominated by Ipomoea imperati (Extine and Stout, 1987). However, they did not report that beach mice eat shoots or seeds.

RESPONSE TO WATER LEVELS

Ipomoea imperati is a terrestrial species. It is subjected to occasional minor flooding associated with storms and high tides. Storm surges often wash away small foredunes where it occurs or covers plants by the deposition of sand and debris.

ECONOMIC IMPORTANCE

Coastal Protection

Ipomoea imperati is an important colonizing species on sandy beaches in the tropics and subtropics where it promotes embryonic dune formation and serves to stabilize topographically important primary dune systems. Rapidly growing stolons trap shifting sand. Some substrate stability is initiated due to the production of shallow, adventitious root systems.

Medicinal Uses

No information is available about medicinal uses of the species.

ACKNOWLEDGMENTS

We thank Dr. Luis Materón for reviewing a draft of the manuscript and Leslie Allison for the preparation of the map. We thank Chris Best, Jim Everitt, and Tim Fulbright for critical reviews of the manuscript.

LITERATURE CITED


