

Biological Flora of Coastal Dunes and Wetlands: *Canavalia rosea* (Sw.) DC

Gabriela Mendoza-González, M. Luisa Martínez, and Debora Lithgow

Instituto de Ecología, A.C. (INECOL)
Antigua Carretera a Coatepec no. 351
El Haya, Xalapa, Veracruz, 91070, Mexico
gaballito@gmail.com



www.cerf-jcr.org



www.JCRonline.org

ABSTRACT

Mendoza-González, G.; Luisa Martínez, M., and Lithgow, D., 0000. Biological flora of coastal dunes and wetlands: *Canavalia rosea* (Sw.) DC. *Journal of Coastal Research*, 00(0), 000-000. Coconut Creek (Florida), ISSN 0749-0208.

The genus *Canavalia* includes 60 species, of which 37 are found in the Neotropics. One of the most common members of this genus is *Canavalia rosea*. In this paper, we present a compilation of the ecological, physiological, and geomorphological biology of this pantropical beach and coastal dune species that will serve as a basis for scientists and managers interested in the species. This legume (Fabaceae) is a perennial trailing vine that grows on five continents and is also found on many islands. The leaves are compound, and the leaflets are roughly circular in shape, with an entire margin and a short petiole. The flowers are small, pink-purple, in racemes and range from 1 to 3 cm in diameter. Blooming takes place with greatest intensity between May and September, although sporadic racemes can be found throughout the year. Fruits are large, 7–12 cm long, with marbled brown dormant seeds. The root is monopodic and presents a mycorrhizal association. It is a successful colonizer of tropical shorelines due to the dispersal of its seeds by ocean currents and a high tolerance to salt spray, burial, low-nutrient substrates, and high temperature. The species is an important sand colonizer and plays a significant role in the geomorphology of beaches and frontal dunes. The species often covers large areas and forms a relatively continuous mat that stabilizes the sandy substrate in which it grows. The leaves, stems, and seeds have many nutritional and medicinal uses due to their high protein content and active bactericidal ingredients.

ADDITIONAL INDEX WORDS: *Dune colonizing, coastal dune vegetation, tolerance to burial, pantropical.*

INTRODUCTION

Canavalia rosea is an herbaceous vine that grows along beaches and coastal dunes. The genus *Canavalia* DC belongs to the family Fabaceae and comprises 52 species, most of which are distributed in the Neotropics (Beyra-Matos *et al.*, 2004). Within the genus, *C. rosea* is the only pantropical species that can be very abundant at the local scale, especially on beaches, where it is able to tolerate sand burial and salinity (Beyra-Matos *et al.*, 2004).

The thick, fleshy stems of *C. rosea* grow to 10 m or more in length and can be quite woody near the base. The branches radiate outwards from the base and form dense mats. These creeping vines climb over dunes or vegetation as they expand inland from the beach (Beyra-Matos *et al.*, 2004). Flowers are pink-purple and are produced throughout the year, but mostly during summer. Following bursting of the woody legumes, the seeds are dispersed by ocean currents (Vatanparast *et al.*, 2011).

Canavalia rosea is an important element in the beach and dune vegetation of the Neotropics, with unique adaptations to this environment. It is part of one of the functional groups of

tropical coastal plants, characteristic of coastal dunes, and is particularly tolerant to soil salinity and burial on accreting beaches (Gallego-Fernández and Martínez, 2011). The uniqueness and relevance of the species have led to it being the subject of studies worldwide since the last century (Berry, 1916, 1930; Chen *et al.*, 2000; D'Arcy, 1980; Kienholz, 1927; Raunkiaer, 1934; Sauer, 1964; Sauer and Kaplan, 1969; Waldren, Florence, and Chepstow-Lusty, 1995; Wilson, 1977); however, the extensive range of information produced by these studies has never been collated. Here, we have compiled information regarding the taxonomy, evolution, geographical distribution, physiology, demography, and ecology of *C. rosea*. The goal was to perform a thorough review of previous studies of *C. rosea* and collate the findings into a single document. This review contributes to the series "Biological Flora of Coastal Dunes and Wetlands," which aims to enhance communication and increase interaction among the different disciplines that work with coastal habitats (Maun and Finkl, 1988). To conduct this review, we compiled peer-reviewed as well as some gray literature, namely, unpublished theses.

TAXONOMY AND VARIATION

Name

The genus name is a Latinized derivation of the Malabar "Kanavali," meaning "forest climber" and "climbing herb"

DOI: 10.2112/JCOASTRES-D-13-00106.1 received 8 May 2013; accepted in revision 21 July 2013; corrected proofs received 18 September 2013.

Published Pre-print online 28 March 2014.

© Coastal Education & Research Foundation 2014

(Austin, 2004). The specific name *rosea* is from the Latin *roseaus*, rosy, and refers to the pink flowers. *Canavalia rosea* is synonymous with *Canavalia apiculata* (Piper), *Canavalia arenicola* (Piper), *Canavalia obtusifolia* (Lam.), *Canavalia maritima* (Aubl.), *Dolichos emarginatus* (Jacq.), *Dolichos roseus* (Sw.), and *Dolichos maritimus* (Aubl.), from the Latin *maritimus* meaning “belonging to the sea.” In English, the species is known as bay bean, seaside jackbean, coastal jackbean, and beach bean. It is called “feijão-depraia” in Brazil, “frijol-de-la-playa” in Costa Rica and Mexico, “mateblanco” or “mate-de-costa” in Cuba, and “Noumahlanga” in various parts of Portuguese-speaking Africa (Corrêa and de Azeredo-Penna, 1984; Kitajima *et al.*, 2008). In Hawaii, several species of the genus *Canavalia* were called “awikiwiki” by native Hawaiians. The name comes from the Hawaiian word for “fast” and means “the very quick one” (Pukui and Elbert, 1986; USDA, 2007).

Taxonomic Description

Kingdom: Plantae
 Subkingdom: Tracheophytas
 Super phylum: Espermatophyta
 Phylum: Magnoliophyta
 Class: Magnoliopsida
 Subclass: Rosidae
 Order: Fabales
 Family: Fabaceae
 Subfamily: Faboideae (Papilionoideae)
 Subtribe: Diocleinae
 Genus: *Canavalia*
 Subgenus: *Canavalia*
 Species: *rosea* (Sw.) DC

The subfamily Faboideae is represented by herbs, subshrubs, shrubs, trees, vines, and lianas. It contains 478 genera and 13,805 species. Woody species are more common in the tropics, whereas temperate regions present more herbaceous species (Lewis *et al.*, 2005). Leaves are trifoliate, and flowers are strongly zygomorphic, exhibiting one petal larger than the others. The location of the genus *Canavalia* within the subtribe Diocleinae is supported by characteristics such as leaflets and glandular calyx; terete style; nodose inflorescences; presence of bracteoles; seeds with linear thread; presence of the amino acid canavanine; and a chromosome number of $2n = 22$ (de Lange, Murray, and Datson, 2004; Lackey, 1981). The genus *Canavalia* is subdivided into four subgenera: *Catodonia* (seven species) from the New World, *Wenderotia* (16 species) from the New World, *Canavalia* (23 species) from the Old and New Worlds, and *Maunaloa* (six species), a subgenus endemic to Hawaii (Beyra-Matos *et al.*, 2004). Of these, the only pantropical species is *C. rosea* (Figure 1).

Seed Morphology

Legumes are $7\text{--}15 \times 2\text{--}2.5$ cm, linear oblong, moderately compressed, initially appressed-pubescent, later glabrous, sometimes pleated, spirally dehiscent or sometimes with explosive dehiscence, and light brown; each valve has sutural ribs and an extra rib 3 cm from the ventral rib. The pods are flat and approximately 10–15 cm long and 2.5 cm wide. They are prominently ridged and woody when mature. Pods contain between four and nine seeds, 12–18 mm \times 7–12 mm in size and

10 mm thick, pale yellow smooth or darker brown, almost black, ellipsoid, slightly compressed, with 7–8.5 mm thread length and 0.57 g in weight (Beyra-Matos *et al.*, 2004; Sauer, 1964). Seeds are dispersed by ocean currents (Beyra-Matos *et al.*, 2004; Sauer, 1964; Vatanparast *et al.*, 2011).

Seedling Morphology

The presence of seedlings on the beach occurs mostly during the rainy season (Martínez and Moreno-Casasola, 1996). Newly germinated seedlings have thick and large cotyledons that can last several weeks until the first leaves are formed. Immature seedlings resemble the adult plants and grow rapidly. The seedlings are capable of extensive lateral spread on bare sand (Moreno-Casasola, Grime, and Martínez, 1994).

Shoot Morphology

Canavalia rosea has a creeping habit. Stems are pubescent with white hairs when young and later glabrate. The thick, fleshy stem of *C. rosea* can grow to 10 m or more in length, and about 2.5 cm in diameter, although it is normally much thinner. The stem is rather woody near the base, and several branches radiate outwards, forming mats of light green semisucculent foliage. The plant is capable of climbing, up to a height of 2 m or more over other vegetation when it reaches further inland from the coastal dunes. Leaves are pinnately trifoliate leaflets. Leaflets are $5\text{--}10 \times 4\text{--}10$ cm, broadly obovate, ovate, or orbicular, apically rounded or emarginate, occasionally short acuminate, broadly cuneate, rounded or truncate at the base, coriaceous, and puberulent with short white hairs on both surfaces or moderately dense on the lower epidermis and the petiolules; petiole is 2–7 cm long; rachis is 1.3–3.7 cm long; petiolules are 3–5 mm long; stipules are deciduous lanceolate and 4 mm long (Beyra-Matos *et al.*, 2004).

Root Morphology

The root of *C. rosea* is deep and largely monopodic; however, with no water or nutrient restrictions, the roots may branch profusely and present greater biomass allocation (Valverde, Pisanty, and Rincón, 1997). The relatively ligneous root forms rhizobial nodules that undertake symbiotic fixation of atmospheric nitrogen. The nodules are located on the lateral roots and are spherical in shape (2–4 mm in diameter) and pink in color (Chen *et al.*, 2000).

Inflorescence

The inflorescences are axillary and racemose. The plant blooms most of the summer and sporadically throughout the rest of the year. Flowers are axillary and racemose, located in small groups along the peduncle, which is thickened at the insertion points, bearing two to six pedicellate flowers, each with two deciduous bracteoles and a calyx at the base. Flowers are zygomorphic and hermaphroditic. The calyx is gamosepalous (sepals fully or partly united), 10–12 mm long, with a tubular base, with sparsely to moderately dense short white hairs. The upper lip is much shorter than the base, with a constricted upper edge behind and not at the apex, apiculate; tooth length is less than 2 mm, sharp, slightly exceeding the sharp side lobes. Free wings standard is rounded or elliptical, 2.5–3 cm long and 1.5–2.1 cm wide, reflexed, narrow, ligulate,



Figure 1. *C. rosea* growing in its natural habitat. (a) Dense mats of *C. rosea* growing at the beach. (b) Close-up of the leaves and inflorescence. (c) Close-up of green pods. (d) *Xylocopa* visiting the flowers of *C. rosea*. (Photo credits: a, b, and c, Gonzalo Castillo; d, Armando Aguirre.)

obtuse, and auriculate at the base; keel is wider than the wings. Sessile ovary is puberulent, multi-ovulate, slim style, and glabrous; stigma is small and terminal. The corolla is zygomorphic, pentamerous, and pink. The typical pea flowers (5 cm long) are pink-purple and are located on erect and long stalks, surpassing the height of the leaf mat (Beyra-Matos *et al.*, 2004).

Chromosome Number

Meiotic chromosome number is $n = 11$ (Goldblatt, 1981) and $2n = 22$ (Lackey, 1981).

Ecotypes

Canavalia veillonii has been considered as a potential ecotype of *C. rosea*, although more information is necessary to confirm the validity of the taxon. This ecotype has a very limited range of occurrence, being restricted to an area of occupancy of 4 km². It is endemic to a single dry forest in New Caledonia, which is among the most threatened ecosystems in

that archipelago, since its dry forests have been dramatically reduced in both size and quality (Hequet, 2010).

Phylogeny

Sauer (1964) suggested that the genus *Canavalia* diverged from other Phaseolae during the Cretaceous. In the Wilcox flora (from sea beaches in the Tennessee-Mississippi region, during the Eocene), the leaves of several fossil plants are very similar to those of *C. rosea*. These fossil plants were named *Canavalia eocenica* (Berry, 1916) and *Leguminosites andiriformis* (Berry, 1930), although the differences in leaf shape between these two forms fall within the natural variation of living species (Sauer, 1964). These findings suggest that the genus *Canavalia* has a New World origin, which coincides with the indirect evidence from the present geography of the genus and its relatives, *i.e.* all the species of three (*Camptosema*, *Cratylia*, and *Cleobulia*) of the five genera of the subtribe Diocleinae are Neotropical, and most of the species of *Dioclea* and *Canavalia* are also from the tropical regions of the New

Table 1. Geographic distribution of the pantropical species *C. rosea*.

Region	Country
New World	
North America	United States (Florida, Texas), Mexico
Central America	Guatemala, Honduras, Belize, El Salvador, Nicaragua, Costa Rica, Panama
Antilles	Cuba, Dominican Republic, Bermuda, Haiti, Jamaica, Puerto Rico, Virgin Islands, Bahamas, Cayman Islands, Swan Island, San Andres, Trinidad & Tobago
South America	Colombia, Venezuela, Brazil, Ecuador, Galapagos Islands, Peru, French Guiana, Guyana, Suriname
Old World	
Africa	Mauritania, Senegal, Portuguese Guinea, Republic of Guinea, Sierra Leone, Liberia, Ivory Coast, Ghana, Thogo, Dahomey, Nigeria, Cameroon, Sao Thome, Gabon, Republic of Congo, Angola, South Africa, Mozambique, Tanganyika, Kenya, Zanzibar, Madagascar, Rodriguez, Seychelles
Asia	India, Nicobar Island, Burma, Malaya, Singapore, Thailand, Cambodia, Vietnam, China, Formosa
Oceania	Philippines, North Borneo, Indonesia, Western New Guinea, northeast of New Guinea, Papua New Guinea, Solomon Islands, New Caledonia, Hawaiian Islands, Australia

World. Pantropical species and subgenera share the capacity for long-distance sea dispersal. The only Old World genus, *Pueraria*, is not particularly closely related to the subgenus *Canavalia* (Sauer, 1964).

Based on several attributes, such as seed and flower morphology, Sauer (1964) reported that the most primitive subgenus was probably *Wenderothia*, while the subgenera *Catodonia* and *Canavalia* probably originated from *Wenderothia*. In turn, the subgenus *Maunaloa* was probably derived from the subgenus *Canavalia* because of the pantropical occurrence of *C. rosea*, which belongs to the subgenus *Canavalia*.

Sauer (1964) considered that *C. rosea* is the “prime seafaring progenitor” of other inland and island *Canavalia* species. It is assumed that, in Mesozoic America, the presumably original *Canavalia* population was small, panmictic, and homogeneous, and that it gradually became specialized with increased geographic expansion (Sauer, 1964). Sauer (1964) noted that *C. rosea* may have dispersed around the tropics of the world and spawned a large number of similar but discrete species, some of which have lost the capacity for long-distance dispersal, as well as adaptations to the shoreline habitat, as is the case with inland *Canavalia* species. The process of speciation is not known; however, given that some of the most morphologically proximal species are geographically discrete, it is likely that allopatric rather than sympatric speciation has taken place.

More recently, the phylogenetic relationships among *C. rosea* and its allied species, as well as the Hawaiian endemic species, were studied using chloroplast DNA (cpDNA) and internal transcribed spacers (ITS) of nuclear ribosomal DNA (nrDNA) (Vatanparast, 2010). The results suggested a rapid speciation

among *C. rosea* and its related oceanic species (Vatanparast, 2010). In agreement with the findings of Sauer (1964), it is suggested that long-distance dispersal has played a role in the expansion of the distribution range of the species, and, as theory predicts, speciation probably occurred in marginal populations because of a reduced and more limited gene flow.

GEOGRAPHIC DISTRIBUTION

The geographic distribution of *C. rosea* is pantropical; the species is naturally found on tropical and subtropical seashores throughout the New and Old World (Table 1 and Figure 2). The highest concentration of species within the genus *Canavalia* occurs in the Neotropics. Thirty-seven species are found in this biogeographic region, whereas only 15 are from the Palearctic, mainly the Indian Ocean and the western portion of the Pacific Ocean (Beyra-Matos *et al.*, 2004).

RANGE OF HABITATS

Zone of Occurrence

Canavalia rosea is ecologically important in coastal ecosystems, where it is a pioneer species on sand dunes and beaches of tropical and subtropical coasts (D’Arcy, 1980). Typical habitats of *C. rosea* are the beach, the backshore above the high tide mark, and the foredunes, but it can sometimes climb over rocks and shrubs. Occasionally, it can also grow near the shore of coastal lagoons and roadsides. It can form monospecific patches with a cover of 25–50%, although it is frequently found with *Ipomoea pes-caprae*, another pantropical vine (Devall, 1992; Moreno-Casasola, 1991).

Substrate Characteristics

Typically, *C. rosea* grows on sandy substrates with low organic matter and nutrient content. Soil analyses have been performed in different parts of the world where *C. rosea* typically grows (Table 2). In general, the results from these studies (Emilio *et al.*, 2006; Henriques and Hay, 1998; Moreno-Casasola, 1982) indicate that *C. rosea* grows in relatively alkaline substrates, featuring extremely low organic matter content and reduced moisture (Table 2). Macronutrients (N, P, K) are also usually low, although they can sometimes be higher and increase progressively with distance inland. It has been observed that micronutrients can sometimes be relatively abundant, as was found in the United States with calcium, indicating calcareous sand, and in Mexico with Na and Cl, providing evidence that *C. rosea* is tolerant to salinity (Table 2). Finally, in the sand where *C. rosea* grows, magnesium levels can vary widely from 15 to almost 190 ppm (Emilio *et al.*, 2006; Henriques and Hay, 1998; Moreno-Casasola, 1982) (Table 2).

Climatic Requirements

We revised the Global Biodiversity Information Facility database (GBIF, <http://www.gbif.org/>) and collated each location where *C. rosea* has been recorded (932 locations throughout the world). We then combined the spatially explicit information regarding mean annual precipitation and temperature (according to WorldClim, <http://www.worldclim.org/>) with the GBIF database, in order to evaluate the weather conditions under which this species grows (Table 3).

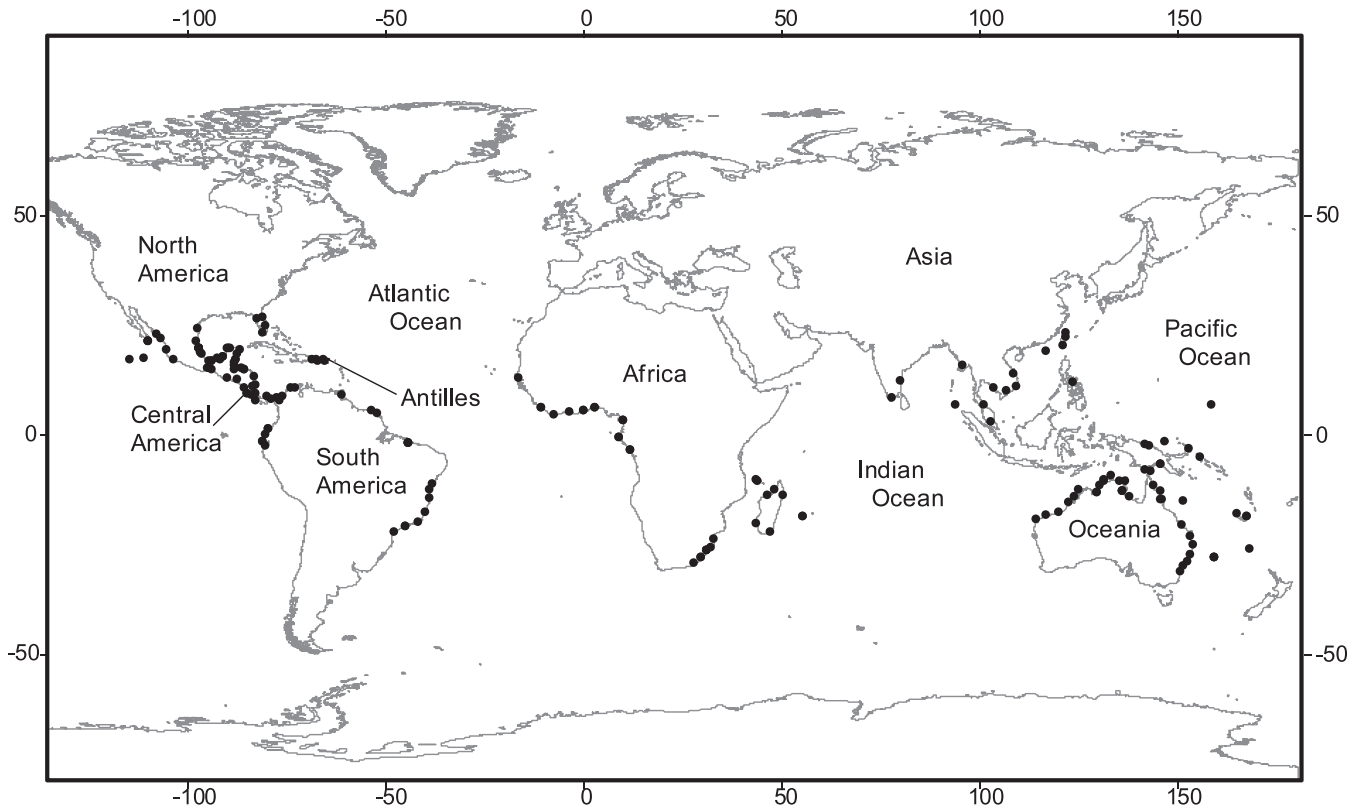


Figure 2. Pantropical distribution of *C. rosea* around the world. Relocated records were obtained from GBIF (Global Biodiversity Information Facility, 2013).

From this analysis, we were able to determine that *C. rosea* generally grows in locations with extreme annual precipitation that fluctuates between 101 to 6717 mm/y. However, the species is most frequent in sites that are moderately rainy, with total annual precipitation ranging from 1000 to 2000 mm. Similarly, mean annual temperature at the locations where this species grows varies drastically and ranges from 15.2 to

28.8°C; however, the species is most abundant where mean annual temperature ranges from 24 to 28°C (Figure 3). The weather regime where *C. rosea* grows varies throughout its distribution (Figure 3). The widest temperature ranges occur in Oceania, varying from 15 to 29°C, whereas the widest precipitation ranges are found in North and South America, where the driest and wettest sites are located. More moderate weather fluctuations occur in Africa and Asia.

Table 2. Soil analysis at locations where *C. rosea* grows.

	Mexico ^a	USA ^b	Brazil ^{c,d}
pH	8.8	7.77–8.51	4.5–7.72
Organic matter (%)	0.17	0.76–3.64	0.3–2.7
Moisture (%)	1.99	1.16–15.93	0.68–6
Ammonium N (ppm)		1.91–4.80	
N (ppm)	70	1.91–4.80	ND ^e
P (ppm)	0.21	2.54–21.50	ND
K (ppm)	15.21	2.11–13.28	ND
Ca (ppm)	47.8	1805–2487	39.1–77.3
HCO ₃ (ppm)	171.34	ND	ND
Na (ppm)	79.81	ND	7.4–10.1
Cl (ppm)	57.155	ND	ND
SO ₄ (ppm)	131.52	ND	ND
Mg (ppm)	15	59.27–189.3	74.2–98.8

^a Data from Moreno-Casasola (1982).

^b Data from Lane *et al.* (2008).

^c Data from Emilio *et al.* (2006).

^d Data from Henriques and Hay (1998).

^e ND = no data.

Mendoza-González *et al.* (2013) modeled the climatic niches of six coastal dunes plant species and projected their future potential distributions based on two climate change scenarios and projections of sea-level rise. Their results suggested that, by 2050 or 2080, the distribution of *C. rosea* in the Gulf of Mexico will be reduced by at least 50% (Mendoza-González *et al.*, 2013).

PLANT COMMUNITIES

Canavalia rosea is a pioneer creeping plant that grows on the beach, foredunes, and occasionally (and less abundantly) towards the thickets in the sheltered zone behind the foredunes. The species is frequently associated with plants that occur on most tropical beaches, such as: *Sporobolus virginicus*, *Sesuvium portulacastrum*, *Remirea maritima*, and *Scaevola plumieri* (Araujo and Pereira, 2004; Castillo and Moreno-Casasola, 1996; Emilio *et al.*, 2006; Florence, Waldren, and Chepstow-Lusty, 1995; Henriques and Hay, 1998; Lane *et*

Table 3. Precipitation and temperature intervals in which *C. rosea* grows.

	Precipitation Interval (mm)	Yearly Precipitation Range where <i>C. rosea</i> is Most Frequent (mm)	Temperature Interval (°C)	Mean Annual Temperature Range where <i>C. rosea</i> is Most Frequent (°C)
North America	115–5826	<2000	20.1–28.2	25–27
South America	101–6717	<3000	21.6–28.3	24–27
Africa	434–4513	1000–3000	18.2–27.2	25–27
Asia	828–2964	1000–3000	21.7–27.2	22–25
Oceania	229–4459	<2000	15.2–28.8	26–28

al., 2008; Lokkers, 2000; Moreno-Casasola, 1982; Moreno-Casasola and Espejel, 1986; Müller-Hohenstein, 1992; Viana and dos Santos, 2002) (Table 4). In particular, *C. rosea* is physiognomically and ecologically similar to *I. pes-caprae* (Convolvulaceae), with which it is frequently associated in pantropical distribution, forming dense communities of low-lying plants (Devall, 1992), although *I. pes-caprae* grows closer to the ocean, while *C. rosea* can cross the first beach ridge (Moreno-Casasola and Espejel, 1986). These species are found throughout the tropical regions of the American and African continents. For example: *Chrysobalanus icaco* and *Dalbergia ecastaphyllum* are present in the transition zone between dunes and saline areas, while *Chromolaena odorata* and *Ipomoea imperati* are found in the foredunes (Castillo and Moreno-Casasola, 1996; Gallego-Fernández and Martínez, 2011; Lane et al., 2008; Müller-Hohenstein, 1992; Siebert and Mössmer, 2002).

Canavalia rosea is frequently associated with cosmopolitan species. In America, Asia, and Oceania, it coexists with *Casuarina equisetifolia*, an invasive species originally from Australia (Castillo and Moreno-Casasola, 1996; Kolbek and Alves, 1993; Lokkers, 2000), and in Africa, Asia, and Oceania, it is found with *Cordia subcordata* (Kingston, Waldren, and Bradley, 2003). On the tropical coastlines of the Americas and

Asia, it is associated with *Catharanthus roseus*, *Chamaesyce hyssopifolia*, *Chamaesyce prostrata*, *Digitaria fucescens*, *Digitaria sanguinalis* cf. var. *pruriens*, *Eleusine indica*, *Portulaca oleracea*, *Stachytarpheta indica*, and *Stenotaphrum secundatum* (Castillo and Moreno-Casasola, 1996; Emilio et al., 2006; Kolbek and Alves, 1993). On the coastline of America and Oceania, *C. rosea* has been described as occurring together with *Cassytha filiformis*, *Cenchrus echinatus*, *Fimbristylis cymosa*, *Paspalum vaginatum*, and *Suriana maritima* (Emilio et al., 2006; Florence, Waldren, and Chepstow-Lusty, 1995; Kingston, Waldren, and Bradley, 2003; Lokkers, 2000).

PHYSIOLOGICAL ECOLOGY

Physiology

The success of *C. rosea* as a pioneer species of beaches and foredunes is related to its capacity for long-distance dispersal but also to its tolerance of salt spray, sand scouring and burial, high substrate temperatures, and low levels of soil nutrients (Moreno-Casasola, Grime and Martínez, 1994). The leaflets close under the hot sun at midday, which reduces evapotranspiration.

Kienholz (1927) observed a rapid elongation in plant stems of *C. rosea* (16 mm in 36 hours), which occurred on a clear and hot day “with little air movement.” Valverde, Pisanty, and Rincón (1997) observed that *C. rosea* was able to survive and reproduce successfully when growing in sand with very low nutrient content, but also that it responded to increased nutrients. In a greenhouse experiment, newly germinated *C. rosea* seedlings were sown under different substrate conditions: continuously nutrient poor, continuously nutrient rich, predictable nutrient pulses, and unpredictable nutrient pulses. Biomass increased markedly in nutrient-rich conditions (Table 5). Plants growing in nutrient-poor sand (watered only with distilled water) showed the lowest biomass values, while the biomass increased to a lesser degree with different nutrient pulses. The same trends were observed in relation to leaf area, which increased with additional nutrients. Biomass partitioning also varied with nutrient treatments. As expected, biomass allocation to roots was higher in low nutrient conditions (even with predictable or unpredictable pulses) (Table 5). Growth rate increased twofold when seedlings were exposed to increased nutrient levels in the sand (Table 5). Interestingly, responses to both predictable and unpredictable pulses were not as evident as in the permanently nutrient-rich environment (Table 3). This study demonstrates the ability of *C. rosea* to tolerate extremely nutrient-limited conditions (Valverde, Pisanty, and Rincón, 1997).

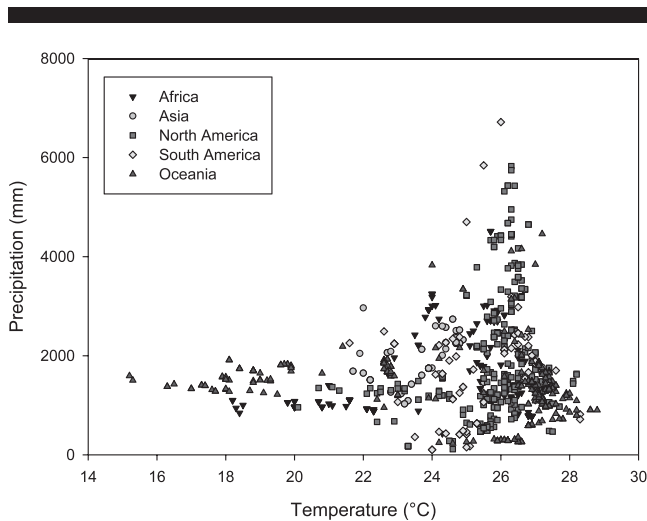


Figure 3. Bidimensional ecological distribution (annual precipitation and mean temperature), considering species locations. Different symbols and gray scale show the pantropical distribution (data from WorldClim, 2013 and GBIF, 2013).

Table 4. Floristic associations of *C. rosea* throughout its pantropical distribution.

Species	America	Africa	Asia	Oceania
<i>Acicapha spathulata</i>	X			
<i>Allophylus rhomboidalis</i>				X
<i>Alyxia fosbergii</i>				X
<i>Alternanthera maritima</i> var. <i>africana</i>		X		
<i>Amaranthus greggii</i>	X			
<i>Ambrosia hispida</i>	X			
<i>Argusia argentea</i>				X
<i>Arundo donax</i>	X			
<i>Bidens alba</i> var. <i>radiata</i>	X			
<i>Bidens hendersonensis</i>				X
<i>Blutaparon portulacoides</i>	X			
<i>Boerhavia tetrandra</i>				X
<i>Borreria capitata</i>	X			
<i>Borreria scabesoides</i>	X			
<i>Caesalpinia major</i>				X
<i>Capparis cordifolia</i>				X
<i>Casuarina equisetifolia</i>	X		X	X
<i>Cakile edentula</i>	X			
<i>Cakile geniculata</i> o <i>C. lanceolata</i>	X			
<i>Catharanthus roseus</i>	X		X	
<i>Cassythia filiformis</i>	X			X
<i>Cenchrus echinatus</i>	X			X
<i>Chamaecrista chamaecristoides</i>	X			
<i>Chamaesyce hyssopifolia</i>	X		X	
<i>Chamaesyce mesembrianthemifolia</i>	X			
<i>Chamaesyce prostrata</i>	X		X	
<i>Chromolaena odorata</i>	X	X		
<i>Chrysobalanus icaco</i>	X	X		
<i>Clerodendrum inerme</i>				X
<i>Cnidoscopus texanus</i>	X			
<i>Coccoloba barbadensis</i>	X			
<i>Coccoloba uvifera</i>	X			
<i>Coccothrinax argentata</i> , <i>C. littoralis</i>	X			
<i>Cocos nucifera</i>	X			
<i>Commelina erecta</i>	X			
<i>Cordia subcordata</i>		X	X	X
<i>Croton punctatus</i>	X			
<i>Crotolaria pumila</i>	X			
<i>Cyperus stolonifera</i>				X
<i>Dalbergia ecastaphyllum</i>	X	X		
<i>Digitaria fuscens</i>	X		X	
<i>Digitaria sanguinalis</i> cf. var. <i>pruriens</i>	X		X	
<i>Diodia radula</i>	X			
<i>Eleusine indica</i>	X		X	
<i>Eugenia reinwardtiana</i>				X
<i>Fimbristylis cymosa</i>	X			X
<i>Fimbristylis spadicea</i>	X			
<i>Geniostoma hendersonense</i>				X
<i>Glochidion pitcairnense</i>				X
<i>Guettarda speciosa</i>				X
<i>Heliotropium anomalum</i>				X
<i>Hydrocotyle bonariensis</i>	X			
<i>Ipomoea imperati</i>	X	X		
<i>Ipomoea littoralis</i>	X			
<i>Ipomoea macrantha</i>				X
<i>Ipomoea pes-caprae</i>	X	X	X	X
<i>Iva imbricata</i>	X			
<i>Lantana involucrata</i>	X			
<i>Lepturus repens</i>				X
<i>Lycium sandwichense</i>				X
<i>Mariscus pedunculatus</i>	X			
<i>Melanthera aspera</i>	X			
<i>Metopium toxiferum</i>	X			
<i>Mollugo verticillata</i>	X			
<i>Momordica charantia</i>	X			
<i>Oenothera drummondii</i>	X			
<i>Okenia hypogaea</i>	X			

Table 4. Continued.

Species	America	Africa	Asia	Oceania
<i>Oxypetalum banksii</i> ssp. <i>corymbiferum</i>	X			
<i>Palafoxia lindenii</i>	X			
<i>Palafoxia texana</i>	X			
<i>Pandanus tectorius</i>				X
<i>Panicum amarum</i>	X			
<i>Panicum racemosum</i>	X			
<i>Paspalum vaginatum</i>	X			X
<i>Pectis saturejoides</i>	X			
<i>Philoxerus vermicularis</i> , <i>Blutaparon vermiculare</i>	X			
<i>Phymatosorus scolopendria</i>				X
<i>Pithecellobium keyense</i>	X			
<i>Pittosporum</i> aff. <i>arborescens</i>				X
<i>Plantago australis</i>	X			
<i>Portulaca lutea</i>				X
<i>Portulaca oleracea</i>	X		X	
<i>Remirea maritima</i>	X			
<i>Santalum insulare</i> var. <i>hendersonense</i>				X
<i>Scaevola plumieri</i>	X	X		
<i>Scaevola sericea</i> o <i>S. taccada</i>				X
<i>Schinus terebinthifolius</i>	X			
<i>Schizachyrium scoparium</i> , <i>S. littorale</i>	X			
<i>Senecio stokesii</i>				X
<i>Serenoa repens</i>	X			
<i>Sesuvium portulacastrum</i>	X	X	X	X
<i>Sphagneticola trilobata</i>	X			
<i>Sophora tomentosa</i>	X			
<i>Sorghum halepense</i>	X			
<i>Sporobolus virginicus</i>	X	X	X	
<i>Stachytarpheta indica</i>	X		X	
<i>Stenotaphrum secundatum</i>	X		X	
<i>Stylosanthes hamata</i>	X			
<i>Suriana maritima</i>	X			X
<i>Thespesia populnea</i>				X
<i>Thuarea involuta</i>				X
<i>Timonius polygamus</i>				X
<i>Tournefortia gnaphalodes</i>	X			
<i>Trachypogon plumosus</i>	X			
<i>Triplasis purpurea</i>	X			
<i>Triumfetta procumbens</i>				X
<i>Uniola paniculata</i>	X			
<i>Vigna luteola</i>	X			
<i>Vigna marina</i>		X		
<i>Wedelia biflora</i>			X	X

Pérez-Maqueo (1995) studied the tolerance of seedlings of *C. rosea* to salinity. In a greenhouse experiment, he exposed two-month-old seedlings to saltwater inundation. He observed that seedlings were able to survive exposure to saltwater for at least 90 days, although their growth rate was inhibited. Biomass accumulation in seedlings exposed to saltwater was around half (0.94 g) that of the control group (2.01 g), a difference which was significant ($P < 0.05$). Relative growth rate was positive in the control group but negative in seedlings exposed to salinity. These results can be interpreted as tolerance to salinity, but with a long-term deleterious effect when exposure to salinity was constant.

Phenology

The phenological behavior of tropical coastal dune plants was observed by Castillo and Carabias (1982). They stated that *C. rosea* is almost always in a leafy condition and only sheds leaves sporadically. New leaves are produced at the beginning

Table 5. Total dry biomass (*B*), root/shoot ratio (*R/S*), leaf area (*LA*), and relative growth rate (*RGR*) of *C. rosea* seedlings, after growing for 90 days under different nutrient regimes. Significant differences between the means are indicated by different lowercase letters ($p < 0.05$, Tukey-Kramer test) (after Valverde, Pisanty, and Rincón, 1997).

Treatment	<i>B</i> (g)	<i>R/S</i>	<i>LA</i> (cm ²)	<i>RGR</i> (g g ⁻¹ d ⁻¹)
Distilled water	2.1 a	0.7 a	64.8 a	0.017 a
Unpredictable nutrient pulses	3.5 b	0.57 ab	93.5 ab	0.022 b
Predictable nutrient pulses	3.7 b	0.53 b	133.6 b	0.024 b
Nutrient-rich	7.2 c	0.53 b	265 c	0.031 b
Significance	0.0001	0.001	0.0001	0.001

of the rainy season. Plants are in flower most of the summer and at the end of the rainy season. Occasionally, flowers were produced throughout the rest of the year. Anthesis was diurnal, beginning around sunrise and lasting about 10 hours. Fructification occurred during the dry season (Beyra-Matos *et al.*, 2004; Moreno-Casasola, Grime, and Martínez, 1994; Martínez and Moreno-Casasola, 1996).

POPULATION BIOLOGY

Perennation

The beach bean is a perennial, climbing or trailing herbaceous vine (Beyra-Matos *et al.*, 2004). It is a chamaephyte, with perennating buds located no more than 25 cm above the soil surface (Raunkiaer, 1934). Sexual reproduction occurs by seed production with dispersal by sea currents (Verçoza, do Nascimento, and Ribeiro, 2010). Seed germination is usually low in *C. rosea* due to hard coat dormancy, but it can germinate readily following imbibition in warm water for several hours (Williams, 2007), and also after extreme temperature fluctuations (Moreno-Casasola, Grime, and Martínez, 1994).

Population Dynamics

Population dynamics of *C. rosea*, in terms of reproduction and survival, have not been studied. Nevertheless, gene flow can be an additional method with which to study population dynamics, in relation to migration between populations. Vatanparast (2010) and Vatanparast *et al.* (2011) employed molecular markers and used short fragments of 6 cpDNA regions to perform a population genetic analysis of *C. rosea* on a global scale. These authors found that frequent gene flow occurs in *C. rosea*. Exchange of genes among populations occurs via pollination and seed dispersal. In the case of *C. rosea*, ample gene flow takes place as a result of the long-distance nature of the seed dispersal.

Vatanparast (2010) and Vatanparast *et al.* (2011) studied the genetic structure of cpDNA sequences of *C. rosea* and related species from 48 populations in 515 individuals and found that: (1) no significant genetic differentiation exists among populations throughout the Pacific and Indian Ocean regions. The same general trends were observed within the Atlantic region, indicating significant long-distance gene flow (transatlantic and transpacific). (2) While there was good evidence of transatlantic long-distance dispersal, seed dispersal limitation caused by the presence of the Isthmus of Panama produced a clear genetic difference between the Pacific and Atlantic

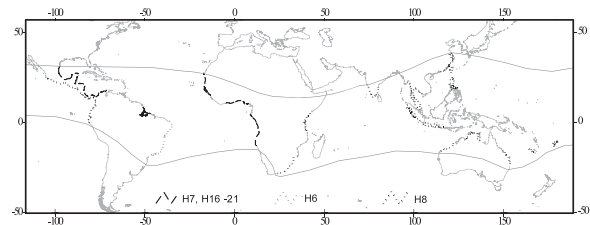


Figure 4. Distribution map of the haplotypes identified by partial sequence. Symbols represent the different haplotypes; gray line represents the pantropical distribution of *C. rosea* (modified from Vatanparast, 2010). Haplotypes H7 and H16–21 are from the Atlantic Ocean, except Brazil, which corresponds to H6. Haplotypes H8 are from Tanzania, India, and Java in the Indian Ocean.

populations in terms of the distribution of the cpDNA haplotype (Figure 4). (3) Populations in southern Brazil were highly different from other populations in the Atlantic, probably because of the action of the bidirectional South Equatorial Current, which bifurcates at the northeastern horn of Brazil; the northbound and southbound currents appear to act as a barrier to gene flow (Figure 4) (Vatanparast, 2010).

REPRODUCTION

Sexual Reproduction

Canavalia rosea produces flowers during the rainy season and fruits and seeds during the dry season. Due to their hard coat dormancy, seeds may fail to germinate unless exposed to extreme temperature fluctuations (Moreno-Casasola, Grime, and Martínez, 1994; Williams, 2007). Seedling mortality is high (D’Cunha and Sridhar, 2011).

Pollination and Fertilization

One of the petals of *C. rosea* is larger and longer (standard) and serves as a landing platform for flower visitors, assisting in the collection of nectar and pollen. These floral attributes are considered as a “melittophily syndrome” (Faegri and van der Pijl, 1979). The large flowers of *C. rosea* are visited by bees of medium and large sizes: *Bombus*, *Centris*, and *Xylocopa* (Endress, 1994; Gross, 1993). Verçoza, do Nascimento, and Ribeiro (2010) observed that *Tetragonisca angustula*, *Trigona spinipes*, and *Apis mellifera* also visited the flowers of *C. rosea*. However, these smaller visitors are considered pollen thieves, since they are of insufficient weight to force the standard petal down and reach the nectar and reproductive organs deeper within the flower. However, large bees such as *Xylocopa frontalis* (carpenter bee) (30 mm long approximately) force the standard petal down and reach the pollen and reproductive organs (Lindsey, 1984; Sugden, 1986). The reproductive organs then come into contact with the body covered with pollen, thus achieving pollination. This bumblebee is therefore considered an effective pollinator of *C. rosea*, making the plant directly dependent upon this bee for fruit and seed production (Verçoza, do Nascimento, and Ribeiro, 2010).

Xylocopa frontalis bees carry out solitary visits throughout the day, but their activity is most intense between 0800 and 1000 h. These bees always visit more than one flower per plant

and flowers from different individuals. This kind of foraging can be explained by the small amounts of nectar produced per flower, which obliges the insect to visit many flowers several times in order to fulfill their feeding requirements. This foraging strategy promotes the flow of pollen between plants and consequently, cross-pollination, which is fundamental for fruit and seed production (Endress, 1994; Frankie *et al.*, 1983). Pollination of *C. rosea* by *X. frontalis* has been observed in different locations, such as Brazil (Gottsberger, Camargo, and Silberbauer-Gottsberger, 1988; Verçoza, do Nascimento, and Ribeiro, 2010), Indonesia (Gross, 1993), and Mexico (field observations). This bumblebee also behaves as a pollinator of some of the sympatric species of *C. rosea*, namely, *I. pes-caprae* and *I. imperati* and back-dune vegetation such as *Crotalaria vitellina* and *Sophora tomentosa* (Leguminosae-Papilionoideae) and *Opuntia monacantha* (Cactaceae) (Prabhu *et al.*, 2010).

Gross (1993) found that autogamy and selfing rendered a null fruit-set, whereas out-crossing was the only pollination treatment that produced seeds. This confirms that the requirement for pollen vectors is obligate in *C. rosea*.

Seed Production

Does a wide distribution range make it a successful colonizer? Gross (1993) studied the reproductive behavior of *C. rosea* in Krakatau (Indonesia), and the findings were contrary to that expected for a pioneer species: The fruit-to-flower ratio was extremely low, ranging from 10 to 19%. Gross (1993) examined the flowering and fruiting phenology, breeding system, and floral visitors and tested whether such a low fruit-set was explained by (1) lack of pollinators, (2) pollinator infidelity, or (3) other limiting resources, such as nutrients. This author observed that neither the presence of pollinators nor the levels of deposited pollen were sufficiently low to explain the low fruit-set in the population. However, when pods were removed, fruit-set increased fivefold on the subsequent flowers, indicating that fruit production was resource-limited.

Dispersal

On maturity, seeds of *C. rosea* are ejected with great force from the twisted pods as they dry and turn brown. Once on the sand, seeds can then be dispersed over great distances by ocean currents (Vatanparast *et al.*, 2011). The seeds are buoyant and germinate and begin the process of colonization upon reaching new shores. Interestingly, Gross (1993) reported that *C. rosea* was recorded on Krakatau Island only 3 years after the catastrophic eruption of 1883, which demonstrates the colonizing ability of this species.

Seed Bank and Seed Size

The pods, which are produced at the end of the rainy period, are flat and about 10–15 cm long and 2.5 cm wide. They are prominently ridged and woody when mature and usually contain about six seeds per pod (Beyra-Matos *et al.*, 2004). Mean seed weight varies from 0.5 to 0.65 g (Arun *et al.*, 2003; Corkidi and Rincón, 1997; Moreno-Casasola, Grime, and Martínez, 1994), and mean seed length is 1.4 cm (Moreno-Casasola, Grime, and Martínez, 1994). Mean cotyledon weight is 0.35 ± 0.07 g, and mean seed coat weight is 0.15 ± 0.02 g (Arun and Sridhar, 2004). No seed banks have been reported.

However, it is reasonable to assume that a seed bank could exist because of the long-lasting hard-coat dormancy of the seeds (Moreno-Casasola, Grime, and Martínez, 1994). Additionally, Gross (1993) suggested that all year-round seed production could lead to accumulation of seeds in the sand. This would guarantee the presence of seeds in the ground when environmental conditions are favorable, thus enabling germination. This feature further enhances the colonizing success of this pioneer species.

Germination Ecology

Seeds of *C. rosea* are hard-coated and thus unable to germinate easily, unless this dormancy is broken. Moreno-Casasola, Grime, and Martínez (1994) studied the germination ecology of hard-coated seeds from coastal dune species. They used daily fluctuating temperatures and moisture regimes to test how dormancy was broken without mechanical scarification. Maximum temperature was 60°C, which naturally occurs on dry sand on a hot summer day with no shade from the sun. These authors found that *C. rosea* seeds presented highest germination percentages under moderate temperature fluctuations (20°C daily), in both laboratory and field experiments (Figure 5). Moreover, germination was higher in both cases when moderate temperature fluctuations coincided with dry conditions, rather than wet/dry cycles. Dormancy is probably broken during the dry season by the moderate to extreme temperature fluctuations that occur prior to the rainy season, when seedlings germinate. The seeds that did not germinate in these experiments were viable, since they germinated readily after mechanical scarification, meaning that they are capable of accumulation in the seed bank until dormancy is finally broken.

Vegetative Reproduction

Canavalia rosea produces long creeping or stoloniferous branches. It is not known whether vegetative propagation can occur when branches are cut from the mother plant (Moreno-Casasola, 1997). However, adventitious roots can be produced from the nodes, providing additional anchorage for runners in the sand (Gross, 1993; Williams, 2007). *In vitro* propagation is also possible with the addition of auxins, and this has been used successfully in the rehabilitation and revegetation of coastal regions (D'Cunha and Sridhar, 2011).

GEOMORPHOLOGICAL INTERACTIONS

Response to Burial

Burial is one of the major factors that affect plants in coastal areas (Gilbert and Ripley, 2010), and many seedlings are lost because of burial by sand (Devall, Thien, and Platt, 1991). Due to the length of the stems in *C. rosea*, sand rarely covers the entire plant. Instead, blowing sand often only covers portions of the stems, and the portions that remain exposed generate new runners. In this way, the plant responds to burial and moves across the beach and foredunes (Britton and Morton, 1989). In common with other coastal dune plants (Disraeli, 1984; Maun and Lapierre, 1984, 1986; Perumal and Maun, 1999; Yuan, Maun, and Hopkins, 1993; Zhang and Maun, 1992), burial in *C. rosea* can increase plant vigor. Martínez and Moreno-Casasola (1996) performed a greenhouse experiment in which six beach

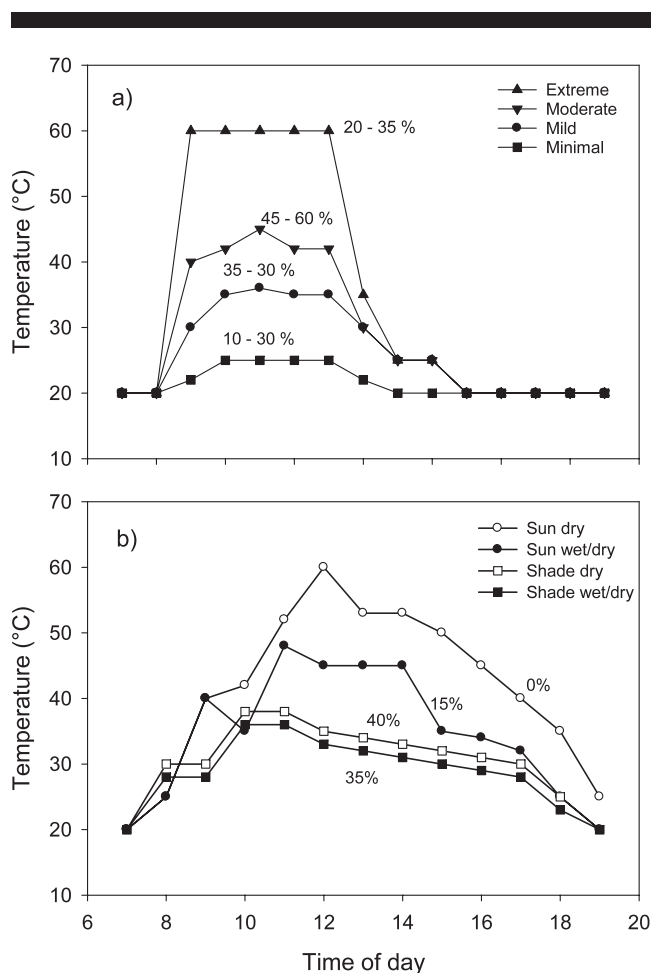


Figure 5. Germination of *C. rosea* seeds following exposure to fluctuating temperature and moisture conditions in the laboratory (a) and in the field (b). Lines show the different treatments to which seeds were exposed for 90 days, and percentage values represent the maximum germination percentage. The first percentage value in the laboratory experiment was under wet/dry conditions, and the second was under dry conditions (after Moreno-Casasola, Grime, and Martínez, 1994).

and coastal dune species were buried. Treatments consisted of the following levels of burial: 0% (control: no burial), 50% (one half of the meristems were buried), and 100% (all the meristems, including the apical meristem, were buried). In all cases, some green tissue was left above the artificially accreted sand. These authors observed that biomass accumulation in *C. rosea* increased after burial by sand, especially when seedlings were 17 weeks old (Figure 6). Root/shoot ratios did not differ significantly between treatments and were always <1 , meaning that more biomass was allocated to shoots than to roots. Finally, leaf area followed the same trend as biomass, with greater than fourfold increases when seedlings were buried by sand at 17 weeks old. These results provide evidence that *C. rosea* is not only tolerant to burial by sand, but is in fact stimulated by it. The increased biomass allocated to shoots and leaf area indicates a mechanism that enables buried plants to reemerge after being covered by sand.

Martínez *et al.* (2002) studied the effects of burial by sand on seed germination in five tropical beach species. In these greenhouse burial experiments, mechanically scarified seeds were placed on a water-saturated bed of sand and then covered by 0 (control), 4 cm, and 16 cm of dry sand. In general, it was observed that seedling emergence took longer with increasing burial depths. Seed burial stimulated germination since seeds covered by 4 cm of sand presented a significantly higher germination percentage (98%) than unburied control seeds (58%). *Canavalia rosea* was the only species with a significantly high germination percentage after burial with 16 cm of sand.

Role in Geomorphology

Beach and coastal dune geomorphology is largely affected by vigorous perennials with extensive root systems that are tolerant to burial by sand. These perennials are normally grasses, but in the tropics, they are replaced by species with trailing vines, such as *C. rosea* and *I. pes-caprae* (Devall, 1992). Specifically, the capacity for lateral growth by means of elongating stolons helps these creeping vines to emerge from accreting sand (Ehrenfeld, 1990). As a consequence, dunes are formed as sand accumulates around the plants and the stolons repeatedly and continuously emerge.

Hesp and Martínez (2008) considered *C. rosea* as a trailing ridge-forming species because of its tolerance to burial and spatial colonization. When these authors examined the evolution and colonization of trailing ridges in central Gulf of Mexico, they found that they were formed after plant colonization of the lateral margins of active dunes (transverse, barchanoidal, transverse, aké, or network dunes). As expected, the early-colonizer dune-forming species were located where substrate mobility was highest, on the youngest end of the trailing ridge. Species such as *Croton punctatus*, *Palafoxia lindenii*, *C. rosea*, and *I. pes-caprae* were most tolerant to burial (Martínez and Moreno-Casasola, 1996), and these were the species that initiated the process of trailing ridge formation (Hesp and Martínez, 2008). With increasing age or inland distance, vegetation cover and diversity increased and sand movement decreased, presenting a successional sequence.

INTERACTIONS WITH OTHER SPECIES

Facilitation

We found no direct evidence of facilitative interactions between *C. rosea* and other accompanying species. Nevertheless, indirect evidence indicates that *C. rosea* probably acts as a nurse plant. On the island of Krakatau, Thornton *et al.* (2002) noted that *C. rosea* was one of the initial beach-colonizing species. The only limitations for successful colonization by *C. rosea* appeared to be the presence of its specific pollinator, the large and solitary carpenter bee *Xylocopa latipes* (Gross, 1993) and the occurrence of *C. rosea* in nearby islands. In addition to efficient colonization, the tolerance to burial and occurrence of nitrogen-fixing nodules in the roots provide evidence that *C. rosea* may potentially be a nurse plant (Thornton *et al.*, 2002).

Symbiosis

Insect herbivores consume both vegetative and reproductive tissues, and damage through herbivory can occur at any stage

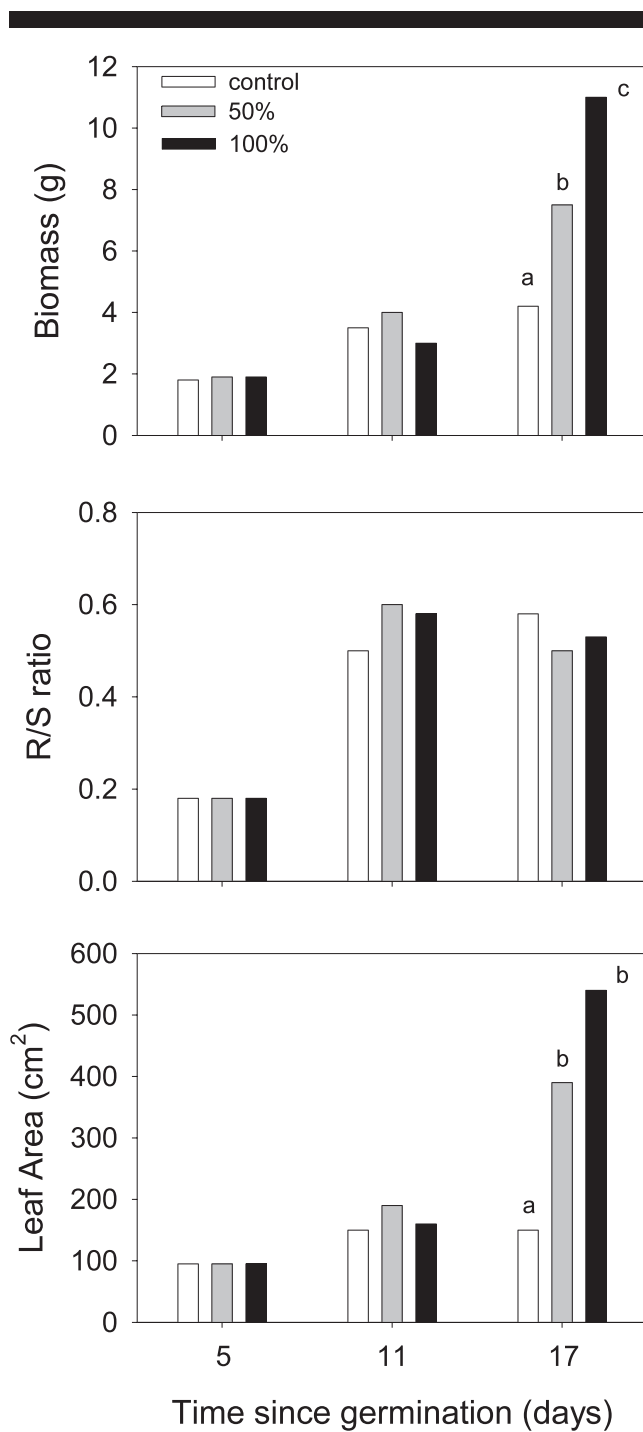


Figure 6. Biomass, root/shoot ratio, and leaf area of seedlings of *C. rosea* exposed to different levels of burial by sand in a greenhouse experiment. Percentage values refer to the percentage of growth of meristems that were artificially covered by dry sand. Different letters indicate significant differences at $p < 0.005$ (after Martínez and Moreno-Casasola, 1996).

of the plant life cycle, with a potentially strong impact on plant fitness (Crawley, 1983). It has therefore been hypothesized that several plant attributes (structural, chemical, physiological) have evolved in response to the selective pressures of

herbivores (Marquis, 1992). The mutualistic interaction between ants and plants is one such defensive strategy, where the plant species produce food rewards, such as extra floral nectaries (EFN). EFNs are nectar-secreting structures that are not directly involved with pollination (Oliveira *et al.*, 1999) and are commonly found in leaves, petioles, stipules, stems, and reproductive structures (Rico-Gray *et al.*, 2004). EFNs attract ants, which, in turn, protect the plant against herbivory by deterring potential herbivores. Ant protection may lead to increased fruit set (Oliveira *et al.*, 1999).

The inflorescences of *C. rosea* have two types of EFNs (Díaz-Castelazo *et al.*, 2005). First, when flower buds are aborted, the pedicel leaves a depression or scar that becomes tumescent and glandular, depositing its sugary content in the scar (Díaz-Castelazo *et al.*, 2005). These scars contain nectar throughout the life of the inflorescence. The second type of EFN is located on the developing shoots along the axils of the leaves. These nectaries are not synchronized with inflorescence production. Instead, they are active during new leaf formation. EFNs from the inflorescence produce more abundant (1.5 μL) and concentrated (16%) nectar than EFNs from the axillary shoots (0.85 μL and 9.5%, respectively) (Díaz-Castelazo *et al.*, 2005). The study of multiple mutualistic interactions between dune plants and ants has demonstrated that *C. rosea* is one of the constant core members of this mutualistic network (Beyra-Matos *et al.*, 2004; Díaz-Castelazo *et al.*, 2010). Díaz-Castelazo *et al.* (2010) observed multiple ant-plant interactions in the coastal dune vegetation of Veracruz, Mexico. Díaz-Castelazo *et al.* (2010) found that *C. rosea* EFNs were frequently visited by *Camponotus planatus*, *Forelius pruinosus*, *Monomorium cyaneum*, *Paratrechina longicornis*, and *Dorymyrmex bicolor*. Other ant visitors were *Camponotus atriceps*, *Leptothorax echinatinodis*, *Pseudomyrmex brunneus*, and *Solenopsis geminata*.

Nitrogen-Fixing Nodules in Roots with Symbiotic Bacteria

Other mutualistic interactions involve root nodules. Several authors have observed that certain seashore species are able to form root nodules with symbiotic bacteria that undertake fixation of atmospheric nitrogen (Chen *et al.*, 2000; Corkidi and Rincón, 1997; D'Cunha and Sridhar, 2011; Kulkarni, Raviraja, and Sridhar, 1997). Corkidi and Rincón (1997) explored the growth response of coastal dune plants from different successional stages, following exposure to arbuscular mycorrhizal fungal (AMF) colonization. They found that leaf area and number of leaves significantly increased with AMF inoculation, although beach and foredune species (*C. rosea*, *I. pes-caprae*, *S. virginicus*, *I. imperati*) were less responsive than species typical of the coastal dune environment (*Chamaecrista chamaecristoides*, *P. lindenii*, and *Trachypogon plumosus*). They also found that stems of inoculated *C. rosea* plants were longer than those of noninoculated plants. This may be ecologically significant in a stoloniferous species, since it helps emergence of the plant following burial by sand.

Kulkarni, Raviraja, and Sridhar (1997) studied spore density and root colonization of arbuscular mycorrhizal fungi in the rhizosphere of 12 coastal dune species from the west coast of India. They found that all 12 plant species either presented

vesicles, arbuscules, or both. However, levels of AMF root colonization were variable and ranged from 34 to 80%. *Canavalia rosea* had the lowest percentage of root colonization (35%), as well as the lowest number of arbuscules in the roots (6 arbuscules cm⁻¹). Six species of AMF were found to be associated with *C. rosea*, including *Glomus albidum*. The spore load in the rhizosphere of *C. rosea* was approximately 0.30 g⁻¹ sand (Kulkarni, Raviraja, and Sridhar, 1997).

Interestingly, these symbiotic rhizobia (*Sinorhizobium*) are halotolerants that grow in 3–3.5% w/v NaCl (Chen *et al.*, 2000). In view of this, and the fact that *C. rosea* grows so close to the shoreline, it has been hypothesized that these symbionts enable the plant to thrive in low-nitrogen and saline environments (Chen *et al.*, 2000). Based on this assumption, Pérez-Maqueo (1995) performed a greenhouse experiment with inoculated and noninoculated seedlings of *C. rosea*, following exposure to two flooding regimes: freshwater and seawater. Flooding treatments aimed to mimic natural flooding conditions: Each tray was saturated with either distilled or seawater, and water was allowed to remain in the pots for 4 days. Subsequently, trays were washed with distilled water (washing the trays decreased the salinity and simulated the effect of rainfall for 4 days) and were then drained. The same treatment was applied 6 days after the first flooding event. Seedlings were harvested immediately after this second flooding event and were then left to recover for one more month, when they were harvested again. Pérez-Maqueo (1995) found that biomass accumulation and specific leaf area were higher in inoculated compared to noninoculated seedlings (Figure 7). In all cases, biomass allocation to the roots was higher than to the shoots. Relative growth rate (RGR) was mostly negative for flooded seedlings, except for freshwater flooding, when seedlings recovered from the flooding event and accumulated a large biomass. The only seedlings that survived seawater flooding were those that had not been inoculated with mycorrhizae. This was interpreted as a negative association when environmental conditions were extreme.

Competition

Throughout its pantropical distribution, it is common to find *C. rosea* growing in the same habitat as *I. pes-caprae* and *S. portulacastrum* (Britton and Morton, 1989; Devall, 1992; Moreno-Casasola, 1991; Wilson, 1977). These species are common on tropical beaches. The appearance of *C. rosea* and *I. pes-caprae* is similar: Both are creeping plants that grow in dense mats above the high tide line with erect leaves rising from the sand. One significant difference between these species is in the leaf morphology, being pinnately trifoliate in *C. rosea* and simple in *I. pes-caprae* (Wilson, 1977, personal observation). These observed similarities in habitat and morphology suggest the possibility of competitive interactions, although there is no empirical evidence of this. However, Wilson (1977) found that, in Costa Rica, *I. pes-caprae* was competitively superior close to the water, while *C. rosea* became dominant 3 m inland (Devall, 1992; Devall and Thien, 1992).

Canavalia rosea and *I. pes-caprae* colonize the beach and foredunes using contrasting growth strategies. Cloning in *C. rosea* is rare, and it seldom forms ramets (I. Pisanty,

unpublished data). The modules of *C. rosea* remain attached to the parent, and water and nutrients are transported from the main root to younger parts of the plant. Some modules function as explorers (I. Pisanty, unpublished data) (Devall, 1992). In contrast, the large-rooted stems of *I. pes-caprae* often break apart from the parent plant, forming independent ramets (Devall, 1992; Devall and Thien, 1992). *Canavalia rosea* probably exploits safe sites where the adults become established, whereas *I. pes-caprae* colonizes new microhabitats that are suitable for the establishment of new ramets.

RESPONSE TO WATER LEVELS

The beach and foredunes where *C. rosea* frequently grows are often subject to flooding by very high tides and by storm surges. The stems of *C. rosea* may be covered by ocean water when these flooding events take place. The water table is usually available for the deep main root (Moreno-Casasola, Grime, and Martínez, 1994). Seeds are mostly buoyant and impermeable to water for at least a year (Beyra-Matos *et al.*, 2004).

Martínez *et al.* (2002) tested the effects of inundation by freshwater and seawater on seed germination of five tropical coastal dune species. These authors had observed during previous study that, depending on the local conditions, seeds of *C. rosea* could potentially be exposed to either relatively permanent or intermittent flooding with both freshwater and seawater. Thus, two irrigation treatments were used, permanent inundation and flooding every 4 days, which were intended to at least partially imitate natural conditions. Flooding experiments were maintained for 50 days. After 25 days, seeds from the seawater treatments were transferred to a substrate saturated with freshwater. Germination was then recorded for another 25 days. Seeds in the control lots were regularly watered with freshwater, but never flooded. In these controls, the hard-coated seeds of *C. rosea* were scarified manually with a knife. This set of experiments showed that the final germination percentage of nonscarified seeds of *C. rosea* exposed to permanent inundation in freshwater and seawater was almost the same as that observed in the control group, reaching almost 60%. The results of this experiment showed that seeds of *C. rosea* were very tolerant to flooding by both freshwater and seawater.

The response of seedlings to flooding with freshwater and seawater was studied by Pérez-Maqueo (1995), who observed that *C. rosea* seedlings were relatively tolerant, especially if they had been previously inoculated with mycorrhizae. However, this association proved to be deleterious under extreme flooding conditions (with seawater), when inoculated seedlings died (a detailed explanation is given in the “Nitrogen-Fixing Nodules in Roots with Symbiotic Bacteria” section).

ECONOMIC IMPORTANCE

Coastal Protection

Canavalia rosea is a dune-forming species in the tropics. The long stolons creep over the sand and cover large areas, forming a continuous mat of vegetation. These plants are commonly used to prevent soil erosion because (1) the dense cover

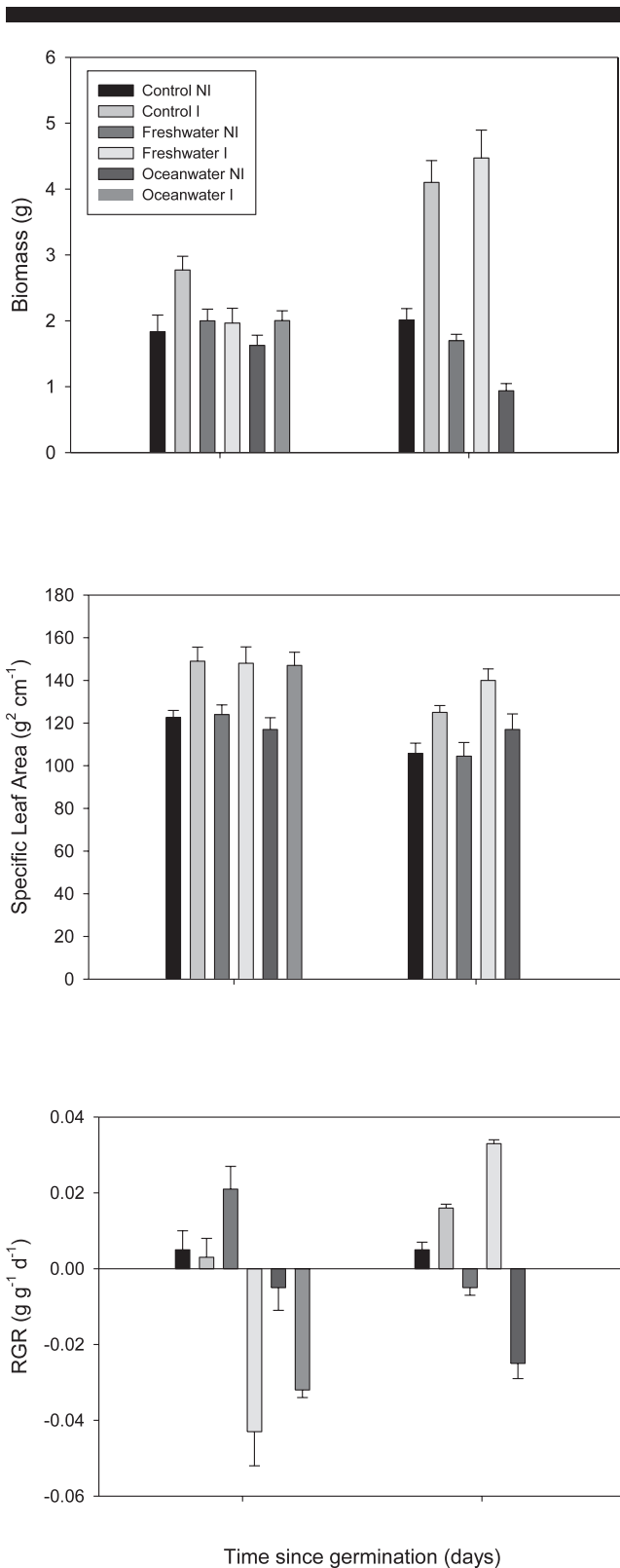


Figure 7. Greenhouse growth experiment of inoculated and noninoculated seedlings of *C. rosea* exposed to freshwater and seawater flooding regimes (after Pérez-Maqueo, 1995).

decreases the impact of storm surges; (2) the roots bind the substrate together and prevent sand from shifting; and (3) the quick growth of the plant enables it to cover even the most mobile dunes. These attributes are particularly important because they enable *C. rosea* to reduce the direct impact of wind and waves on the beach. *Canavalia rosea* is also used as a biomass cover crop (Sridhar and Seena, 2006).

Cultural Uses

Kitajima *et al.* (2008) suggested that *C. rosea* can be used for “xeriscape gardening” and seaside gardens because of its ability to grow rapidly, fix sand dunes, and form aesthetically attractive dense stands. It is especially useful in drought and poor soil conditions. In addition, it is used as green manure in India (D’Cunha and Sridhar, 2011).

Nutritional Uses

Some species of *Canavalia* have been grown since ancient times in different parts of the globe (Rachie, 1979; Sauer and Kaplan, 1969). For example, from 1768 to 1771, *C. rosea* became an important source of food for the British explorer Captain James Cook and his crew during their Pacific voyages (Sridhar and Seena, 2006; Williams, 2007). The young pods and seeds are edible and were probably boiled or roasted when mature and peeled or soaked before being eaten to remove toxins. Roasted and powdered seeds are used as a substitute for coffee powder. Fresh and dried flowers are used as a garnish and for flavoring (Sridhar and Seena, 2006). The plant has been consumed by the aboriginal peoples of Australia, Africa, and Southeast Asia (García, Pinheiro, and Sazima, 2010; Packer *et al.*, 2012; Prabhu *et al.*, 2010).

Canavalia rosea is also used in Africa and Southeast Asia as fodder, because of the high protein content in the leaves, flowers, fruits, and seeds (Beyra-Matos *et al.*, 2004; Wolff and Kwolek, 1971). The conservation and domestication of *C. rosea* may be considered a potential strategy by which to provide an alternative source of protein, because of the proteins, essential amino acids, and low levels of antinutritional factors found in the seeds of *C. rosea* (Arun *et al.*, 2003) (Table 6).

Seena, Sridhar, and Ramesh (2005) assessed the biochemical and protein quality of thermally treated seeds and found that the protein and energy values surpassed those of common pulse crops; the carbohydrates and fatty acids in the test seeds were superior to those of soybean; and the essential amino acids phenylalanine and lysine of treated seeds were higher than the reference pattern of the Food and Agriculture Organization (FAO)/World Health Organization (WHO)/United Nations University (UNU) (FAO/WHO/UNU, 1985) (D’Cunha and Sridhar, 2011; Seena, Sridhar, and Ramesh, 2005; Sridhar and Seena, 2006).

Medicinal Uses

Different parts of *C. rosea* have diverse medicinal properties, and their use may provide health benefits for coastal inhabitants. For instance, a plant shoot decoction has been used to treat tuberculosis, while the roots have been used for the treatment of ciguatera fish poisoning, aches, pains, rheumatism, and leprosy (Bourdy *et al.*, 1992; García, Pinheiro, and Sazima, 2010). Leaf extracts relieve pain, promote healing

Table 6. Proximate and mineral composition of seed flours of *C. rosea* on dry weight basis (n = 5; mean \pm SD). (Data from Arun et al., 2003).

Proximate and Mineral Composition	Values
Moisture (%)	9.3 \pm 0.13
Crude protein (g/100 g)	34.1 \pm 0.52
Crude lipid (g/100 g)	1.7 \pm 0.1
Crude fiber (g/100 g)	10.2 \pm 0.18
Ash (g/100 g)	3.5 \pm 0.18
Crude carbohydrate (g/100 g)	50.5 \pm 0.53
Energy value (KJ/100 g)	1586 \pm 8
Total protein (true protein)	29.3 \pm 0.6
Albumins (g/100 g)	7.6 \pm 0.76
Globulins (g/100 g)	18.8 \pm 0.28
Prolamins (g/100 g)	0.3 \pm 0.02
Glutelins (g/100 g)	2.8 \pm 0.19
Sodium (mg/100g)	47.96 \pm 0.73
Potassium (mg/100g)	974.32 \pm 5.99
Calcium (mg/100g)	86.16 \pm 4.27
Phosphorus (mg/100g)	158 \pm 2.28
Magnesium (mg/100g)	23.13 \pm 0.02
Iron (mg/100g)	4.53 \pm 1.79
Copper (mg/100g)	0.28 \pm 0.11
Zinc (mg/100g)	13.08 \pm 1.2
Manganese (mg/100g)	2.02 \pm 0.21

of burns, stop bleeding, and counter some enteric infections caused by certain gram-positive bacteria (*Bacillus cereus*, *Bacillus megaterium*, *Bacillus stearotherophilus*, *Bacillus subtilis*, *Staphylococcus aureus*, and *Streptococcus faecalis*) (Bhagya and Sridhar, 2009; Packer et al., 2012; Pattamadilok et al., 2008; Prabhu et al., 2010). Moreover, some components of *C. rosea* have been found to be cytotoxic to viruses, bacteria, fungi, and cervical and liver cancer cells and can also act to lower blood sugar (Bhagya and Sridhar, 2009; Morris, 1999).

DISCUSSION AND CONCLUSION

Canavalia rosea is an ecologically important pantropical beach and coastal dune species that has been the subject of study worldwide. We carried out an extensive review of existing studies on *C. rosea* and collated them into one single document. This information could be of interest to a wide array of biologists and resource managers, and it provides a useful basis for people interested in conducting research on *C. rosea*, as well as suggesting new avenues of research.

ACKNOWLEDGMENTS

The collation of studies in order to write this paper was conducted with the financial support of two grants: SEM-ARNAT-CONACYT 23669 and CONABIO JM-027. Mendoza-González and Lithgow are thankful for their Ph.D. scholarships from CONACyT (211507/204461 and 275429/224619, respectively). We are very grateful to the editor and the comments provided by the reviewers, which largely improved earlier versions of the manuscript. Thanks are also due to Keith MacMillan for his thorough and detailed editing.

LITERATURE CITED

Araujo, D.S.D. and Pereira, M.C.A., 2004. Sandy coastal vegetation. In: *Encyclopedia of Life Support Systems*. Oxford, UK: Developed under the auspices of the United Nations Education, Scientific, and Cultural Organization, Eolss Publishers. [http://](http://www.eolss.net/ebooks/Sample%20Chapters/C20/E6-142-TB-08.pdf)

- www.eolss.net/ebooks/Sample%20Chapters/C20/E6-142-TB-08.pdf.
- Arun, A.B. and Sridhar, K.R., 2004. Symbiotic performance of fast-growing rhizobia isolated from the coastal sand dune legumes of west coast of India. *Biology and Fertility of Soils*, 40(6), 435–439.
- Arun, A.B.; Sridhar, K.R.; Raviraja, N.S.; Schmidt, E., and Jung, K., 2003. Nutritional and antinutritional components of *Canavalia* spp. seeds from the west coast sand dunes of India. *Plant Foods for Human Nutrition*, 58(3), 1–13.
- Austin, D.F., 2004. *Florida Ethnobotany*. Boca Raton, Florida: CRC, 909p.
- Berry, E.W., 1916. The Lower Eocene floras of southeastern North America. *U.S. Geological Survey Professional Paper 91*, 481p.
- Berry, E.W., 1930. Revision of the Lower Eocene Wilcox flora of the southeastern states with descriptions of new species, chiefly from Tennessee and Kentucky. *U.S. Geological Survey Professional Paper 156*, 1–144.
- Beyra-Matos, A.; Reyes, G.; Hernández, L., and Herrera P., 2004. Revisión taxonómica del género *Canavalia* DC. (Leguminosae-Papilionoideae) en Cuba. *Revista de la Academia Colombiana de Ciencias Exactas*, 28(107), 157–175.
- Bhagya, B. and Sridhar, K.R., 2009. Ethnobiology of coastal sand dune legumes of southwest coast of India. *Indian Journal of Traditional Knowledge*, 8(4), 611–620.
- Bourdy, G.; Cabalion, P.; Amade, P., and Laurent, D., 1992. Traditional remedies used in the western Pacific for the treatment of ciguatera poisoning. *Journal of Ethnopharmacology*, 36(2), 163–174.
- Britton, J.C. and Morton, B., 1989. *Shore Ecology of the Gulf of Mexico*. Austin, Texas: University of Texas Press, 387p.
- Castillo, S. and Carabias, J., 1982. Ecología de la vegetación de dunas costeras: fenología. *Biotica*, 7(4), 551–568.
- Castillo, S. and Moreno-Casasola, P., 1996. Coastal sand dune vegetation: an extreme case of species invasion. *Journal of Coastal Conservation*, 2(1), 13–22.
- Chen, W.M.; Lee, T.M.; Lan, C.C., and Cheng, C.P., 2000. Characterization of halotolerant rhizobia isolated from root nodules of *Canavalia rosea* from seaside areas. *FEMS-Microbiology Ecology*, 34(1), 9–16.
- Corkidi, L. and Rincón, E., 1997. Arbuscular mycorrhizae in a tropical sand dune ecosystem on the Gulf of Mexico. II. Effects of arbuscular mycorrhizal fungi on the growth of species distributed in different early successional stages. *Mycorrhiza*, 7(1), 17–23.
- Corrêa, M.P. and de Azeredo-Penna, L., 1984. *Dicionário das Plantas Úteis do Brasil e das Exóticas Cultivadas*. Volume III. Rio de Janeiro, Brazil: Ministério da Agricultura, Instituto Brasileiro de Desenvolvimento Florestal, 448p.
- Crawley, M.J., 1983. *Herbivory: The Dynamics of Animal-Plant Interactions*. Berkeley, California: University of California Press, 437p.
- D'Arcy, W.C., 1980. *Canavalia*. In: Woodson, R. and Schery, R.W. (eds.), *Flora de Panama*. (Leguminosae). *Annals of the Missouri Botanical Garden*, 67(3), 562–571.
- D'Cunha, M. and Sridhar, K.R., 2011. Micropropagation of the wild legume *Canavalia rosea* (Sw.) DC. from coastal sand dunes. *Biological Letters*, 48(1), 85–96.
- de Lange, P.J.; Murray, B.G., and Datson, P.M., 2004. Contributions to a chromosome atlas of the New Zealand flora—38. Counts for 50 families. *New Zealand Journal of Botany*, 42(5), 873–904.
- Devall M., 1992. The biological flora of coastal dunes and wetlands. 2. *Ipomoea pes-caprae* (L.) Roth. *Journal of Coastal Research*, 8(2), 442–456.
- Devall, M.S. and Thien, L.B., 1992. Self-incompatibility in *Ipomoea pes-caprae* (Convolvulaceae). *American Midland Naturalist*, 128(1), 22–29.

- Devall, M.S.; Thien, L.B., and Platt, W.J., 1991. The ecology of *Ipomoea pes-caprae*, a pantropical strand plant. In: *Proceedings of the Symposium on Coastal Sand Dunes* (Guelph, Ontario, . University of Guelph, Canada), p. 471.
- Díaz-Castelazo, C.; Guimarães, P.R., Jr.; Jordano, P.; Thompson, J.N.; Marquis R.J., and Rico-Gray, V., 2010. Changes of a mutualistic network over time: reanalysis over a 10-year period. *Ecology*, 91(3), 793–801.
- Díaz-Castelazo, C.; Rico-Gray, V.; Ortega, F., and Ángeles, G., 2005. Morphological and secretory characterization of extrafloral nectaries in plants of coastal Veracruz, Mexico. *Annals of Botany*, 96(7), 1175–1189.
- Disraeli, D.J., 1984. The effect of sand deposits on the growth and morphology of *Ammophila breviligulata*. *Journal of Ecology*, 72(1), 145–154.
- Ehrenfeld, J.G., 1990. Dynamics and processes of barrier island vegetation. *Aquatic Sciences*, 2(3–4), 437–480.
- Emilio, T.C.; Cunha, S.R.; Araujo, A.C.; Pinheiro, G.F.; Gomes Neto, A.; Tognella-de-Rosa, M.M.P., and Klein, A.H.F., 2006. Distribution and abundance of plant communities in dunes of Barra Velha beach, Santa Catarina, southern Brazil. In: Klein, A.H.F. and Finkl, C.W. (eds.), *Proceedings of the 8th International Coastal Symposium (ICS 2004), Itajai/Itapema, Santa Catarina, Brazil*. Journal of Coastal Research, Special Issue No. 39, pp. 1181–1185.
- Endress, P.K., 1994. *Diversity and Evolutionary Biology of Tropical Flowers*. Cambridge, UK: Cambridge University Press, 420p.
- Faegri, K. and Van der Pijl, L., 1979. *The Principles of Pollination Ecology*, 3rd ed. London: Pergamon, 224p.
- FAO/WHO/UNU (Food and Agriculture Organization/World Health Organization/United Nations University), 1985. *Energy and Protein Requirements*. Geneva: WHO, *Technical Report 724*, <http://www.fao.org/docrep/003/aa040e/aa040e00.HTM>.
- Florence, J.; Waldren, S., and Chepstow-Lusty, A.J., 1995. The flora of the Pitcairn Islands: a review. *Biological Journal of the Linnean Society*, 56(1–2), 79–119.
- Frankie, G.W.; Haber, W.A.; Opler, P.A., and Bawa, K.S., 1983. Characteristics and organization of the large bee pollination system in the Costa Rica dry forest. In: Jones, C.E. and Little, R.J. (eds.), *Handbook of Pollination Biology*. New York: Van Nostrand Reinhold Company, Inc., pp. 411–448.
- Gallego-Fernández, J.B. and Martínez, M.L., 2011. Environmental filtering and plant functional types on Mexican foredunes along the Gulf of Mexico. *Ecoscience*, 18(1), 52–62.
- García, V.L.; Pinheiro M., and Sazima, M., 2010. *Sophora tomentosa* e *Crotalaria vitellina* (Fabaceae): biologia reprodutiva e interações com abelhas na restinga de Ubatuba, São Paulo. *Biota Neotropica*, 10(1), 185–192.
- Gilbert, M.E. and Ripley, B.S., 2010. Resolving the differences in plant burial responses. *Austral Ecology*, 35(1), 53–59.
- GBIF (Global Biodiversity Information Facility). 2013. *Global Biodiversity Information Facility*. <http://www.gbif.org/>.
- Goldblatt P., 1981. Cytology and the phylogeny of the Leguminosae. In: Polhill, R. and Raven, P.H. (eds.), *Advances in Legume Systematics: Part 2*. Kew, UK: Royal Botanic Gardens, pp. 427–463.
- Gottberger, G.; Camargo, J.M.F., and Silberbauer-Gottsberger, I., 1988. A bee pollinated tropical community: the beach dune vegetation of Ilha de São Luís, Maranhão, Brazil. *Botanische Jahrbücher für Systematik*, 109(4), 469–500.
- Gross, C.L., 1993. The reproductive ecology of *Canavalia rosea* (Fabaceae) on Anak Krakatau, Indonesia. *Australian Journal of Botany*, 41(5), 591–599.
- Henriques, R.P.B. and Hay, J.D., 1998. The plant communities of a foredune in southeastern Brazil. *Canadian Journal of Botany*, 76(8), 1323–1330.
- Hequet, V., 2010. *Canavalia veillonii*. In: *IUCN 2012. IUCN Red List of Threatened Species*. Version 2012.2. <http://46.137.138.24/details/biblio/177879/0/print>.
- Hesp, P. and Martínez, M.L., 2008. Transverse dune trailing ridges and vegetation succession. *Geomorphology*, 99(1), 205–213.
- Kienholz, R., 1927. Shrinkage and growth in plant stems. *Botanical Gazette*, 83(1), 103–105.
- Kingston, N.; Waldren, S., and Bradley, U., 2003. The phyto-geographical affinities of the Pitcairn Islands—a model for south-eastern Polynesia? *Journal of Biogeography*, 30(9), 1311–1328.
- Kitajima, E.W.; de Alcántara, B.K.; Madureira, P.M.; Alfenas-Zerbini, P.; Rezende, J.A.M., and Zerbini, F.M., 2008. A mosaic of beach bean (*Canavalia rosea*) caused by an isolate of Cowpea aphid-borne mosaic virus (CABMV) in Brazil. *Archives of Virology*, 153(4), 743–747.
- Kolbek, J. and Alves, R.J.V., 1993. Some vicariating plant communities in Brazil, Malaysia and Singapore. *Vegetatio*, 109(1), 15–27.
- Kulkarni, S.S.; Raviraja, N.S., and Sridhar, K.R., 1997. Arbuscular mycorrhizal fungi of tropical sand dunes of west coast of India. *Journal of Coastal Research*, 13(3), 931–936.
- Lackey, J.A., 1981. Phaseoleae. In: Polhill, R.M. and Raven, P.H. (eds.), *Advances in Legume Systematics: Part 1*. Kew, UK: Royal Botanical Garden, pp. 301–327.
- Lane, C.; Wright, S.J.; Roncal, J., and Maschinski, J., 2008. Characterizing environmental gradients and their influence on vegetation zonation in a subtropical coastal sand dune system. *Journal of Coastal Research*, 24(4C), 213–224.
- Lewis, G.; Schrire, B.; Mackinder, B., and Lock, M., 2005. *Legumes of the World*. Kew, UK: Royal Botanical Gardens, 577p.
- Lindsey, A.H., 1984. Reproductive biology of Apiaceae. I. Floral visitors to *Thaspium* and *Zizia* and their importance in pollination. *American Journal of Botany*, 71(3), 375–387.
- Lokkers, C., 2000. *Survey of Coastal Vegetation in Council Reserves at Horseshoe Bay*. Townsville, Australia: Earthworks Environmental Services Pty, Ltd., and Townsville City Council, Earthworks Report 00c01a, 14p.
- Marquis, R.J., 1992. Selective impact of herbivores. In: Fritz, R.S. and Simms, E.L. (eds.), *Plant Resistance to Herbivores and Pathogens: Ecology, Evolution, and Genetics*. Chicago: The University of Chicago Press, pp. 301–325.
- Martínez, M.L. and Moreno-Casasola, P., 1996. Effects of burial by sand on seedling growth and survival in six tropical sand dune species. *Journal of Coastal Research*, 12(2), 406–419.
- Martínez, M.L.; Vázquez, G.; White, D.A.; Thivet, G., and Brengues, M., 2002. Effects of burial by sand and inundation by fresh and seawater on seed germination of five tropical beach species. *Canadian Journal of Botany*, 80(4), 416–424.
- Maun, M.A. and Finkl, C.W., 1988. The biological flora of coastal dunes and wetlands: a format. *Journal of Coastal Research*, 4(2), 511–513.
- Maun, M.A. and Lapierre, J., 1984. The effects of burial by sand on *Ammophila breviligulata*. *Journal of Ecology*, 72(3), 827–829.
- Maun, M.A. and Lapierre J., 1986. Effects of burial by sand on seed germination and seedling emergence of four dune species. *American Journal of Botany*, 73(3), 450–455.
- Mendoza-González G.; Martínez M.L.; Rojas-Soto, O.R.; Vázquez, G., and Gallego-Fernández, J.B., 2013. Ecological niche modeling of coastal dune plants and future potential distribution in response to climate change and sea level rise. *Global Change Biology*, 19(8), 2524–2535. doi:10.1111/gcb.12236.
- Moreno-Casasola, P., 1982. Ecología de la vegetación de dunas costeras: factores físicos. *Biotica*, 7(4), 577–602.
- Moreno-Casasola, P., 1991. Sand dune studies on the eastern coast of Mexico. In: Davidson-Arnot, J. (ed.), *Proceedings of the*

- Symposium on Coastal Dunes* (Guelph, Ontario, University of Guelph), pp. 215–230.
- Moreno-Casasola, P., 1997. Vegetation differentiation and environmental dynamics along the Mexican Gulf coast. In: van der Maarel, E. (ed.), *Dry Coastal Ecosystems*, Volume 2C. Amsterdam: Elsevier, pp. 469–482.
- Moreno-Casasola, P. and Espejel, I., 1986. Classification and ordination of coastal sand dune vegetation along the Gulf of Mexico and Caribbean Sea. *Vegetatio*, 66(3), 147–182.
- Moreno-Casasola, P.; Grime, J.P., and Martínez, M.L., 1994. A comparative study of the effects of fluctuation in temperature and moisture supply on hard coat dormancy in the seeds of coastal tropical legumes in Mexico. *Journal of Tropical Ecology*, 10(1), 67–86.
- Morris, J.B., 1999. Legume genetic resources with novel “value added” industrial and pharmaceutical use. In: Janick, J. (ed.), *Perspectives on New Crops and New Uses*. Alexandria, VA: ASHS Press, pp. 196–201.
- Müller-Hohenstein, K., 1992. Las dunas como ecosistemas: experiencias en Europa, Arabia y Africa. *Bosque*, 13(1), 9–12.
- Oliveira, P.S.; Rico-Gray V.; Díaz-Castelazo C., and Castillio-Guevara C., 1999. Interaction between ants, extrafloral nectaries and insect herbivores in Neotropical coastal sand dunes: herbivore deterrence by visiting ants increases fruit set in *Opuntia stricta* (Cactaceae). *Functional Ecology*, 13(5), 623–631.
- Packer, J.; Brouwer, N.; Harrington, D.; Gaikward, J.; Heron, R.; Yeagl Community Elders; Ranganathan, S.; Velmulpad, S., and Jamie, J., 2012. An ethnobotanical study of medicinal plants used by the Yaegl Aboriginal community in northern New South Wales, Australia. *Journal of Ethnopharmacology*, 139(1), 244–255.
- Pattamadilok, D.; Pengsuparp, T.; Phummiratch, D.; Ongpipatanakul, B.; Meksuriyen, D.; Kawanishi, K.; Kaneda, N., and Suttisri, R., 2008. Canarosine: a new guanidine alkaloid from *Canavalia rosea* with inhibitory activity on dopamine D1 receptors. *Journal of Asian Natural Products Research*, 10(10), 915–918.
- Pérez-Maqueo, O., 1995. Análisis del efecto de los disturbios en la dinámica de la playa del Morro de la Mancha, Veracruz. México City, México: Universidad Nacional Autónoma de México (UNAM), Master’s thesis.
- Perumal, J.V. and Maun, M.A., 1999. The role of mycorrhizal fungi in growth enhancement of dune plants following burial in sand. *Functional Ecology*, 13(4), 560–566.
- Prabhu, S.; Raj, L.J.M.; Britto, S.J., and Senthilkumar, S.R., 2010. Antibacterial activity and preliminary phytochemical analysis of leaf extract of *Canavalia rosea* (Sw.) DC. (beach bean). *International Journal of Research in Pharmaceutical Sciences*, 1(4), 428–434.
- Pukui, M.K. and Elbert, S.H., 1986. *Hawaiian Dictionary: Hawaiian-English, English-Hawaiian*, 6th edition. Honolulu: University of Hawai’i Press, 575p.
- Rachie, K.O., 1979. *Tropical Legumes: Resources for the Future*. Washington, D.C.: National Academy of Sciences, 331p.
- Raunkiaer, C., 1934. *The Life Forms of Plants and Statistical Plant Geography: Being the Collected Papers of C. Raunkiaer*. Oxford: Clarendon, 632p.
- Rico-Gray, V.; Oliveira, P.S.; Parra-Tabla, V.; Cuautle, M., and Díaz-Castelazo, C., 2004. Ant-plant interactions: their seasonal variation and effects on plant fitness. In: Martínez, M.L. and Psuty, N. (eds.), *Coastal Dunes, Ecology and Conservation*. Berlin: Springer-Verlag, Ecological Studies 171, pp. 221–239.
- Sauer, J., 1964. Revision of *Canavalia*. *Brittonia*, 16(2), 106–181.
- Sauer, J. and Kaplan, L., 1969. *Canavalia* beans in America prehistory. *American Antiquity*, 34(4), 417–424.
- Seena, S.; Sridhar, K.R., and Ramesh, S.R., 2005. Nutritional and protein quality evaluation of thermally treated seeds of *Canavalia maritima* in the rat. *Nutrition Research*, 25(6), 587–596.
- Siebert, S. and Mössmer, M., 2002. Newsletter of the Southern African Botanical Diversity Network. *Sabonet News*, 7(1), 1–29.
- Sridhar, K.R. and Seena, S. 2006. Nutritional and antinutritional significance of four unconventional legumes of the genus *Canavalia*—a comparative study. *Food Chemistry*, 99(2), 267–288.
- Sugden, E.A., 1986. Anthecology and pollinator efficacy of *Styrax officinale* subsp. *redivivum* (Styracaceae). *American Journal of Botany*, 73(6), 919–930.
- Thornton, I.W.B.; Runciman, D.; Cook, S.; Lumsden, L.F.; Partomihardjo, T.; Schedvin, N.K.; Yukawa, J., and Ward, S.A. 2002. How important were stepping stones in the colonization of Krakatau?. *Biological Journal of Linnean Society*, 77(3), 275–317.
- USDA (United States Department of Agriculture), 2007. Genus *Canavalia* Adans. Germplasm Resources Information Network (GRIN). Online database. Beltsville, Maryland: National Germplasm Resources Laboratory. <http://www.ars-grin.gov/cgi-bin/npgs/html/genus.pl?2025>.
- Valverde, T.; Pisanty, I., and Rincón, E., 1997. Growth response of six tropical dune plant species to different nutrient regimes. *Journal of Coastal Research*, 13(2), 497–505.
- Vatanparast, M., 2010. Phylogeography of a pantropical plant with sea-drifted seeds: *Canavalia rosea* (Sw.) DC. (Fabaceae). United Kingdom: Graduate School of Science, Chiba University, PhD thesis, 89p.
- Vatanparast, M.; Takayama, K.; Sousa, M.S.; Tateishi, Y., and Kajita, T., 2011. Origin of Hawaiian endemic species of *Canavalia* (Fabaceae) from sea-dispersed species revealed by chloroplast and nuclear DNA sequences. *The Journal of Japanese Botany*, 86(1), 15–25.
- Verçoza, F.C.; do Nascimento, E.C., and Ribeiro, I.M., 2010. Melitofilia em *Canavalia rosea* (Sw.) DC. (Leguminosae-Papilionoideae). *Entomo Brasiliis*, 3(3), 73–76.
- Viana, B.F. and Alves dos Santos, I., 2002. Bee diversity of the coastal sand dunes of Brazil. In: Kevan, P. and Imperatriz-Fonseca, V.L. (eds.), *Pollinating Bees. The Conservation Link between Agriculture and Nature*. Brasilia, Brazil: Ministry of Environment, pp. 135–153.
- Waldren, S.; Florence, J., and Chepstow-Lusty, A.J., 1995. A comparison of the vegetation communities from the islands of the Pitcairn Group. In: Benton, T.G. and Spencer, T. (eds.), *The Pitcairn Islands: Biogeography, Ecology and Prehistory*. Biological Journal of the Linnean Society, Special Issue No. 56, pp. 121–144.
- Williams, M.J., 2007. *Native Plants for Coastal Restoration: What, When, and How for Florida*. Brooksville, Florida: USDA, NRCS, Brooksville Plant Materials Center. 51p. <http://www.fl.nrcs.usda.gov/programs/pmc/flplantmaterials.html>.
- Wilson, E., 1977. Ecological observations of the tropical strand plants *Ipomoea pes-caprae* (L.) R. Br. (Convolvulaceae) *Canavalia maritima* (Aubl.) Thou. (Fabaceae). *Brenesia*, 10(11), 31–42.
- Wolff, I.A. and Kwolek, W.F., 1971. Lipids of the Leguminosae. In: Harborne, J.B.; Boulter, D., and Turner, B.L. (eds.), *Chemotaxonomy of the Leguminosae*. London: Academic, pp. 231–255.
- Worldclim, 2013. *Global Climate Data*. <http://www.worldclim.org/>.
- Yuan, T., Maun, M.A., and Hopkins, W.G., 1993. Effects of sand accretion on photosynthesis, leaf water potential and morphology of two dune grasses. *Functional Ecology*, 7(6), 676–682.
- Zhang, J. and Maun, M.A., 1992. Effects of burial in sand on the growth and reproduction of *Cakile edentula*. *Ecography*, 15(3), 296–302.

□ RESUMEN □

El género *Canavalia* incluye 60 especies de las cuales 37 se encuentran en la región Neotropical. Uno de los miembros más extendidos del género es *Canavalia rosea*. En este trabajo presentamos una recopilación de la literatura, que no ha sido reunida previamente sobre la biología de esta especie, la cual es importante debido a su amplia distribución en el mundo. Esta leguminosa (Fabaceae) posee una distribución pantropical en las playas arenosas y dunas frontales de los cinco continentes y tiene la habilidad de dispersarse por corrientes marinas. *C. rosea* posee ramas que pueden medir más de ocho metros de largo, con hojas compuestas y folíolos orbiculares con margen entero y tallo corto. Las inflorescencias son de color rosado o púrpura. La floración ocurre entre mayo y septiembre con mayor intensidad, aunque puede ser esporádica durante el resto del año. Los frutos son vainas de 7–12 cm de largo con semillas latentes, redondas y de color café. La raíz es profunda, monopódica y posee asociaciones micorrícicas. Es una colonizadora exitosa de las costas tropicales gracias a su capacidad de dispersión a larga distancia por medio de las corrientes marinas y a su alta tolerancia al spray salino, al enterramiento y a sustratos con altas temperaturas y bajas cantidades de nutrientes. Esta colonizadora desempeña un papel muy importante en la geomorfología de las playas y dunas frontales ya que es capaz de cubrir grandes áreas y formar tapetes casi continuos que ayudan a fijar la arena y mantienen el sustrato aglutinado. Además, las hojas, tallos y semillas tienen múltiples usos alimenticios y medicinales por su alto contenido en proteínas y principios bactericidas activos.