Reprinted from THE SOUTHWESTERN NATURALIST
Vol. 50, No. 3, September 2005
Made in United States of America

INLAND OCCURRENCE OF THE STRAND PLANT *IPOMOEA PES-CAPRAE* (CONVOLVULACEAE) AROUND LAKE NICARAGUA

MARGARET S. DEVALL* AND LEONARD B. THIEN

U.S. Forest Service, Center for Bottomland Hardwoods Research, P.O. Box 227, Stoneville, MS 38776 (MSD)
Department of Cell and Molecular Biology, Tulane University, New Orleans, LA 70118 (LBT)
**Correspondent: mdevall@fs.fed.us*

ABSTRACT—*Ipomoea pes-caprae* (L.) Roth (railroad vine, Convolvulaceae) is a pantropical, perennial beach plant that forms large patches just above the high tide line on coastal beaches and dunes throughout tropical and subtropical areas of the world. In spite of its wide distribution, only rare occurrences of *I. pes-caprae* have been documented in inland habitats. Here we report on an extensive population of *I. pes-caprae* growing on the shores of Lake Nicaragua in the interior of Nicaragua.

RESUMEN—*Ipomoea pes-caprae* (L.) Roth (la riñonina, Convolvulaceae) es una planta perenne y pantropical que forma parches grandes arriba de la línea de la marea alta en playas costeras y en dunas en áreas tropicales y subtropicales del mundo. A pesar de su amplia distribución, *I. pes-*

caprae ha sido documentado rara vez en hábitats tierra adentro. Aquí informamos de una población extensa de *I. pes-caprae* habitando la orilla del Lago Nicaragua en el interior de Nicaragua.

Ipomoea pes-caprae (L.) Roth (railroad vine, Convolvulaceae) is a pantropical perennial beach plant with showy, pink flowers and water-dispersed seeds. The plant possesses a self-incompatibility mechanism, although it is a pioneer species (Martin, 1970; Devall and Thien, 1989). *Ipomoea pes-caprae* forms patches just above the high-tide line on coastal beaches and dunes throughout tropical and subtropical areas of the world. The size of a patch varies depending on whether the beach is accreting or eroding, the recency and intensity of storms, and human activity. *Ipomoea pes-caprae* is one of the most widely distributed beach plants (Ridley, 1930) and is often a component of the strand (Austin and Weise, 1972; Porter, 1973; Whitten et al, 1984; Moreno-Casasola and Espejel, 1986; Devall, 1992). The primary pollinators of *I. pes-caprae* are bees, although butterflies, moths, flies, beetles, wasps, and ants also visit the flowers (Devall and Thien, 1989). Seeds of *I. pes-caprae* often are parasitized by the beetle *Megacerus leucospilus* (Bruchidae) (Teran and Kingsolver, 1977).

Ipomoea pes-caprae occurs on the coastal beaches of 5 continents and most tropical islands, as well as on warm temperate shores (St. John, 1970). In spite of its wide distribution, only rare occurrences of *I. pes-caprae* in inland habitats have been documented (Guppy, 1906; St. John, 1970; Austin, 1982; Austin and Cavalcante, 1982). Here we report on an extensive population of *I. pes-caprae* growing on the shores of Lake Nicaragua in the interior of Nicaragua, also listed in Taylor (1963) and Austin (2001).

Lake Nicaragua is 8,000 km^2 in area, with a mean elevation of 25 m, and has a total dissolved solid content of 0.07%, mostly sodium bicarbonate (Taylor, 1963). Sandy beaches are common on the western and northern shore of the lake, and the southern shore is rocky. We sampled the beach along Lake Nicaragua near the town of Malacatoya (Fig. 1) in November 1997 and October 1998 and in the city of Granada in October 2000. The sandy beach near Malacatoya is approximately 15 m wide and slopes down toward the water. In Granada, there are a low seawall and a narrow sandy beach with occasional large rocks.

We studied *I. pes-caprae* on the shore of Lake Nicaragua following the methods of Devall and Thien (1989). We placed 15 1-m^2 quadrats 5 m apart along a transect that paralleled the beach, beginning near the front of the population (close to the water). The exact location of the first quadrat along the transect was randomly chosen by drawing a number. Two other transects were located parallel to the first, with 5 m between each transect. *Ipomoea pes-caprae* stems root adventitiously, and the extent of an individual plant cannot be easily determined, so we counted stems longer than 30 cm in length to determine density. Within each quadrat, we counted flowers, fruits, and seedlings. We also collected *I. pes-caprae* seeds at Malacatoya, stored them in plastic bags, and checked for bruchid (*Megacerus*) beetle larvae.

Thick mats of *I. pes-caprae* occur almost continuously from Granada to Malacatoya. The plants grow from the upper boundary of the beach to the high tide line. Other species in this area include water hyacinth (*Eichhornia crassipes* (Martins) Solms), pennywort (*Hydrocotyle bonariensis* Lam.), and water lettuce (*Pistia stratiodes* L.). Beyond the beach are grasses. In June 2002, *I. pes-caprae* colonies occurred on the beach at the village of Sapoá, in disturbed areas, and at Cárdenas and Colón on the south shore of the lake, in patches at the high tide line. The species was present along the rocky shores of some small islands in the lake near Granada, with abundant water hyacinth surrounding the shores, and on San Fernando and small islands in the Solentiname archipelago. *Ipomoea pes-caprae* also grew at the ferry landing at San Jorge near Rivas and in the town of Moyogalpa on the large island of Ometepe.

Mean stem density of the *I. pes-caprae* patch at Malacatoya was 16.6/m^2 (Table 1). Mean flower density was 3/m^2, and mean fruit density was 4.3/m^2. No seedlings were observed in the quadrats. *Megacerus leucospilus* parasitized 9.9% of *I. pes-caprae* seeds (n = 344). There were fewer stems, flowers, and fruits in quadrats along transects at Granada, but a few seed-

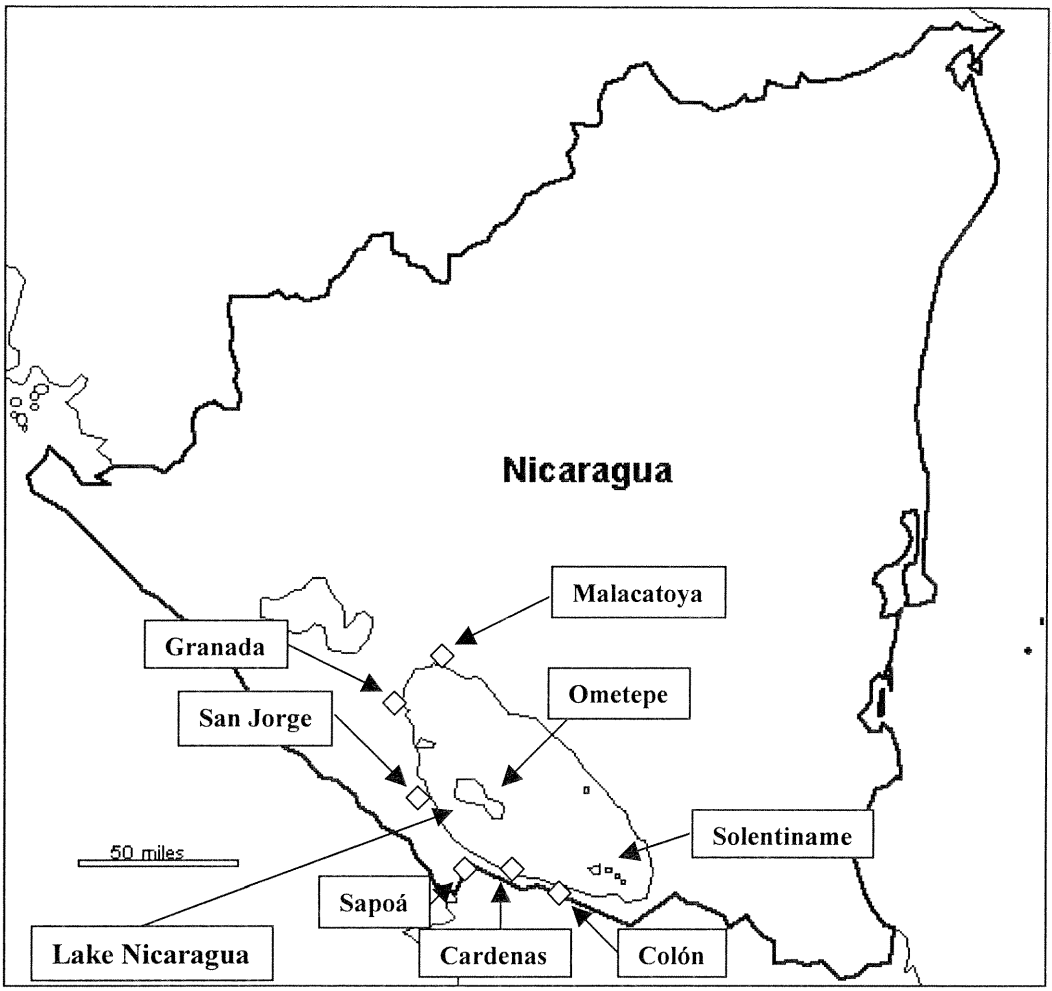

FIG. 1—Map of Nicaragua showing Lake Nicaragua, the city of Granada, and other locations where *Ipomoea pes-caprae* was observed. Copyright Enchanted Learning. Used by permission.

TABLE 1—Mean (± *SD*) stem, flower, fruit, and seedling density (number per m^2) of *Ipomoea pes-caprae* on the northern shore of Lake Nicaragua. Data were collected from 45 1-m^2 quadrats (each location) at Malacatoya in October of 1998 and from Granada in October of 2000. Flower data from around the Gulf of Mexico after Devall (1987); stem, fruit, and seedling density after Devall and Thien (1989).

Location	Stem density	Flower density	Fruit density	Seedlings
Malacatoya, Nicaragua	16.6 (7.6)	3.0 (3.3)	4.3 (5.6)	0
Granada, Nicaragua	7.8 (7.3)	0.4 (1.1)	4.1 (9.1)	0.2 (0.6)
Progreso, Yucatan, Mexico	5.8 (3.6)	0.4 (0.7)	3.5 (8.1)	0*
S. Padre Island, Texas, USA	3.6 (4.1)	2.0 (4.5)	0.3 (0.5)	0
Grand Isle, Louisiana, USA	0.6 (1.4)	0.5 (1.2)	1.6 (5.1)	0
Uaymitun, Yucatan, Mexico	6.4 (5.7)	0.1 (0.3)	0	0
San Bruno, Yucatan, Mexico	5.4 (4.5)	0	0	0

* One seedling was sampled.

lings were noted (Table 1). The stem densities of *I. pes-caprae* at Malacatoya and Granada were greater than that at 5 coastal locations around the Gulf of Mexico (Devall and Thien, 1989), where the mean stem density ranged from 0.6 to 5.8/m^2 (Table 1). We suggest the density of *I. pes-caprae* stems was greater around Lake Nicaragua because the plants were more protected from storms and hurricanes than are coastal populations. Herbivory of *I. pes-caprae* in populations around the Gulf of Mexico is slight, and the species tolerates human disturbance (Devall, 1987). Fruit density was also greater at Malacatoya (4.3/m^2) compared to 0–3.5/m^2 around the Gulf of Mexico. No seedlings were found at Malacatoya or at 4 of 5 locations around the Gulf of Mexico (Devall and Thien, 1989); in contrast, a few seedlings (0.2/m^2) were present at Granada. *Megacerus leucospilus* were found in 0.5–16% of seeds around the Gulf of Mexico, with more southerly populations exhibiting greater percentages of parasitized seeds; the rate was 9.9% at Malacatoya.

The occurrence of this large inland population of *I. pes-caprae* is unusual. *Ipomoea pes-caprae* is a widely distributed colonizing strand species on tropical beaches throughout the world (Sauer, 1959, 1967; St. John, 1970; Austin and Cavalcante, 1982; Fang and Staples, 1995; Austin, 2001). It has reached nearly all the locations at which it occurs by drifting of its seeds in the sea (Ridley, 1930). The species also occurs on the back margins of beaches, along coastal roads (Wilson, 1977), and in coastal villages, where it is dispersed by transportation of sand. It does not naturally invade inland habitats (St. John, 1970). Ridley (1930) stated that *I. pes-caprae* is never found inland, unless temporarily, after the seeds have been carried in sand. The landward extent of the species is limited by dispersal, competition, and shading by plants beyond the strand (Devall, 1992).

It was formerly thought that Lake Nicaragua and Lake Managua were formed when a large bay was cut off from the Pacific Ocean by volcanic activity (Hayes, 1899). Today it is thought that the Nicaraguan depression, including the 2 lakes, is a graben formed by subsidence during the late Tertiary and Quaternary (Thorson et al., 1966) or during the late Miocene (McBirney and Williams, 1965; Morris et al., 1990). Mann et al. (1990) considered it a Quaternary structural depression that subsided as an asymmetric half graben along boundary faults on its southwestern side. It seems that the lakes were never connected to the Pacific.

For about 100 years after its founding in 1524, Granada was a thriving seaport for ships of up to 120 tons that traveled up the San Juan River, which connects Lake Nicaragua with the Caribbean. After that time, changes in the riverbed, as well as Dutch and English pirates, made the passage of large ships impossible, but small vessels continued to use the river to reach Granada (Carr, 1953).

A shark (*Carcharhinus leucas*), as well as sawfish and tarpon (all marine species), occur in the freshwater of Lake Nicaragua and the San Juan River. Thorson (1971) demonstrated that the sharks swim back and forth from the Caribbean to the lake along the river. The river, however, flows from the lake to the Caribbean (approximately 175 km), drops about 393 m, and contains several sections with named rapids. Because *I. pes-caprae* seeds did not float up the river, we suggest that the seeds were inadvertently carried up the river on ships traveling to Granada, perhaps as early as the 1500s, or were carried inland even earlier, given that the plant has been used medicinally for thousands of years. Water hyacinth, pennywort, and water lettuce are all non-natives and known "hitchhikers", but all 3 are medicinal, so purposeful introductions around Lake Nicaragua cannot be excluded. We have not observed birds eating *I. pes-caprae* seeds, which contain ergot alkaloids (Jirawongse et al., 1979), but this would not preclude birds from eating them if the birds did not break the seed coats. It is possible that seeds were carried on the feet or feathers of birds that were wet or muddy. *Megacerus leucospilus* could have arrived in parasitized seeds along with viable seeds. The extensive spread of the plant around the lake indicates that it has been present for some time.

We thank A. Rigamer and V. Rico-Gray for helpful reviews of the manuscript, and we thank J. Kingsolver for insect identification. We appreciate information about birds from P. Hamel. We obtained the map of Nicaragua from Enchanted Learning and added names of sites where *I. pes-capre* occurs.

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Submitted 20 April 2004. Accepted 15 December 2004. Associate Editor was Chris Lauver.