

# Ecological Characteristics of *Batis maritima* in Florida and Belize

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**ABSTRACT.** *Batis maritima*, a low-growing perennial species with woody stems and succulent leaves, occurs in mangroves and, to a lesser degree, in salt marshes in the Neotropics. It spreads by clonal growth, occurs in a wide range of habitats, and at times forms monotypic stands. Sites that are permanently flooded or are flooded regularly by tides and salt pans are the only mangrove habitats in which *B. maritima* does not occur or occurs as a few scattered plants. On mangrove-dominated islands in Belize, the coverage and height of *B. maritima* were highest in open habitats, including sites disturbed by human activities. In a mangrove-dominated mosquito impoundment in Florida, *B. maritima* occurred in all habitats sampled and, similar to observations in Belize, coverage and height were greatest in the most open habitats. The abundance and, at times, dominance of *B. maritima* suggests that it may play an important role in the dynamics of mangrove ecosystems, especially in the recruitment and establishment of mangrove seedlings. Mangrove seedlings and saplings were present in most of the plots that were sampled in Belize and Florida, but there was no relationship between the percent cover of *B. maritima* and the density of seedlings and saplings.

## INTRODUCTION

*Batis*, the only genus in the family Bataceae, has two species. *Batis maritima* L. occurs in the Neotropics in coastal salt marshes and mangroves from Georgia and Brazil on the Atlantic coast and California to Peru on the Pacific Coast of North and South America. The species is widely distributed in the Caribbean basin. The second species, *Batis agrillicola* P. Royan, is endemic to coastal areas of northern Australia.

*Batis maritima*, a low-growing C<sub>3</sub> perennial species with woody stems and succulent leaves, is associated with saline soils and has been described as a species that responds to disturbance in mangroves and salt marshes (Rey et al., 1990; Pennings and Richards, 1998; Pennings and Callaway, 2000). An important ecophysiological characteristic of *B. maritima* is the ability to adjust photosynthetic rates to increasing soil salinity by making adjustments to leaf sap osmolalities (Lüttge et al., 1989). The ability to propagate clonally (Pennings and Callaway, 2000) is another characteristic that enables it to respond rapidly to altered environmental conditions.

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Despite its widespread distribution, there have been relatively few ecological studies of *B. maritima*. In Georgia salt marshes, Pennings and Richards (1998) found a positive relationship between the presence of wrack (accumulated litter) and the abundance of *B. maritima*. Pennings and Callaway (2000) found that clonal integration was an important factor in the ability of the species to colonize bare salt pans. The responses of *B. maritima* to altered hydrological conditions appear to vary with differing environmental settings. In hypersaline coastal wetlands in Texas, *B. maritima* cover expanded following inundation with freshwater (Alexander and Dunton, 2002). Conversely, the opposite occurred in Baja California (México) where its cover increased following the construction of a dike that eliminated tidal flooding and increased soil salinity (Ibarra-Obando and Poumian-Tapia, 1991). *Batis maritima* cover was also dynamic in mangroves in Florida that were impounded for mosquito control. The cover of all herbaceous halophytic species, including *B. maritima*, decreased following the construction of dikes and the subsequent impoundment and flooding of mangroves in the Indian River (Rey et al., 1990). Several years later, when tidal exchange between the impoundment and estuary was restored, *B. maritima* recolonized areas that were no longer flooded continuously. Another important ecological feature of *B. maritima* is its inability to tolerate prolonged periods of shade in mangrove-dominated wetlands (López-Portillo and Ezcurra, 1989). Along Florida's Gulf Coast, Milbrandt and Tinsley (2006) observed a greater number of black mangrove (*Avicennia germinans* (L.) Stearn) seedlings in existing *B. maritima* patches compared to surrounding mudflats. They hypothesized that this improved seedling success was the result of a slight increase in elevation provided by the *B. maritima* root system. In contrast, McKee et al. (2007) found that on offshore islands in Belize *B. maritima* did not appear to have an effect on recruitment of red mangrove (*Rhizophora mangle* L.) seedlings.

Other than the experimental research on coastal salt marshes (Pennings and Richards, 1998; Pennings and Callaway, 2000), little is known about the ecological role of *B. maritima* in coastal wetlands, especially in mangroves where it most frequently occurs. Is it a fugitive species that only persists because it is capable of responding to changing environmental conditions? Alternatively, is it an important species in mangroves because of its impact on patterns of nutrient cycling or its ability to influence the establishment of mangrove trees (i.e., *R. mangle*, *A. germinans*, *Laguncularia racemosa* (L.) Gaertn. f. [white mangrove], *Conocarpus erectus* L. [buttonwood])? Although

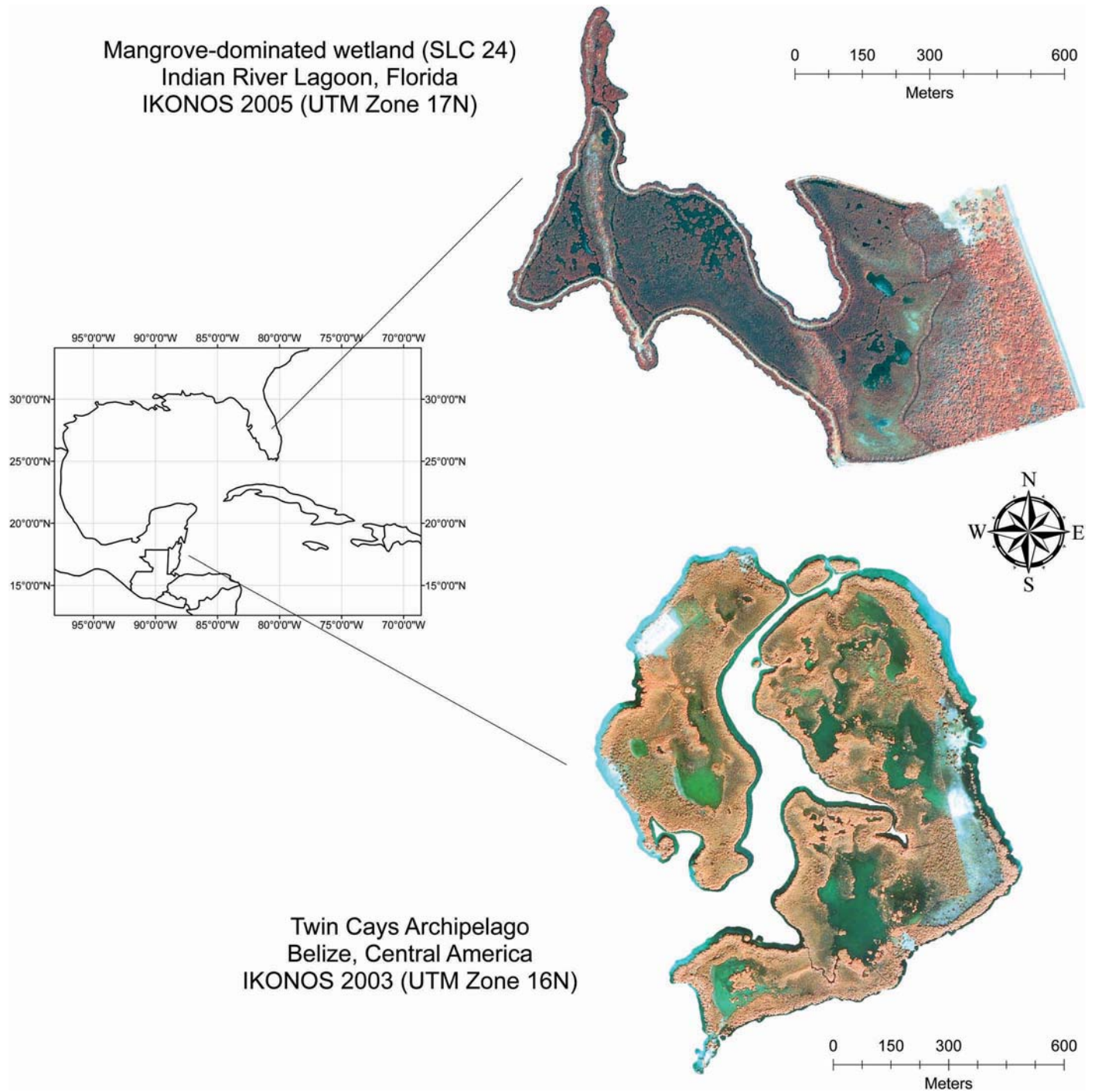
*B. maritima* is a common component of mangrove forests throughout the Neotropics, there is limited knowledge on distribution patterns within the intertidal landscape or on the ecological roles of this species across a range of mangrove habitats.

Our objective was to describe the distribution of *B. maritima* in Florida and Belize as part of our overall goal to determine its ecological role in mangrove ecosystems. Here we describe our initial efforts to characterize the ecology of *B. maritima* at two of the Smithsonian's long-term research sites (Figure 1) that also represent the range of conditions (subtropical and tropical) where this species associates with mangroves. For Florida (subtropical), we focus on *B. maritima* in four habitats in a mangrove-dominated impoundment along the Indian River Lagoon (IRL) that has a history of intervention for purposes of mosquito control (Rey et al., 1990). For Belize (tropical), we focus on *B. maritima* in disturbed and undisturbed sites on offshore mangrove islands. For both sites, we also present data on the relationships between percent cover of *B. maritima* and the density of mangrove seedlings.

## STUDY SITES

### BELIZE

Twin Cays is the focus of our *B. maritima* studies in Belize. Twin Cays (91.5 ha) is an archipelago of peat-based mangrove islands (Figure 1) located near the crest of the barrier reef of central Belize. These islands are located approximately 17 km east of the mainland, and the only source of freshwater is precipitation. Vegetation on Twin Cays is dominated by the mangroves *R. mangle*, *A. germinans*, and *L. racemosa*. The forest structure is heterogeneous and characterized by gradients in hydrology and tree height that include a seaward fringe of *R. mangle* around the periphery of the islands, along tidal creeks, and in perennially flooded ponds (Feller et al., 1999). *Avicennia germinans* and *L. racemosa* primarily occur in habitats that are not water covered at low tide. Vegetation patterns on Twin Cays are complex, and the dynamics have been the focus of many studies (Feller, 1995; Feller and McKee, 1999; Rodriguez and Feller, 2004; Lovelock et al., 2006a). However, none of the previous research has focused on the distribution or ecology of *B. maritima* even though it occurs in almost all habitats except those that do not experience prolonged flooding (D. Whigham, personal observation). Human activities have altered parts of Twin Cays (Rodriguez and Feller, 2004; McKee et al., 2007), and the primary anthropogenic activity has been the clearing



**FIGURE 1.** Approximate locations of SLC24 and Twin Cays (inset map) and IKONOS images of the two study sites. For SLC 24, the white line that is seen around the impoundment is a dike. Dark areas within the impoundment are dredged from adjacent subtidal habitats. Darker areas on the two large islands are internal tidally influenced ponds that are most often shallowly water covered.

of mangroves with or without the addition of sediments dredged from nearby subtidal habitats. In this study, we compared the distribution of *B. maritima* in disturbed and undisturbed mangrove habitats at Twin Cays (described in further detail below).

## FLORIDA

An impounded, mangrove-dominated wetland (SLC 24) in St. Lucie County in the IRL is the focus of the Florida studies (see Figure 1). SLC 24 has been managed in a variety of ways since it was diked in 1970. Rey et al. (1990) describe management activities and patterns of vegetation change in SLC 24 between 1970 and 1987. SLC 24 was hydrologically isolated from the IRL by a dike (Figure 1) until 1985 when a culvert was installed to remove excess water deposited during two tropical storms. Once water levels were lowered, the culvert was sealed, and the impoundment remained isolated until 1987 when the culvert was reopened and other culverts were installed. The cover of all vegetation decreased from 75% to near 30% following construction of the diked impoundment in 1970. Over subsequent years, the cover of herbaceous halophytes, including *B. maritima*, changed in response to variations in the timing and duration of flooding and the establishment and growth of mangroves. Rey et al. (1990) concluded that a steady decline in the cover of herbaceous halophytes after 1984 was primarily caused by shading as the canopies of mangroves developed. Vegetation patterns are also complex in the numerous impoundments that have been established in the IRL, and they have been the focus of several studies focused primarily on nutrient limitation within mangroves (Feller et al., 2003; Lovelock and Feller, 2003; Lovelock et al., 2006b). We sampled *B. maritima* in three mangrove-dominated habitats and areas associated with salt pans where dwarf *A. germinans* (sensu Feller et al., 2003) occurs as scattered individuals or in patches with almost continuous cover. Details of sampling locations and methods are given below.

## METHODS

### BELIZE

We sampled *B. maritima* in two disturbed sites and six undisturbed sites on Twin Cays. One disturbed site is a 2 ha area on West Island that was cleared of mangroves and burned in 1991 and covered with material dredged from the adjacent subtidal area in 1995 (Rodriguez and Feller, 2004; McKee et al., 2007). The other disturbed site was clear cut in 2004, but no dredged material was added. In

both disturbed sites, we sampled *B. maritima* in 10 randomly located plots (each 1 × 1 m) in which we made visual estimates of its cover, measured its height at five randomly chosen locations in each plot, and identified and counted all mangrove seedlings and saplings. Seedlings of *A. germinans* and *L. racemosa* had cotyledons present. Seedlings of *R. mangle* were individual, with no more than one pair of true leaves. Saplings were defined as individuals less than 50 cm in height with no cotyledons present, or with more than one pair of true leaves in the case of *R. mangle*.

For our undisturbed sites at Twin Cays, we sampled *B. maritima* in three forested habitat types (Fringe, Transition, Interior), which were located at different distances from the ecotone between the mangrove forest and open water. Fringe habitats, which were dominated by trees 4 to 5 m tall, were at the outer boundary between mangroves and open water, either along ponds located in the interior of Twin Cays or along the ocean. *Avicennia germinans* was the dominant tree in the three Fringe habitats adjacent to interior ponds. *Rhizophora mangle* was the dominant tree in the three Fringe habitats adjacent to the ocean. Transition and Interior habitats were all dominated by *A. germinans*. Transition habitats were located approximately 15 m further into the mangrove forest from the Fringe habitats, and Interior habitats were located approximately an additional 15 m beyond the Transition habitats. We sampled 5 randomly located plots (same procedures as described above) in each of the 90 plots (5 plots × 3 habitat types × 6 sites) in undisturbed mangrove.

### FLORIDA

We sampled *B. maritima* in SLC 24 in four habitat types (Fringe = *R. mangle*, Dense = *A. germinans*, Sparse = *A. germinans*, Dwarf = *A. germinans*). The Fringe habitats, dominated by *R. mangle* 4 to 6 m tall with scattered *A. germinans*, were located at the boundary between mangroves and open water. The two habitats dominated by taller (3–6 m) *A. germinans* (Dense, Sparse) differed in the size and spatial configuration of the dominant trees. The Dense *A. germinans* habitat had trees that were mostly 4 to 6 m tall and formed a continuous canopy dominated by *A. germinans*. The Sparse *A. germinans* habitat was also dominated by *A. germinans* but the trees were usually shorter (3–5 m) and were more widely spaced, resulting in a more open canopy. The Dwarf *A. germinans* habitat was always adjacent to salt pans that were mostly unvegetated or only had a few scattered dwarf trees (usually less than 1 m tall). We sampled *B. maritima* in one randomly located plot in each of the replicate sites for each habitat

type. In each  $1 \times 1$  m plot, we made the same set of measurements as described above for Belize.

## DATA ANALYSIS

Because of the different sampling regimes, we made separate statistical comparisons for the Belize and Florida data sets. Based on initial screening of the data (Proc Univariate; SAS Institute, 1990), we determined that none of the data were normally distributed either in their original form or any of the possible transformations. We used the nonparametric PROC NPAR1WAY (SAS Institute, 1990) to make comparisons of *B. maritima* data (percent cover, height) and the number of mangrove seedlings + saplings for the different habitat types at both locations.

## RESULTS

### BELIZE

Percent cover of *B. maritima* differed (Figure 2a) significantly ( $df = 4$ , chi-square for Kruskal–Wallis test = 27.9272,  $P < 0.0001$ ) among the sites on Twin Cays. Mean percent cover ranged from 50% to 53% for the two disturbed sites and the undisturbed Fringe habitat. Percent cover decreased from the Fringe to the Transition ([mean  $\pm 1$  SE] =  $35.5\% \pm 4.7\%$ ) and Interior ( $16.9\% \pm 2.9\%$ ) undisturbed sites. The average height of *B. maritima* also differed significantly between sites (Figure 2b;  $df = 4$ , chi-square for Kruskal–Wallis test = 29.0273,  $P < 0.0001$ ). Heights were similar at the two disturbed sites ( $24.4 \pm 2.3$  cm = clear-cut + fill;  $26.4 \pm 1.0$  cm = clear-cut). At the undisturbed sites, height was greatest at the Fringe habitat ( $61.7 \pm 18.5$  cm) and decreased toward the interior of the mangrove forest ( $40.4 \pm 2.2$  = Transition;  $34.7 \pm 2.0$  = Interior).

The number of mangrove saplings + seedlings also differed across sites (Figure 2c), and there were significant differences for all three species and for the total of all species ( $df = 4$ , chi-square for Kruskal–Wallis test = 38.9958,  $P < 0.0001$ ; 12.5551,  $P > 0.0137$ ; 11.3187,  $P < 0.0232$ ; 15.5953,  $P < 0.0036$  for *R. mangle*, *A. germinans*, *L. racemosa*, and total mangroves, respectively).

The total number of mangrove saplings + seedlings was higher at the clear-cut and filled site ( $24.6 \pm 13.8$  m<sup>-2</sup>) compared to the clear-cut site ( $2.5 \pm 0.8$  m<sup>-2</sup>) and undisturbed mangrove habitats (mean for all three undisturbed sites was  $7.3 \pm 1.2$  m<sup>-2</sup>). *Avicennia germinans* saplings + seedlings at the clear-cut and filled site were less than 1 m<sup>-2</sup> (Figure 2c). *Rhizophora mangle* was the most abundant species at the Fringe habitat, whereas *A. germinans* was

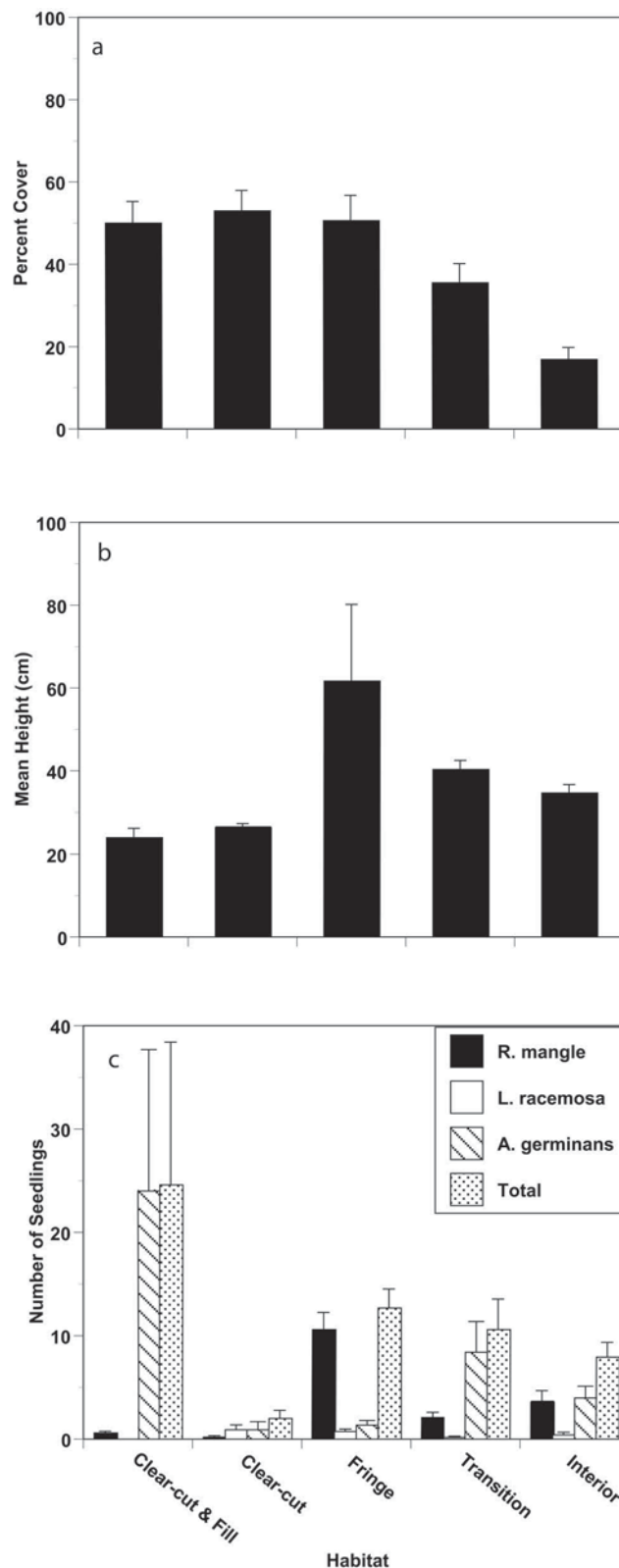


FIGURE 2. Cover (a), height (b), and sapling + seedling (c) data for two disturbed and three undisturbed habitats on Twin Cays (Belize). Values are means  $\pm 1$  SE.

the most abundant species at the Transition and Interior habitats.

#### FLORIDA

Percent cover ( $df = 3$ , chi-square for Kruskal–Wallis test = 38.9252,  $P < 0.0001$ ) and height ( $df = 3$ , chi-square for Kruskal–Wallis test = 33.0923,  $P < 0.0001$ ) of *B. maritima* differed between the four habitat types in SLC 24 (Figure 3a). There was no *B. maritima* in the plots that were sampled in the Fringe *R. mangle* habitat, and the cover ( $2.8\% \pm 1.2\%$ ) was very low in the Dense *A. germinans* habitat. Percent cover was  $42.9 \pm 8.1$  and  $27.8 \pm 4.6$  in the Sparse and Dwarf *A. germinans* habitats, respectively. Height differences (Figure 3b) among the four habitats had the same pattern with the tallest plants occurring in the Sparse *A. germinans* habitat ( $48.9 \pm 4.5$ ) and shortest in the Dense *A. germinans* habitat ( $13.1 \pm 5.4$ ). The total number of saplings + seedlings and the means for each mangrove species also differed significantly (Figure 3c) among the four habitat types ( $df = 3$ , chi-square for Kruskal–Wallis test = 11.5483,  $P < 0.0091$ ; 12.7678,  $P < 0.0052$ ; 16.4377,  $P < 0.0009$ ; 13.4660,  $P < 0.0037$  for *R. mangle*, *A. germinans*, *L. racemosa*, and total mangroves, respectively).

### DISCUSSION

The objective of this initial investigation of *Batis maritima* was to quantify aspects of its distribution in a variety of habitats in mangroves at long-term Smithsonian study sites in Belize and Florida. The impetus for the research was the observation that *B. maritima* is widespread in mangroves and, in some habitats, its high abundance and cover suggest that it potentially plays an important role in these systems. There have, however, been few studies that shed light on its possible ecological importance in mangroves. Studies in salt marshes near its northern limit found that it was not a dominant species and did not compete well with other marsh plants (Zedler, 1977). There is some suggestion that *B. maritima* may be a fugitive species because it is common in disturbed sites (Milbrandt and Tinsley, 2006). Pennings and Richards (1998), for example, found that stands of *B. maritima* were associated with areas that were disturbed by wracks of litter in a Georgia salt marsh.

*Batis maritima* has been described as a species that does not do well in shaded conditions or under conditions of continuous flooding (Rey et al., 1990; Alexander and Dunton, 2002). However, Keer and Zedler (2002) found

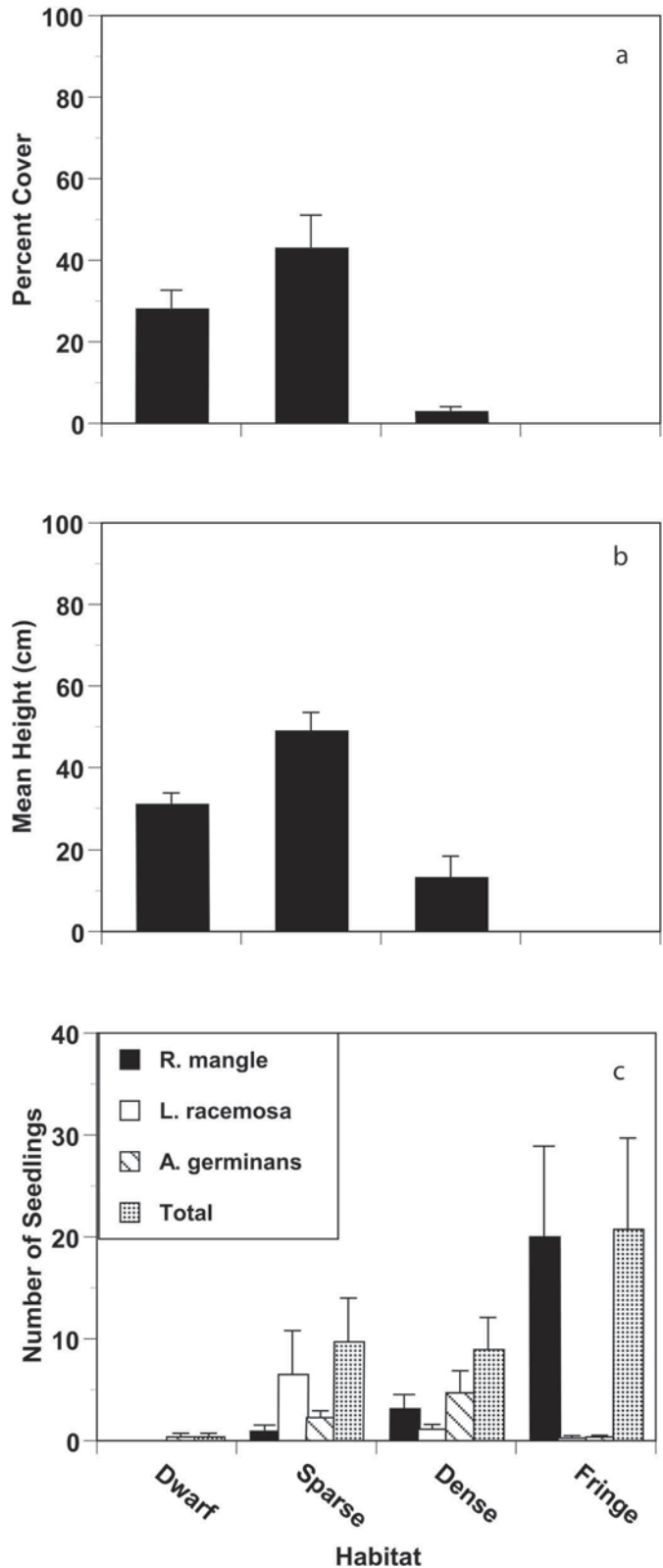


FIGURE 3. Cover (a), height (b), and sapling + seedling (c) data for four habitats in mosquito impoundment SCL 24 in the Indian River Lagoon, Florida. Values are means  $\pm$  1 SE.

that it can tolerate prolonged flooding, and it does well in waterlogged conditions when light is not limiting (Zedler, 1980). It also responds positively to increasing salinity (Ibarra-Obando and Poumian-Tapia, 1991) but is eliminated under hypersaline conditions (Zedler et al., 1986; Dunton et al., 2001).

The only long-term study of *B. maritima* in changing environmental conditions occurred in one of our study sites, SCL 24 in Florida. Rey et al. (1990) examined a sequence of aerial photographs taken over a period of time when hydrological conditions varied from years when there was continuously flooding, to years when the impoundment was drained, and to years when there was partial tidal exchange with the IRL. Vegetation almost completely disappeared when the impoundment was continuously flooded. Once the impoundment was opened to limited tidal exchange, herbaceous halophytes increased in abundance and cover and *B. maritima* eventually became the dominant species. Over time, mangroves recruited and eventually dominated the vegetation in most parts of the impoundment. As the abundance and size of mangroves increased, *B. maritima* declined along with other herbaceous halophytes in response to increased shading by mangroves (Rey et al., 1990).

Results of our surveys support several of the earlier studies and suggest that light levels, regular tidal flooding, and soil salinity are three important factors that determine where *B. maritima* occurs and how abundant it is. There have been at least two studies (Pennings and Richards, 1998; Milbrandt and Tinsley, 2006) suggesting that *B. maritima* is a fugitive species that colonizes high-light disturbed sites. In Belize, the highest percent cover was at the two disturbed sites and the Fringe habitat in the undisturbed mangroves (see Figure 2a). Even though the mean cover of *B. maritima* in the undisturbed sites on Twin Cays was lower ( $34.3\% \pm 3.1.9\%$ ) than the disturbed sites, the highest *B. maritima* cover ( $80.3\% \pm 2.6\%$ ) of any of the habitats sampled was in the three Fringe habitats that were associated with interior ponds. Edge habitats associated with interior ponds are mostly in full sun and are exposed to tidal flooding, but the flooding is rarely more than a few centimeters deep (D. Whigham, personal observations). The substrates are almost always waterlogged, and the sediments are soft, mostly composed of floc that accumulates on the downwind side of the interior ponds. The highest *B. maritima* cover in SLC 24 in Florida also occurred at sites that had no overhead mangrove canopy or only a discontinuous canopy.

The mean cover of *B. maritima* was least in the shaded habitats in Florida and Belize, supporting the suggestions of López-Portillo and Ezcurra (1989) that low light levels

can limit its abundance and distribution. The absence of *B. maritima* in the sample plots at the Fringe habitat associated with SLC 24 and the lower cover in the Fringe habitats closest to the ocean on Twin Cays ( $20.9\% \pm 2.9\%$ ) also support the suggestions that regular inundation by tidal flooding has a negative effect on the species (Alexander and Dunton, 2002).

The mean height of the *B. maritima* canopy also varied among habitats, and the patterns are most likely the result of variations in light and salinity (Zedler et al., 1986; Dunton et al., 2001). In SLC 24, mean height decreased from the more open Dwarf and Sparse *A. germinans* habitats to the shadier Dense *A. germinans* habitat (Figure 3b). At the undisturbed sites in Belize, mean height decreased from the Fringe to the Interior, most likely in response to decreasing light. The height of the plants was greatest in the Fringe habitat associated with the Edge sites that were closest to the Interior ponds. Mean height at the Fringe habitats associated with the ponds was  $85.4 \pm 27.1$  cm compared to  $40.4 \pm 2.2$  at the more shaded Fringe habitats closest to the ocean. Taller average height associated with the Edge habitats may be the result of higher phosphorus concentrations in the sediments. In a separate fertilization experiment, we found that *B. maritima* responded significantly to the addition of phosphorus at all the undisturbed sites on Twin Cays, but the smallest response was at the Edge habitat associated with interior ponds, suggesting that phosphorus was more available in those sediments (D. Whigham, unpublished data). Compared to the Fringe habitats on Twin Cays and the Sparse *A. germinans* habitat in the SLC 24, mean height decreased toward the sites with no mangrove canopy (Dwarf *A. germinans* habitat in SLC 24 and the two disturbed sites at Twin Cays). Lower mean height at the open sites is likely the result of increased salinity as the Dwarf *A. germinans* site in SLC 24 is hypersaline (i.e., soil salinity as high as 100‰; D. Whigham unpublished data). In addition, soil salinity at the clear-cut and filled site on Twin Cays, while variable during an annual cycle, can be more than 60‰ (McKee et al., 2007).

Mangrove seedlings are widely dispersed, and their occurrence varies spatially in response to light levels and their ability to withstand flooding, salinity, and attacks from herbivores (Ellison and Farnsworth, 1993; Olusegun and Creese, 1997). If *B. maritima* facilitates the establishment of mangrove seedlings, we would expect a positive relationship between percent cover and the number of seedlings + saplings for one or more of the mangrove species. Milbrandt and Tinsley (2006) found that the presence of *B. maritima* had a positive effect on the survival of *A. germinans* seedlings. McKee et al. (2007), however, found that *B. maritima* had no effect on the recruitment and survival

of mangrove seedlings, even though mangrove seedlings benefited by the presence of other herbaceous species (i.e., *Distichlis spicata*, *Sesuvium portulacastrum*) at clear-cut and filled sites sampled in this study. Although there were habitat differences in the number of seedlings + saplings, the presence of seedlings + saplings in 88% of the plots sampled in Belize and 55% of the plots in Florida indicated that mangrove establishment may have been facilitated by *B. maritima*. We found no relationship, however, between the amount of *B. maritima* cover and the density of seedlings + saplings for any of the mangrove species (Figure 4). The potential for *B. maritima* to influence the distribution and growth of mangroves trees and other mangrove plants and animals remains unknown. But, given the abundance of the species across a range of habi-

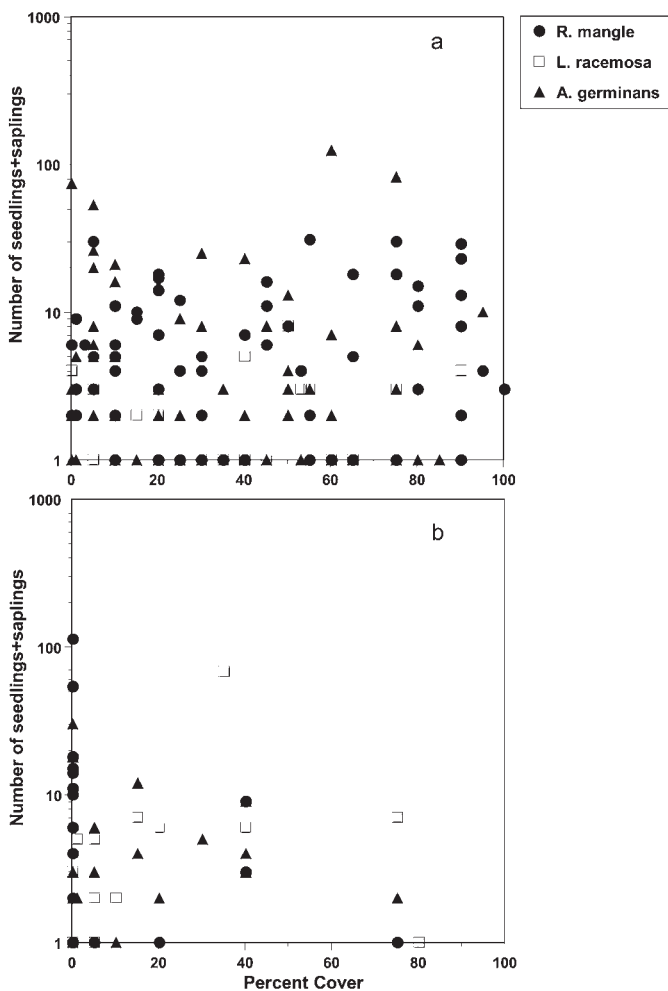


FIGURE 4. Number of mangrove saplings + seedlings ( $\# \text{ m}^{-2}$ ) plotted against percent cover of *Batis maritima* for  $1 \times 1 \text{ m}$  plots sampled in Belize (a) and Florida (b) study sites.

tats, the potential seems high, especially in areas where it is the dominant species.

In summary, *B. maritima* was widespread in most mangrove habitats at both our study locations, and there were significant interhabitat differences in all the variables measured. Mangrove seedlings and saplings were common in areas occupied by *B. maritima*, but we found no evidence that the establishment of mangroves benefited by increasing cover of this common halophytic species. The ubiquitous distribution of *B. maritima* at all the sites sampled, however, indicates that its role in mangrove ecosystems deserves further consideration.

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