

## MANGROVE RECRUITMENT AFTER FOREST DISTURBANCE IS FACILITATED BY HERBACEOUS SPECIES IN THE CARIBBEAN

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**Abstract.** Plant communities along tropical coastlines are often affected by natural and human disturbances, but little is known about factors influencing recovery. We focused on mangrove forests, which are among the most threatened ecosystems globally, to examine how facilitation by herbaceous vegetation might improve forest restoration after disturbance. We specifically investigated whether recovery of mangrove forests in harsh environments is accelerated by nurse plants and whether the beneficial effects are species-specific. Quantification of standardized effects allowed comparisons across performance parameters and over time for: (1) net effect of each herbaceous species on mangrove survival and growth, (2) effects of pre- and post-establishment factors associated with each herbaceous species, and (3) need for artificial planting to enhance growth or survival of mangrove seedlings. Mangrove recruitment in a clear-cut forest in Belize was accelerated by the presence of *Sesuvium portulacastrum* (succulent forb) and *Distichlis spicata* (grass), two coastal species common throughout the Caribbean region. The net effect of herbaceous vegetation was positive, but the magnitude of effects on mangrove survival and growth differed by species. Because of differences in their vegetative structure and other features, species effects on mangroves also varied by mechanism: (1) trapping of dispersing propagules (both species), (2) structural support of the seedling (*Distichlis*), and/or (3) promotion of survival (*Sesuvium*) or growth (*Distichlis*) through amelioration of soil conditions (temperature, aeration). Artificial planting had a stronger positive effect on mangrove survival than did edaphic conditions, but planting enhanced mangrove growth more in *Sesuvium* than in *Distichlis* patches. Our study indicates that beneficial species might be selected based on features that provide multiple positive effects and that species comparisons may be improved using standardized effects. Our findings are not only relevant to the coastal environments found in the Caribbean region, but our assessment methods may be useful for developing site-specific information to restore disturbed mangrove forests worldwide, especially given the large pool of mangrove associates (>45 genera) available for screening.

**Key words:** coastal wetland; disturbance; facilitation; forest regeneration; mangrove associate; nurse plant; patch dynamics; restoration; Rhizophora; seed dispersal; seedling recruitment; stress.

### INTRODUCTION

Knowledge of mechanisms influencing plant establishment and growth is not only important to an understanding of how plant communities are organized, but also in the enhancement of restoration of important ecosystems. Rapid reestablishment of native vegetation, particularly after a large-scale disturbance, can be critical in preventing soil erosion, invasion by exotics, and other unwanted outcomes. Recolonization of disturbed sites may be slow and unpredictable, especially if seed sources are remote. Recovering plant communities are also shaped by the positive and negative interactions among component species. Although competition has been emphasized as an organizing force, a large body of information supports facilitation as a

mechanism influencing plant distribution and success (see Connell 1983, Hunter and Aarssen 1988, Goldberg and Barton 1992, Callaway 1995, Bertness and Leonard 1997, Bruno et al. 2003).

Ecological restoration may involve not only artificial reintroduction of the original community dominants, but also nurse species that improve seed trapping and establishment (Day and Wright 1989), attract seed carriers (Robinson and Handel 1993), enhance soil conditions through organic matter or nutrient accumulation (Pugnaire et al. 1996, Maestre et al. 2001), or provide protection of sensitive seedlings (Martinez 2003, Gomez-Aparicio et al. 2004). Ecological restoration approaches, however, must be based on a thorough understanding of the natural successional dynamics of the system as well as the growth requirements of the dominant plant species. This understanding is particularly important in forested systems in which the age-determined features of ecosystem structure and function are slow to recover.

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The current challenge in ecological restoration is to manipulate development so that recovery of the entire suite of structural and functional features is achieved as quickly as possible (Dobson et al. 1997). However, for many types of ecosystems the information necessary to make critical decisions about species introductions is not currently available. Few studies have experimentally examined facilitation in the context of restoration (Maestre et al. 2001, Gomez-Aparicio et al. 2004). Consequently, the scientific and resource community has been hesitant to apply facilitation to restoration practices. A better understanding of plant interactions, particularly facilitation, may lead to better techniques that support and encourage ecological restoration approaches.

A key question is whether facilitation is species-specific (i.e., involves specific traits of the benefactor) or those positive effects on the beneficiary are due to environmental changes that can be generated by any morphologically similar species or even nonliving objects such as rocks or woody debris. The answer to this question has clear relevance for ecological restoration. Facilitation may not only involve amelioration of environmental conditions that promote growth of a beneficiary species, but can also arise from effects on dispersal and establishment, e.g., trapping of seeds or propagules. A benefactor species that increases the rate of seedling establishment and generates conditions conducive to growth of established seedlings would have a greater influence on seedling dynamics than a species that provides a single effect. Studies have generally investigated facilitation by one of these processes, but not of both simultaneously (Callaway 1995). Consequently, the necessary information needed to select beneficiary species is often lacking to support restoration efforts.

Facilitation has been studied in extreme environments such as salt marshes (Bertness 1991, Bertness and Hacker 1994, Egerova et al. 2003), where plants must cope with stresses such as salinity, flooding, and variable sediment and nutrient supplies. Mangroves are the tropical equivalent of temperate salt marshes, but in contrast to marsh grasses that can propagate vegetatively, these tidal forests are dominated by tree species dependent upon seedling recruitment for regeneration. Mangroves are frequently disturbed by hurricanes and human activities, which severely damage or eliminate the forest community. Mangroves are considered to be one of the most endangered ecosystems in the world, with ~35% of the original area degraded or destroyed since 1980 (Valiela et al. 2001; Food and Agricultural Organization of the United Nations database, *available online*).<sup>5</sup> Mangrove loss is particularly devastating to the Caribbean region (~28% loss between 1980 and 2000), where they constitute a critical habitat intimately linked to adjacent seagrass and coral reef ecosystems (Rivera-Monroy et al. 2004). Such losses may be reversed through application of the principles of ecological restoration.

Recent work emphasizes the use of ecological engineering to achieve cost-effective restoration by properly preparing soil elevations (Lewis 2005). Complimentary approaches that promote rapid revegetation and also minimize cost and effort are needed, especially for developing countries with few resources and incentives to restore degraded forests (Kaly and Jones 1998, Alongi 2002, Barbier 2006). Here we document the potential for use of nurse plants to promote mangrove recruitment in large disturbed sites where harsh conditions limit mangrove recovery.

Mangrove plant communities often contain herbaceous species, which are common components of the tropical beach habitat, salt marshes, or other wet coastal communities (Tomlinson 1994). Such “mangrove associates” may occur naturally as understory, inhabit a back-mangal ecotone, or invade only upon disturbance of the dominant mangrove vegetation. Their presence could positively influence mangrove reestablishment and growth and, consequently, be used to accelerate natural or managed recovery from disturbance. Although factors influencing mangrove recruitment such as seed and seedling predators (McKee 1995a, Lindquist and Carroll 2004), flooding and salinity (McKee 1995b, Elster et al. 1999, Sherman et al. 2000), and sedimentation (Elster 2000) have been studied in neotropical forests, effects of herbaceous associates are relatively unstudied (Flower 2004, Milbrandt and Tinsley 2006). Mangroves may be extremely slow to recolonize and grow, especially in harsh (e.g., arid, hypersaline) environments of the Caribbean region (Cintron et al. 1978, Feller 1995, McKee 1995b, Imbert et al. 2000, Feller et al. 2003, Flower 2004, Milbrandt and Tinsley 2006). Mangrove ecosystems thus constitute not only a critical habitat with important ecological and societal benefits, but are systems in which facilitative interactions might be applied to improve restoration techniques. Furthermore, an understanding of how benefactors may facilitate survival and growth of mangroves will lead to identification of vegetative characteristics to screen potential candidates for restoration projects.

In this study, we examined mangrove seedling establishment and subsequent growth in response to two herbaceous species, *Distichlis spicata* (L.) Greene (Poaceae) and *Sesuvium portulacastrum* L. (Aizoaceae), which are common halophytes found along shorelines in the Caribbean region. We hypothesized that in extreme environments such as those found on intertidal Caribbean islands, these two species would have a positive effect on mangrove recruitment in large disturbed areas. Because of differences in vegetative structure and other features (grass vs. succulent forb), we further hypothesized that effects of herbaceous species on mangroves would differ. These hypotheses were tested at a long-term study site (Twin Cays, Belize) that has been the focus of research by the Smithsonian Institution since the early 1970s (Rützler and Feller 1996).

<sup>5</sup> <http://www.fao.org/docrep/007/j1533e/J1533E00.htm>

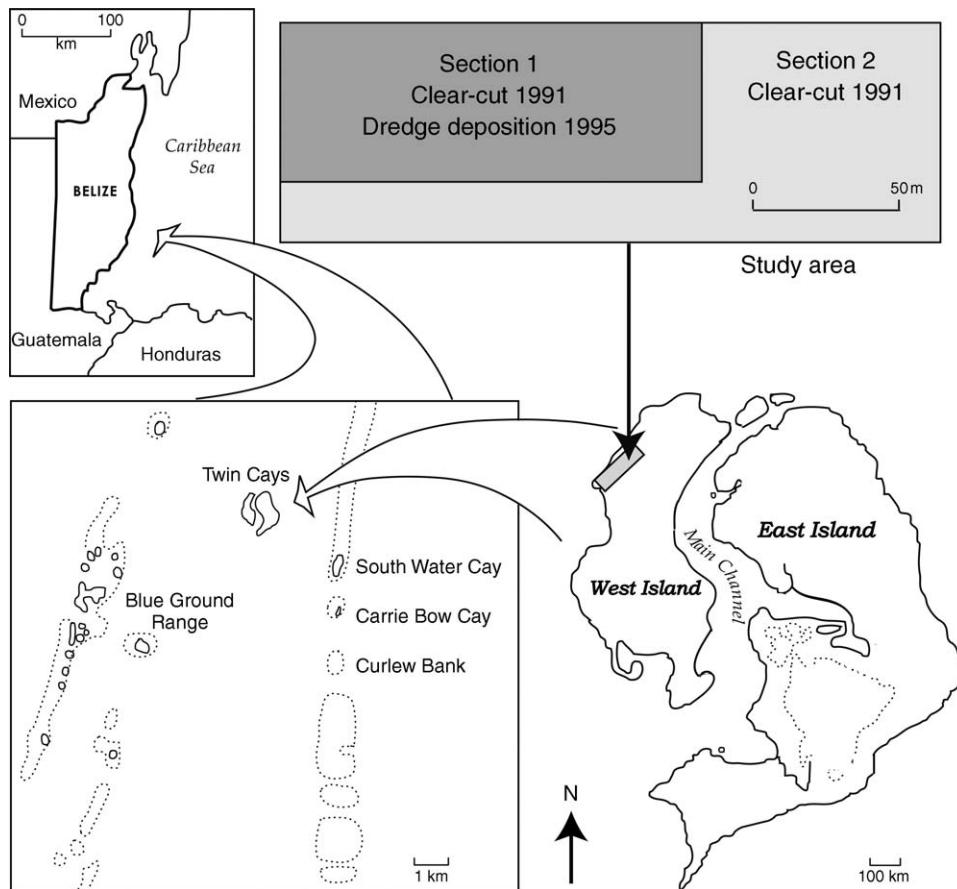


FIG. 1. Map showing location of the study area at Twin Cays, Belize, and the study site that was clear-cut in 1991. Section 1 was monitored until it was backfilled with sand in 1995; section 2 continued to regenerate and was reassessed in 2001.

## METHODS

### Study site

The study was conducted at Twin Cays, a 75-ha archipelago located in the shoreward lagoon of the MesoAmerican barrier reef system, ~12 km from the mainland of Belize (16°50' N, 88°06' W; Fig. 1). Twin Cays is a series of low-relief, intertidal islands that are peat-based (Rützler and Feller 1996). Mangrove islands in this part of the reef complex established on a Pleistocene platform approximately 8000 years ago and have been mangrove communities throughout the Holocene (Macintyre et al. 2004, McKee et al. 2007). The mangrove forest is the oceanic-island type, and species composition is typical of the Caribbean region with *Rhizophora mangle* L. (red mangrove, see Plate 1), *Avicennia germinans* (L.) Stearn. (black mangrove), and *Laguncularia racemosa* (L.) Gaertn. f. (white mangrove). The dominant species is *R. mangle*, which forms monospecific stands along the shoreline and in the interior forest. The topography is heterogeneous with vegetated areas interrupted by tidal creeks, open flats, and shallow ponds. The system is intertidal (20–30 cm range), and the only source of freshwater is rainfall,

which averages <1000 mm/yr. Salinity consequently varies from near sea-strength (36‰) to hypersaline (80–90‰). Nutrient availability is low, and external inputs are limited to seawater and rainfall. Detailed information on the vegetation, geomorphology, chemistry, and hydrology is available elsewhere (Wright et al. 1991, McKee 1993a, Feller 1995, Woodroffe 1995).

Historically, Twin Cays has experienced little human influence, making it a valuable experimental field site. More recently, human impact on Twin Cays and other mangrove islands in the vicinity has escalated through clear-cutting of mangroves for construction of fishing camps and tourist resorts and dredging to raise soil elevations. However, because the substrate is peat and maintenance of soil elevations relative to sea level is dependent upon inputs of organic matter from mangroves (McKee and Faulkner 2000, Macintyre et al. 2004, McKee et al. 2007), these areas rapidly subside and are ultimately abandoned.

This study focused on a 2-ha area cleared of mangroves in 1991 on the western island of Twin Cays (Fig. 1). Colonization by herbaceous vegetation and mangroves was monitored in permanent plots during the first three years after disturbance (January 1992–

January 1995). However, in 1995, part of the recovering area was covered with dredge material (sand and peat) to raise elevations above the intertidal zone. Because the majority of permanent plots were destroyed, further monitoring of mangrove recovery was not possible. Part of the original clear-cut area (~0.7 ha) was not impacted, and this site was used in 2000–2001 to experimentally examine effects of herbaceous vegetation on mangrove recruitment.

#### *Initial vegetative colonization*

In January 1992, 16 plots (4 × 4 m) were established in a stratified random design across the 2-ha clear-cut area. Measurements of edaphic factors were conducted in the center of each plot as described previously (McKee et al. 1988, McKee 1995b). Percent cover of herbaceous vegetation by species was estimated visually in each plot, and all mangrove seedlings were counted and identified to species. Measurements were repeated at approximately six-month intervals for three years. In 1995, this effort was suspended when the area was partially backfilled, and 10 of the 16 plots were permanently buried.

Changes in herbaceous plant cover and soil variables for three years after clear-cutting were analyzed with a repeated-measures ANOVA ( $n = 16$  plots) (SAS 2002). A one-way repeated-measures ANOVA with mangrove species and time as grouping factors was conducted on mangrove density. Contrasts of interest (1 df) were conducted when a significant interaction was found. Relationships between herbaceous plant cover and soil variables were examined by correlation analysis.

#### *Herbaceous patch characterization*

In February 2001, soil and plant measurements were again undertaken to characterize herbaceous patches in an area unaffected by dredge deposition (section 2, Fig. 1). Discrete patches dominated by either *S. portulacastrum* or *D. spicata* (see Plate 1) were identified, and a subset of three patches per species was randomly selected for study. Sampling positions were established with two stations at each of the following positions along a transect traversing each patch: outside patch in unvegetated ground (1 m from the patch edge), patch edge (outer 50 cm), and patch interior (25–50 cm from the center). The two patch types were compared using stem density, canopy height, and rooting depth to characterize above- and belowground vegetative structure. Total number of stems and maximum stem height were measured in 0.1-m<sup>2</sup> circular plots. Shallow cores (15 cm depth × 4 cm diameter) were taken in the same locations, and rooting depth was measured. Soil redox potentials and soil temperature (pH/temperature/mV meter, model 5938-10; Cole-Parmer, Chicago, Illinois, USA) were measured over depth at each sampling station. Cores (12 cm depth × 1.2 cm diameter) were collected with a piston corer and stored in a watertight plastic bag for analysis of salinity, bulk density, water

content, and organic content. After obtaining the wet mass of the core, water was extracted by centrifugation, and the supernatant was measured for salinity and pH. The soil was dried at 80°C to constant mass and reweighed to determine bulk density and water content. The dried soil was ashed at 550°C for 6 h to determine mineral mass after organic loss on ignition. Additional soil samples were analyzed for C and N contents (ThermoQuest Flash EA 1112 Series CHN Analyzer; CE Elantech, Lakewood, New Jersey, USA). Plant and soil variables were analyzed using a split-plot model, with patch species as the main plot and spatial position as the subplot (SAS 2002).

#### *Mangrove distribution and status in patches*

To determine whether distribution and condition of mangroves differed between patch and non-patch environments, mangroves growing inside and outside selected herbaceous patches were examined in detail. The design was a split-plot replicated three times. Each main plot contained one of the herbaceous patches selected previously and an adjacent bare area equivalent in size to the patch. All mangrove seedlings and saplings in the subplots were identified to species and counted. Mangrove condition inside and outside patches was assessed for the dominant species, *R. mangle*. The height, number of nodes, number of growing points (terminal buds), and reproductive output (number of fruit or propagules per plant) were determined on every individual present in patch and bare plots. An index of plant vigor was calculated by dividing the total number of growing points by the number of nodes on the main axis. Total mangrove and individual species densities and *R. mangle* condition were examined using a split-plot model with patch species as the main plot and spatial position (inside, outside) as the subplot (SAS 2002). Frequency distribution of node range for *R. mangle* recruits was examined for each patch type separately by fitting a normal distribution to the data and examining the line of fit generated from the quantile plot (SAS 2002).

#### *Manipulative experiment*

In August 2001, mature *R. mangle* propagules were collected from trees in the undisturbed forest and placed within patches dominated by either *S. portulacastrum* or *D. spicata* and in adjacent bare areas to examine patch effects on establishment and early growth of mangrove seedlings. Propagules were selected based on uniformity in size and labeled by writing directly on the hypocotyl with a permanent marker. The propagules of *R. mangle* are large (mean wet mass = 10 g) and elongated (~25 cm in length), and the primary mode of dispersal is water (McKee 1995a). Vegetated patches and bare-ground plots containing few or no mangroves initially were identified, and propagules were randomly assigned to them. Two types of planting conditions were also used to separate patch effects on establishment from effects

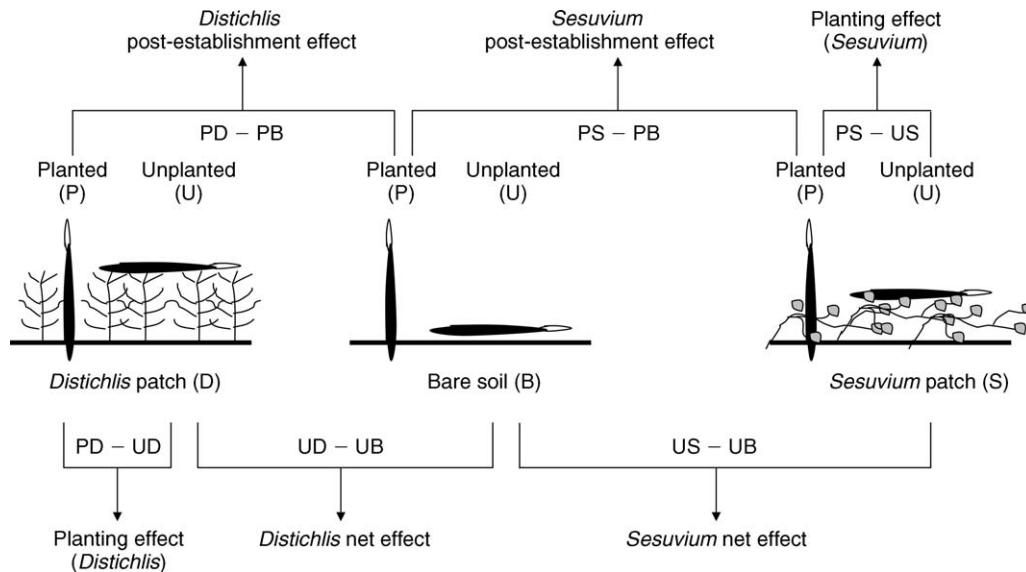


FIG. 2. Experimental design to assess effects of herbaceous patches dominated by *Sesuvium portulacastrum* and *Distichlis spicata* and planting treatment (planted, unplanted) on establishment, survival, and growth of *Rhizophora mangle* seedlings. Net, post-establishment (edaphic), and artificial planting effects were calculated as shown adjacent to each patch type-treatment combination. Net effects of herbaceous patches were estimated by calculating differences in performance between unplanted seedlings in each patch type and unplanted seedlings placed on bare soil (UD - UB, US - UB). Post-establishment (e.g., edaphic) effects were estimated by calculating differences in performance between planted seedlings in each patch type and planted seedlings placed on bare soil (i.e., without trapping and structural support effects; PD - PB, PS - PB). Effects of artificial planting were estimated by calculating differences in performance between planted and unplanted seedlings in each patch type (PS - US, PD - UD).

on subsequent survival and growth. In each of the replicate plots, 10 propagules were planted in an upright position by inserting the radical tip into the soil and another 10 propagules remained unplanted, i.e., deposited untethered in a horizontal position. Deployment of unplanted propagules was conducted to simulate deposition by tides in vegetated or unvegetated plots, i.e., propagules were laid gently in a horizontal position on the herbaceous plant canopy (or bare ground) during an ebb tide. Survival and condition (unrooted or rooted and upright) of seedlings was determined at 6-, 12-, and 24-month intervals. Cumulative leaf production on established seedlings was used as an index of growth.

The data were analyzed as a split-plot with patch type (*S. portulacastrum*, *D. spicata*, and bare ground) as the main plot and treatment (planted, unplanted) as the subplot ( $n=3$ ). Net effects of patches and effects of post-establishment conditions (edaphic) and planting treatment were quantified by making comparisons indicated in Fig. 2. Net effects of herbaceous patches were estimated by calculating differences in performance between unplanted seedlings in each patch type with unplanted seedlings placed on bare soil. Post-establishment (e.g., edaphic) effects were estimated by calculating differences in performance between planted seedlings in each patch type with planted seedlings placed on bare soil (i.e., without trapping and structural support effects). Effects of artificial planting were estimated by

calculating differences in performance between planted and unplanted seedlings in each patch type.

The magnitudes of all effects were standardized to allow comparison across performance parameters and over time. The standardization procedure followed that described previously (Holzapfel and Mahall 1999) based on recommendations for treatment comparisons used in meta-analysis (Gurevitch and Hedges 1993). Each effect was calculated by subtracting the means of the performance parameters and dividing by the pooled standard deviation:

$$d = \frac{\bar{X}_1 - \bar{X}_2}{s_p} J \quad (1)$$

$$s_p = \sqrt{\frac{(N_1 - 1)(s_1)^2 + (N_2 - 1)(s_2)^2}{N_1 + N_2 - 2}} \quad (2)$$

where  $d$  is the effect size,  $\bar{X}$  is the mean of group 1 or 2,  $s_p$  is the pooled standard deviation of groups 1 and 2,  $s$  is the standard deviation of groups 1 or 2, and  $N$  is the total number of individuals in groups 1 or 2. We corrected for sample-size bias by multiplying the term  $J$ :

$$J = 1 - \left( \frac{3}{4(N_1 + N_2 - 2) - 1} \right). \quad (3)$$

The variance associated with each standardized effect was then calculated as recommended (Gurevitch and Hedges 1993):

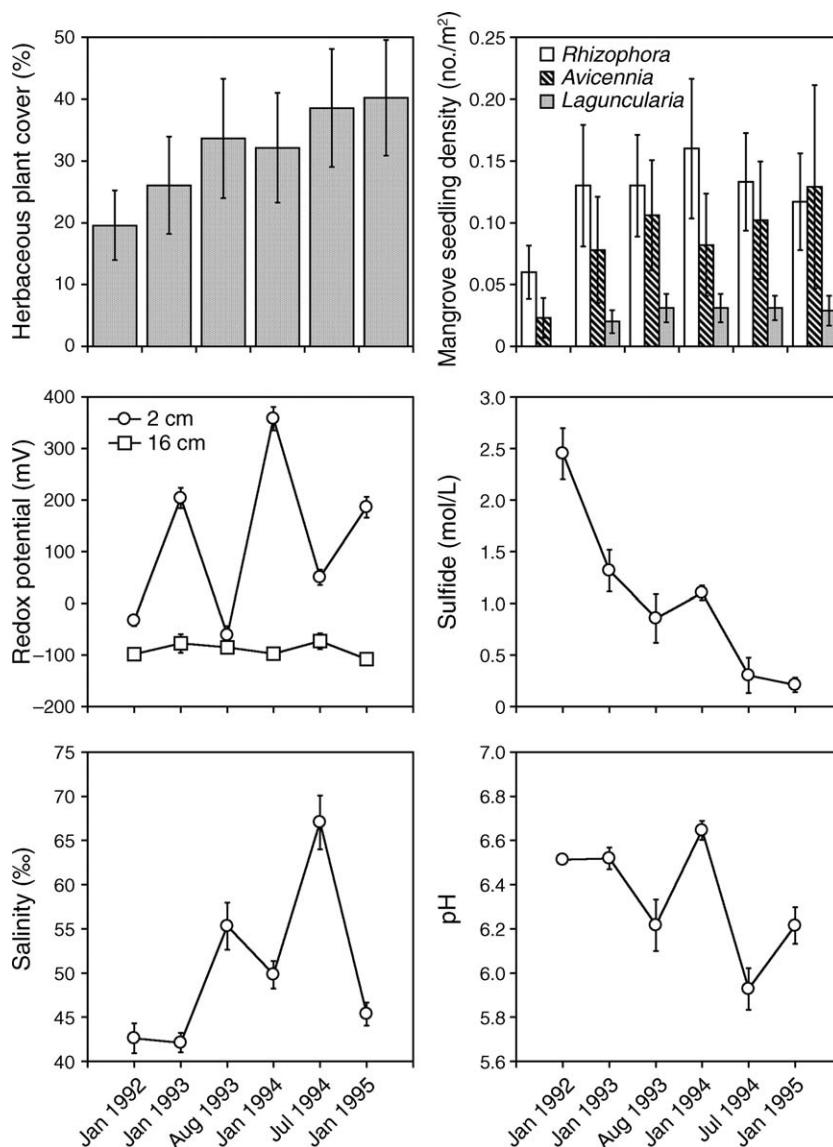


FIG. 3. Changes from 1992 to 1995 in plant and soil conditions measured in replicate plots across the study site where mangroves were clear-cut in 1991: percent cover of herbaceous vegetation; density of mangrove seedlings; soil redox potential ( $E_h$ ) at two depths (2 and 16 cm); sulfide concentrations; porewater salinity; and pH. Measurements were made at intervals until January 1995, when the site was partially buried by dredge material. Values are mean  $\pm$  SE ( $n = 16$  replicate plots per sample date).

$$v = \frac{N_1 + N_2}{N_1 N_2} + \frac{d^2}{2(N_1 + N_2)} \quad (4)$$

where  $v$  is the variance.

## RESULTS

### Initial condition and vegetative colonization of the clear-cut area

The clear-cut area was initially completely devoid of vegetation (see Plate 1), except for three mature *A. germinans* trees left by the cutting crew. By January 1992 when the study was initiated, there was  $\sim 20\%$  vegetative cover, and this gradually increased to 40% over the next three years (Fig. 3). The herbaceous vegetation was

initially dominated by *Batis maritima* (see Plate 1), which increased in percent cover until January 1995. Although *D. spicata* (6–7% cover) and *S. portulacastrum* (<1% cover) were present in some plots, they did not increase significantly during this observation period. Mangrove seedling density was low, but increased significantly at a rate of 0.03 seedlings·m<sup>-2</sup>·yr<sup>-1</sup> ( $F_{5,37} = 4.95$ ,  $P = 0.001$ ). Seedlings of all mangrove species recruited at similar rates, although total density of *L. racemosa* was lower overall compared to *R. mangle* and *A. germinans* ( $F_{2,41} = 2.87$ ,  $P = 0.068$ ; Fig. 4). Mangrove seedlings established naturally in areas devoid of vegetation as well as in areas with herbaceous cover.

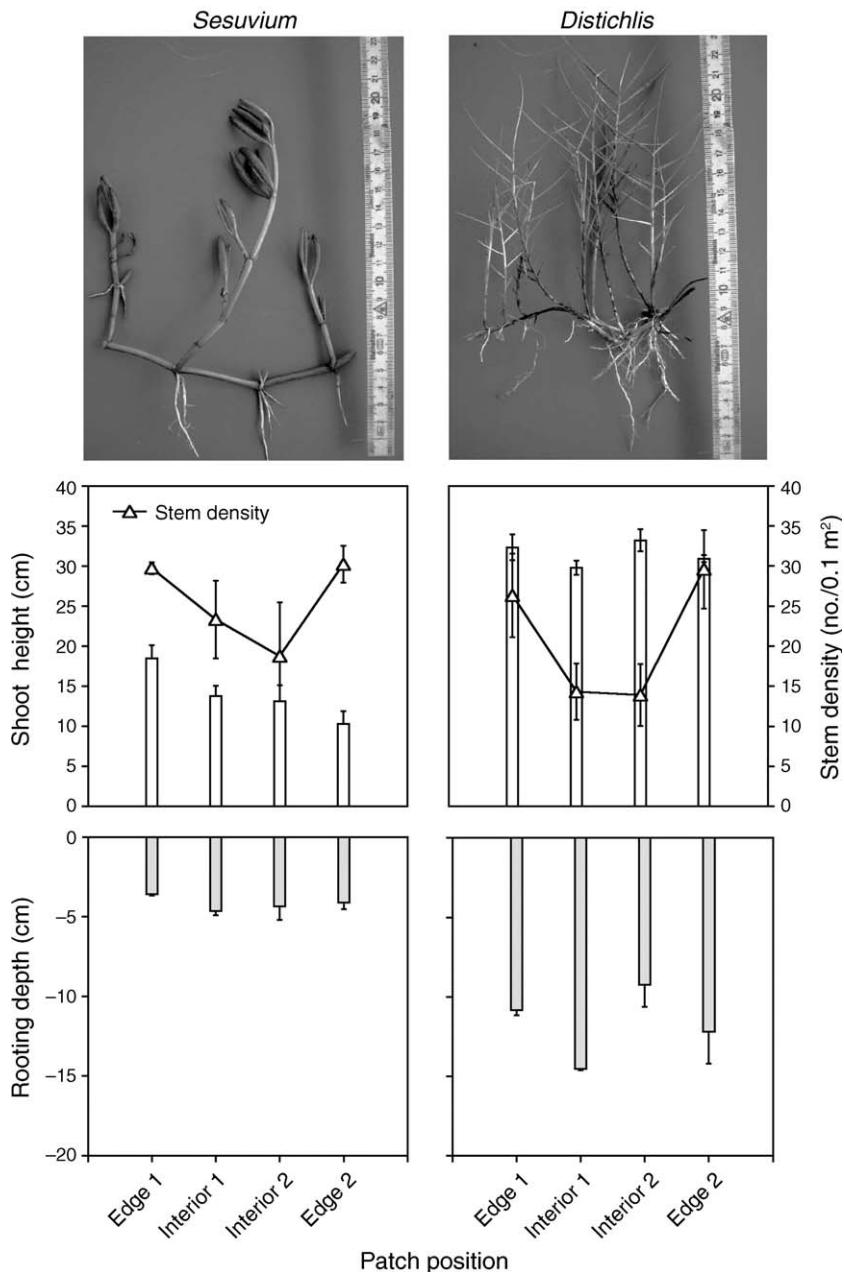


FIG. 4. Structural characteristics of herbaceous patches dominated by either *Sesuvium portulacastrum* or *Distichlis spicata* determined in 2001. Sampling positions occurred across each patch from the edge to interior. Values are mean  $\pm$  SE ( $n = 3$  replicate patches per patch type [each position associated with each patch is the mean of three replicate measurements]).

However, no spatial pattern in mangrove establishment was obvious during early recolonization of the site.

Edaphic conditions in the plots changed significantly (Fig. 3). Soil redox potential,  $E_h$ , which indicates the degree of soil oxidation/reduction and reflects soil waterlogging, remained low at a 16 cm depth, but fluctuated seasonally near the soil surface. Porewater pH and concentrations of sulfide gradually declined over time. Porewater salinity fluctuated during the first two years after clear-cutting, mainly between wet/cool

(January) and dry/hot (July) seasons, but showed no consistent trend over time. Significant correlations between herbaceous plant cover and soil  $E_h$  ( $R = 0.66$ ,  $P = 0.0017$ ) and sulfide ( $R = -0.55$ ,  $P = 0.0126$ ) were found, with the soil becoming less reducing over time as herbaceous cover increased.

When part of the clear-cut area was backfilled in 1995, further monitoring of the original plots was not possible. The area not impacted by backfilling continued to develop, however, and in February 2001 it contained

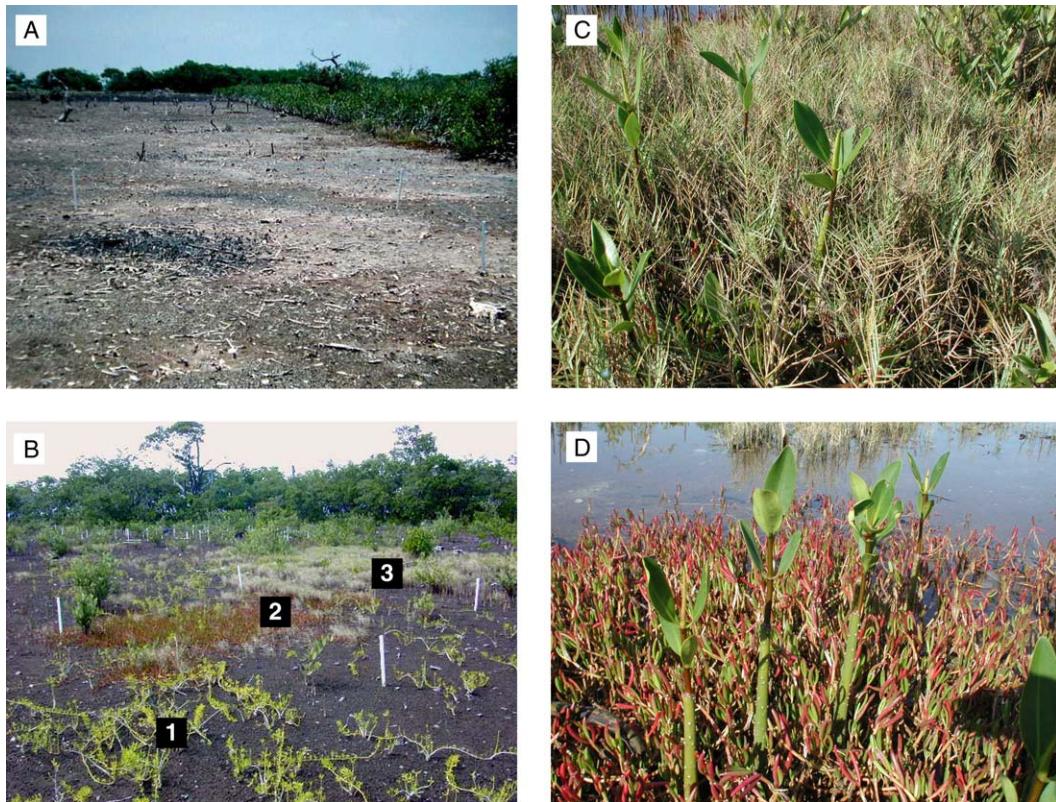


PLATE 1. Ground view of study site in (A) July 1992 just after clearcutting and (B) February 2001 showing patches of three herbaceous species colonizing the clearcut area: (1) *Batis maritima*, (2) *Sesuvium portulacastrum*, and (3) *Distichlis spicata*. Uncut forest can be seen in the background. (C, D) *Rhizophora mangle* (red mangrove) seedlings growing in (C) *D. spicata* and (D) *S. portulacastrum* patches. Photo credits: K. McKee.

numerous monospecific patches of herbaceous vegetation, either *D. spicata* or *S. portulacastrum*. Although *B. maritima* was still present in some spots, it had decreased in abundance and did not form distinct patches.

#### *Structure of herbaceous patches and associated soil physicochemistry*

Herbaceous patches were typically circular in shape and appeared as islands of vegetation surrounded by bare substrate. Patches ranged in size from 8 to 24 m<sup>2</sup> and were distributed throughout the cleared area that had not been backfilled (Plate 1, Fig. 1). Some patches had coalesced to form larger vegetated areas, but ~30% of section 2 remained unvegetated. The transition from patch to surrounding area was abrupt, with little or no decrease in vegetative cover near the patch edge.

The morphological traits of the two herbaceous species differed substantially (Fig. 4). *Distichlis spicata*, a perennial grass with spike-like shoots, was ~30 cm tall and occurred in densities of 600–1200 culms/m<sup>2</sup>. *Sesuvium portulacastrum*, a succulent groundcover, had stem densities similar to that of *D. spicata*, but was considerably shorter in stature (10–15 cm), with a more prostrate growth form. Stem density of both herbaceous

species was greatest at the patch edge ( $F_{2,20} = 7.43$ ,  $P \leq 0.01$ ). Rooting depth of the two species also differed, with that of *D. spicata* three times greater than *S. portulacastrum* ( $F_{1,2} = 213$ ,  $P \leq 0.01$ ). Both shoot height and rooting depth of each species were relatively consistent across the patches.

Significant differences in several soil factors were found between patches and bare ground and between patch types (Fig. 5). Soil  $E_h$  (2 cm depth) was significantly higher in patches than in unvegetated areas ( $F_{4,30} = 3.46$ ,  $P \leq 0.05$ ). At 16 and 32 cm depths,  $E_h$  was less variable, with no significant differences between patch species or between patch and bare ground. The depth profiles of soil  $E_h$ , however, were closely associated with the rooting depths of the two species (Fig. 6). Soil temperature also exhibited spatial variation and was on average 5°–8°C lower inside patches compared to bare soil ( $P \leq 0.0001$ ; Fig. 5). This spatial pattern was most distinct at a 1-cm depth where temperature decreased from outside to the interior of patches (~6°C for *D. spicata* and ~3°C for *S. portulacastrum*; Fig. 5). Salinity in unvegetated areas was typically high ( $\geq 45\%$ ), but was lower inside *D. spicata* patches ( $< 40\%$ ;  $F_{4,30} = 5.88$ ,  $P \leq 0.01$ ; Fig. 5).

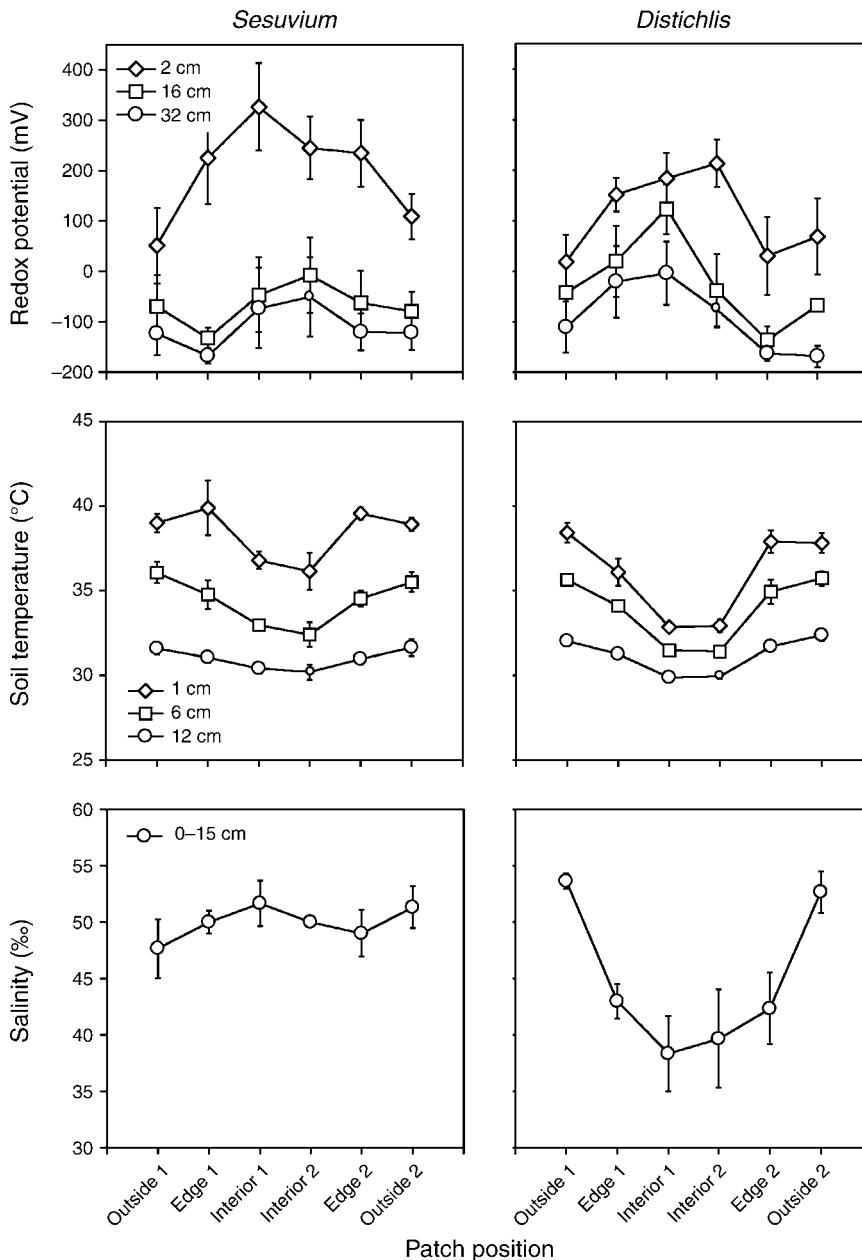


FIG. 5. Variation in selected soil variables across herbaceous patches dominated by either *Sesuvium portulacastrum* or *Distichlis spicata* determined in 2001. Sampling positions occurred across each patch from ~1 m outside where no vegetation occurred (bare soil) and at different soil depths (as indicated for each variable). Values are mean  $\pm$  SE ( $n = 3$  replicate patches per patch type [each position associated with each patch is the mean of three replicate measurements]).

In contrast, the salinity in *S. portulacastrum* patches (47–51‰) was similar to adjacent bare soil. Soil bulk density also decreased from outside to the interior of patches (0.16–0.13 g/cm<sup>3</sup>;  $F_{4,30} = 3.52$ ,  $P \leq 0.05$ ), but was generally low overall. Soil moisture content (83–85%) and organic matter content (71–73%) varied slightly from outside to interior patches, but showed no significant differences between patch types or with position. Soil N content (~20 mg/g soil) was similar between patches and spatial positions.

#### Density, size, and vigor of natural mangrove recruits in patches

By February 2001, three mangrove species had established naturally in the herbaceous patches and in adjacent bare areas of the clear-cut site, but the density of mangroves was several-fold higher inside compared to outside patches (Fig. 7). Density of *R. mangle* was not different between *S. portulacastrum* and *D. spicata* patches (1 df contrast:  $t$  ratio = 0.21,  $P > 0.05$ ), whereas

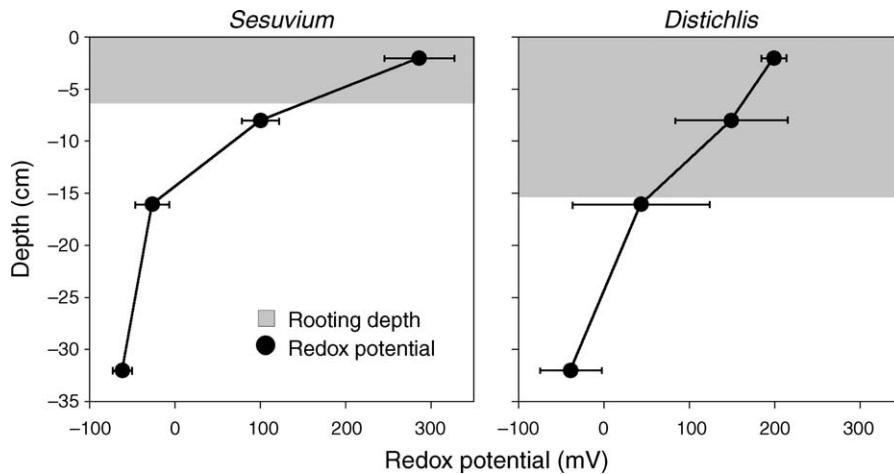


FIG. 6. Variation in soil redox potential with depth in herbaceous patches dominated by either *Sesuvium portulacastrum* or *Distichlis spicata* determined in 2001. Values are mean  $\pm$  SE ( $n$  is the mean of all within-patch positions [4]  $\times$  replicate patches [3] per patch type = 12). The shaded area shows rooting depth for each species.

that of *A. germinans* was higher in *D. spicata* patches (1 df contrasts:  $t$  ratio = 13.80, respectively,  $P \leq 0.0001$ ). Density of *L. racemosa* was also higher in *D. spicata* patches, although the difference was not significant (1 df contrast:  $t$  ratio = 1.62,  $P > 0.05$ ). In addition to higher densities of recruits, the height, vigor, and reproductive output of mangroves were also greater in patches compared to bare ground. Maximum height and vigor of *R. mangle* in *D. spicata* patches was greater than adjacent bare soil (Fig. 8; 1 df contrasts:  $t$  ratio = -3.00

and 4.62,  $P \leq 0.05$ ). However, height and vigor of *R. mangle* was lower in *S. portulacastrum* patches and not significantly different from that in bare soil. Approximately 20% of *R. mangle* individuals within patches were reproductive, whereas none growing outside patches reproduced during the study (Fig. 8). However, there were no significant differences in *R. mangle* reproduction between *S. portulacastrum* and *D. spicata* patches (1 df contrast:  $t$  ratio = 0.63 and 1.28,  $P > 0.05$ , number of

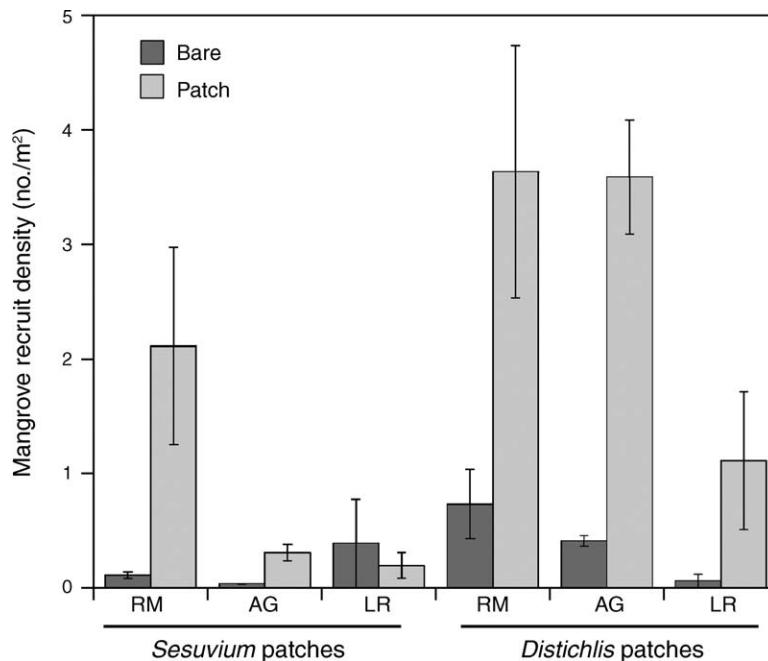


FIG. 7. Density of mangrove recruits (seedlings and saplings) in patches dominated by either *Sesuvium portulacastrum* or *Distichlis spicata* compared to bare soil adjacent to each patch determined in 2001. Mangrove species are *Rhizophora mangle* (RM), *Avicennia germinans* (AG), and *Laguncularia racemosa* (LR). Values are mean  $\pm$  SE ( $n = 3$  replicate patches per patch type [each position associated with each patch is the mean of three replicate measurements]).

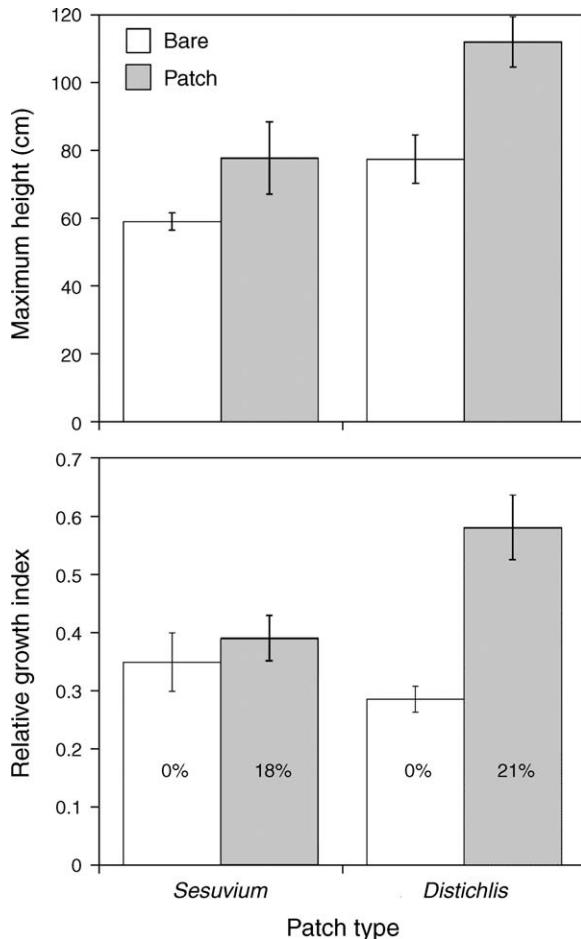


FIG. 8. Maximum height and relative growth index (number of growing points per node on the main shoot axis) of *Rhizophora mangle* recruits in patches dominated by either *Sesuvium portulacastrum* or *Distichlis spicata* compared to bare soil adjacent to each patch determined in 2001. The percentage of reproductive mangroves in each patch type is indicated by inset numbers. Values are mean  $\pm$  SE ( $n = 3$  replicate patches per patch type [each position associated with each patch is the mean of three replicate measurements]).

reproductive trees and number of fruit per tree, respectively).

Qualitative observations indicated that herbaceous patches contained self-regenerating colonies of mangroves with reproductive saplings and numerous seedlings (<10 node class). An analysis of node class distribution of *R. mangle* growing in patches and bare ground showed differences in population structure, which agreed with the observations of reproductive output (Fig. 9). Node class distribution of mangroves growing on bare ground followed a normal distribution with a peak in the 20–24 node class, whereas the pattern for herbaceous patches was skewed due to high numbers in the 0–4 or 5–9 node classes in *D. spicata* (10 individuals) or *S. portulacastrum* (9 individuals) patches, respectively.

#### Effects of patches on trapping, establishment, and growth of mangroves

Transplantation of *R. mangle* propagules into patches and bare areas indicated effects of herbaceous vegetation on trapping, vertical orientation, rooting rate, and subsequent growth of established seedlings (Fig. 10a–d). Artificial planting of mangrove propagules not only prevented removal by tides but also promoted rapid rooting. All artificially planted propagules became rooted within the first six months and survived for two years in bare areas and in *S. portulacastrum* patches; four planted seedlings in *D. spicata* patches were killed by crabs, but the remainder rooted and survived (Fig. 10a). The majority (~75%) of unplanted propagules placed in bare areas was washed away by tides, and those few that were retained either never rooted or never achieved a vertical axis. Many of the unrooted and/or prostrate seedlings exhibited signs of sunburn and desiccation of the hypocotyl. Approximately 40–55% of unplanted propagules deployed into patches were also removed by tidal action, but many became rooted and ultimately achieved a vertical orientation (43–57%). All of the propagules surviving in *S. portulacastrum* patches rooted in a prostrate position, but ultimately became upright through curvature of the hypocotyl. However, propagules placed in *D. spicata* patches slipped into a vertical position (with the radical end touching the soil) soon after deployment and remained so through structural support by the stiff shoots of this grass. Long-term survival was most strongly affected by

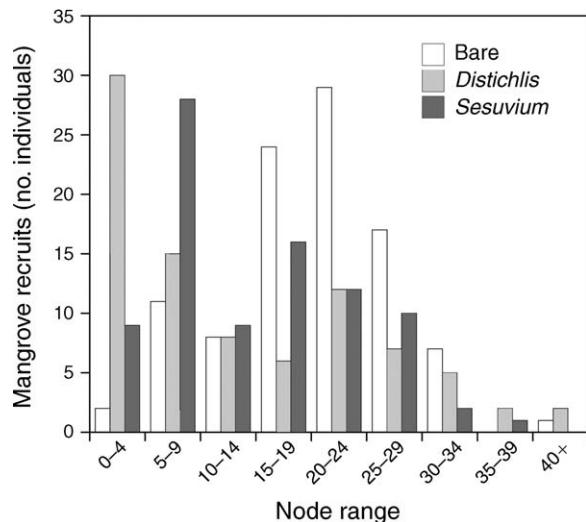


FIG. 9. Frequency distribution of node range for *Rhizophora mangle* recruits in patches dominated by either *Sesuvium portulacastrum* or *Distichlis spicata* compared to bare soil determined in 2001. Values are the mean of numbers of individuals in each node class and patch type. Nodes were counted on all seedling and saplings in each patch and adjacent bare soil plots ( $n = 3$  replicate patches per patch type [each position associated with each patch is the mean of three replicate measurements]).

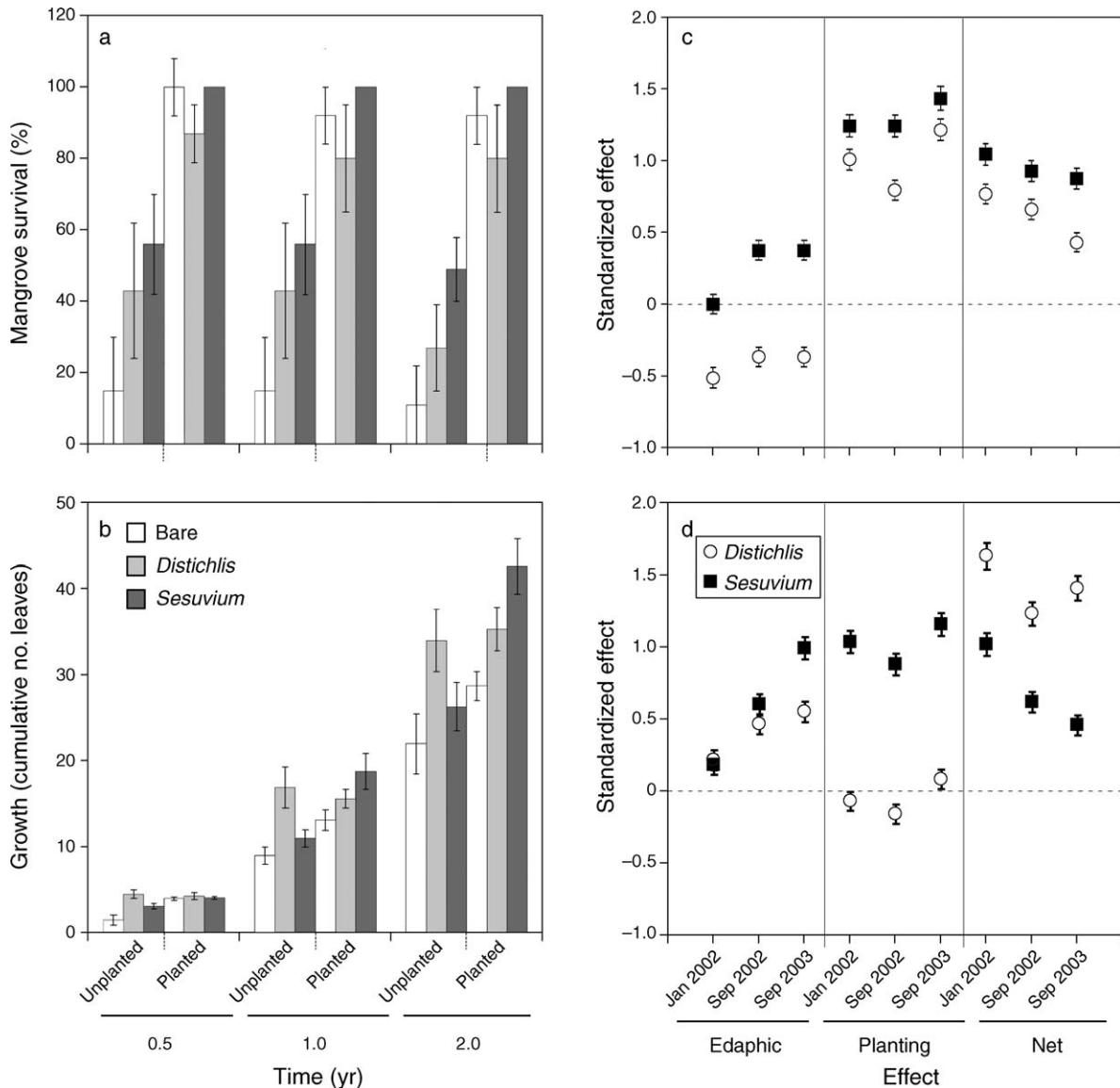


FIG. 10. Survival and growth (cumulative leaf production) of *Rhizophora mangle* seedlings transplanted to patches dominated by either *Sesuvium portulacastrum* or *Distichlis spicata* or to bare soil. Propagules were either planted or placed unplanted and unrestrained in each position, and the positions were then monitored for two years. Values are means  $\pm$  SE ( $n = 3$  replicates per treatment [planted, unplanted]  $\times$  location [*Sesuvium*, *Distichlis*, bare] combination). Left panels show absolute values, and right panels show standardized effects of herbaceous patches over time. See Fig. 2 and *Methods* for calculations of standardized effects and variances.

artificial planting; percentage of survival of planted propagules was 80–100% regardless of location (Fig. 10a). In contrast, survival of unplanted propagules was <60%, with lowest values occurring in bare areas. Comparison of standardized effects indicated that planting had a stronger positive effect on mangrove survival in both *S. portulacastrum* and *D. spicata* patches than did post-establishment conditions (Fig. 10c). Although both herbaceous species had a strong effect on mangrove survival, the net effect of *S. portulacastrum* was slightly higher than *D. spicata* (Fig. 10c).

Cumulative leaf production showed how growth of surviving mangrove seedlings was affected by patch type (Fig. 10b). The seedlings planted in *S. portulacastrum* produced more leaves than in any other treatment combination (1 df contrast:  $t$  ratio = 2.78,  $P = 0.0066$ ) and significantly more than unplanted seedlings (1 df contrast:  $t$  ratio = -3.44,  $P = 0.0009$ ), which fared no better than those deployed to bare sediment (Fig. 10b). *Distichlis spicata* also promoted growth of *R. mangle* seedlings, regardless of whether they were planted or not (1 df contrast:  $t$  ratio = 2.07,  $P = 0.041$ ). Bare areas were

least conducive to the growth of seedlings, regardless of planting treatment (1 df contrast:  $t$  ratio =  $-2.13$ ,  $P = 0.0359$ ). Although both herbaceous species had a positive net effect on mangrove growth, *D. spicata* had a stronger effect than did *S. portulacastrum* (Fig. 10d). Planting increased mangrove leaf production in *S. portulacastrum*, but had no effect in *D. spicata*. Post-establishment effects on growth became more positive over two years in *S. portulacastrum*, whereas the positive effect of *D. spicata* became weaker over time (Fig. 10d).

#### DISCUSSION

Facilitative interactions have been identified in a variety of plant communities, either through spatial associations of species or field or laboratory experiments (Callaway 1995). Clear demonstration of facilitation and its potential value in restoration practices is not always straightforward, however. An experimental approach is required to demonstrate the interference type of plant interaction (Olofsson et al. 1999), and the same is certainly true of plant facilitation. However, of 179 studies of plant facilitation, only 20% employed a manipulative field experiment that produced evidence of the mechanism(s) involved (Callaway 1995). The objective of most field manipulations has been to separate effects of the benefactor species from spatial variation in abiotic factors. This approach typically involves examination of the beneficiary species performance (1) with and without the natural presence of the benefactor species and/or (2) after removal of the benefactor species (e.g., manipulation of canopy or roots). These types of manipulations are required to demonstrate a cause and effect relationship and, further, to determine how the benefactor species is improving the performance of the beneficiary species. However, interpretation of such studies may be problematic due to failure of the manipulation to completely eliminate the influence of the benefactor (e.g., removal of root influence, but not canopy [Cook and Ratcliff 1984]) or to unintended disturbance of the soil, which confounds the effects of benefactor removal (Callaway 1995). A preferred approach is to introduce the beneficiary species as a seed or transplant into areas with and without the benefactor to examine effects on the early life history of the target species. This approach assumes that positive interactions are more prevalent in highly disturbed landscapes (e.g., during secondary succession) in which the benefactor is the precursor to the existence of the beneficiary (Brooker and Callaghan 1998).

In our investigation, herbaceous vegetation clearly facilitated recolonization of mangroves in a disturbed forest. This mangrove ecosystem was characterized by low sediment supply and low nutrients, low elevations (allowing overwashing by tides), high temperatures, hypersalinity, and strongly reducing soils with accumulation of plant phytotoxins, such as sulfide (McKee et al. 1988, McKee 1993b, 1995b) (Fig. 3). Consequently, facilitation of mangrove recruitment might involve

alteration of one or more of these stressful factors. Patches of herbaceous vegetation may promote mangrove recolonization of disturbed areas by (1) trapping dispersing propagules, (2) promoting establishment and rooting, and/or (3) enhancing survival and growth of seedlings through amelioration of physicochemical conditions. Differences in herbaceous patch structure and soil physicochemical factors demonstrated the heterogeneity of conditions at the study site. Although spatial patterns of mangrove recruitment were not evident initially (at three years post-clear-cut), they did appear later after monospecific patches of *D. spicata* and *S. portulacastrum* developed.

Where species-specific facilitation exists, the differences among potential beneficial species may be due to variation in ability to generate a positive effect, but also to relative differences in negative effects (e.g., competition or allelopathy [Mahall and Callaway 1992]). By combining observations of natural recruitment rates and patterns with experimental manipulations, we were able to evaluate the various ways herbaceous vegetation controlled mangrove recolonization of the disturbed forest at Twin Cays.

#### *Facilitation of seedling establishment through propagule trapping and structural support*

Although mangrove seedlings were readily dispersed to the clear-cut site from nearby sources and began establishing within a year after disturbance, recruitment was slow for the first three years. *Batis maritima*, which was initially dominant, did not appear to have an effect on early mangrove recruitment rates or patterns, as reported for degraded forests in south Florida (Milbrandt and Tinsley 2006). However, this disagreement may reflect differences in mangrove species, environmental conditions, timing, presence of other herbaceous species, or other factors in the two locations and points to the need for site-specific information. Nine years post-clear-cut, mangrove recruitment had increased, but more so in herbaceous patches of *D. spicata* or *S. portulacastrum*. Tidal fluctuation readily removes any unrestrained and buoyant object such as propagules (McKee 1995a). The higher densities of natural recruits in patches compared to bare ground may reflect propagule trapping, combined with the stranding requirement for propagule rooting (McKee 1995a). Experimental dispersal of *R. mangle* propagules showed that most unplanted *R. mangle* propagules were washed away from bare ground, but about half were retained in the patches.

Greater height and stiffer structural support provided by the *D. spicata* canopy promoted greater retention of both natural and experimental mangrove recruits. Densities of *A. germinans* and *L. racemosa* recruits were in fact higher in *D. spicata* compared to *S. portulacastrum* patches, possibly due to trapping of these smaller and more buoyant propagules (McKee 1995a). The densities of natural *R. mangle* recruits were not

significantly different between the two patch types, however. Also, retention of unplanted *R. mangle* propagules was about the same in *D. spicata* and *S. portulacastrum* patches. It is possible that the relative trapping influence of these species is less important for larger, heavier propagules such as *R. mangle*. However, the aboveground structure of *D. spicata* patches clearly provided structural support for *R. mangle*, while canopies (30–35 cm height) were not tall enough to shade the seedlings (>30 cm height). Since an upright posture promotes long-term survival of *R. mangle* (McKee 1995b), structural support may be an additional factor affecting recruitment. In contrast, all unplanted survivors in *S. portulacastrum* patches established in a prostrate position and later curved upward. A shorter, weaker seedling axis may explain slower growth of unplanted seedlings in *S. portulacastrum* (Fig. 10d). Such species-specific differences in nurse plants could be exploited to assist in seedling success when artificial planting of mangroves is not feasible.

#### *Facilitation through amelioration of physicochemical conditions*

Some species can act as autogenic engineers by altering the physical state of an environment and modifying a resource that benefits another species (Jones et al. 1994). The effects may be species-specific or provide a broad range of advantages to several related species. Since our study was not designed to experimentally show patch effects on physicochemical conditions, we cannot say with certainty whether the herbaceous vegetation altered the environmental conditions of the clear-cut site or plants simply established in areas with different edaphic features. However, the results are most consistent with the former explanation. Soil conditions were stressful across the entire clear-cut area in January 1992 (Fig. 3). Over the next three years, soil  $E_h$  increased and sulfide decreased along with increasing plant cover.

Comparison of patches dominated by *D. spicata* and *S. portulacastrum* provided additional insight into how herbaceous vegetation might influence environmental conditions. The taller canopy of *D. spicata* patches shaded the soil and reduced soil temperatures more than *S. portulacastrum*, and these changes were associated with lower salinities (Fig. 5). Also, the close association between rooting depth and soil redox potential (Fig. 6) suggests that the herbaceous vegetation was oxidizing the sediment through oxygen release from roots, as demonstrated for salt marsh species (Mendelssohn and Morris 2000) and mature mangroves (McKee et al. 1988, McKee 1993b).

Comparison of experimental mangrove recruits also indicated species-specific facilitation by the herbaceous vegetation. When net effects were compared using standardized units, *S. portulacastrum* was found to be better at promoting mangrove establishment and long-term survival, but *D. spicata* enhanced growth of survivors (Fig. 10c, d). A comparison of planting effects

in the two patch types indicates how much each patch species promoted mangrove survival and growth through trapping and structural support. *Distichlis spicata* apparently promoted growth of unplanted mangroves through physical support. Effects of post-establishment conditions on mangrove growth were not strong initially (at six months), but became increasingly positive over time as the plants became larger (Fig. 10d). This finding may reflect lower temperature and salinity and less reducing soils in patches compared to bare ground (Fig. 5).

Facilitation and competition can occur simultaneously between co-growing species (Holmgren et al. 1997), and this may be the case for mangroves and herbaceous associates. Effects of post-establishment conditions on mangrove growth were more positive for *S. portulacastrum* compared to *D. spicata*, especially over time (Fig. 10d). Both *S. portulacastrum* and *D. spicata* ameliorated stressful soil conditions (Figs. 4, 5). However, since *S. portulacastrum* roots were relatively shallow, they were not competing for nutrients at lower depths. *Distichlis spicata* had deeper root systems, overlapping that of mangrove recruits (up to 50 cm deep). Thus, even though *D. spicata* patches had lower soil temperatures, lower salinities, and higher redox potentials than bare soil, competition for nutrients may have partially counteracted the positive effects.

Establishment of herbaceous vegetation may be an important first step in site preparation for mangrove revegetation where stressful conditions prevail. Initial colonization of the clear-cut site by *B. maritima* may have ameliorated soil conditions, but had little direct effect on trapping and establishment of mangrove seedlings. *Distichlis spicata* and *S. portulacastrum*, which established later, increased propagule trapping and also ameliorated stressful conditions. Herbaceous patches additionally promoted growth and reproduction by mangrove recruits (Figs. 8–10). Many patches contained reproductive saplings surrounded by numerous propagules and seedlings; this pattern was not seen in unvegetated areas (Fig. 9). This pattern likely reflects trapping not only of propagules dispersed from surrounding areas, but of patch-borne propagules. Rapid development of self-regenerating colonies of mangroves may be important in areas in which dispersal from mature forests is limited (Imbert et al. 2000).

#### *Implications for mangrove restoration*

Although many restoration projects involve planting of mangroves (Field 1996), little information exists on factors determining seedling survival and subsequent growth rates in degraded, restored, or created mangrove forests (Day et al. 1999, Elster 2000, Bosire et al. 2003, Milbrandt and Tinsley 2006). The finding that some herbaceous species can have a positive effect on mangrove recruitment suggests that natural regeneration of large disturbed areas may occur much faster if beneficial species are present (Milbrandt and Tinsley

2006). However, our work shows that effects of herbaceous vegetation on mangrove regeneration may depend upon the species involved as well as the factors affecting mangrove recruitment in each geographic area. Consequently, nurse species might be identified based on positive features such as shoot structure affecting shading and amelioration of soil temperature and salinity, propagule trapping and retention, and root effects on soil aeration and competition for nutrients or water. Additionally, such comparisons may be improved using standardized effects as illustrated here. Quantification of standardized effects showed: (1) the net effect of each herbaceous species on mangrove survival and growth, (2) effects of pre- and post-establishment factors associated with each patch type, and (3) the need for artificial planting to enhance growth or survival.

Our work provides an example of how facilitation might promote mangrove regeneration and how such effects might be assessed. However, application to restoration projects will require site-specific information as well as an understanding of the mechanisms involved. Although we directly compared the effects of only two herbaceous species, extensive lists of mangrove associates worldwide include more than 25 plant families and more than 45 genera (Tomlinson 1994). Growth forms include grasses, rushes, sedges, succulents, forbs, and ferns. This large pool of mangrove associates, many of which are cosmopolitan, indicates the potential for selection of beneficial species in other geographic regions. Future work should develop a broader picture of how herbaceous associates interact with mangroves to influence forest regeneration rates and patterns in a variety of environmental conditions. This type of information will be increasingly important as human pressures on the coastal zone grow and the need for better management and restoration strategies increases.

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#### LITERATURE CITED

- Alongi, D. M. 2002. Present state and future of the world's mangrove forests. *Environmental Conservation* 29:331–349.
- Barbier, E. B. 2006. Natural barriers to natural disasters: replanting mangroves after the tsunami. *Frontiers in Ecology and the Environment* 4:124–131.
- Bertness, M. D. 1991. Interspecific interactions among high marsh perennials in a New England salt marsh. *Ecology* 72:125–137.
- Bertness, M. D., and S. Hacker. 1994. Physical stress and positive associations among marsh plants. *American Naturalist* 144:363–372.
- Bertness, M. D., and G. H. Leonard. 1997. The role of positive interactions in communities: lessons from intertidal habitats. *Ecology* 78:1976–1989.
- Bosire, J. O., F. Dahdouh-Guebas, J. G. Kairo, and N. Koedam. 2003. Colonization of non-planted mangrove species into restored mangrove stands in Gazi Bay, Kenya. *Aquatic Botany* 76:267–279.
- Brooker, R. W., and T. V. Callaghan. 1998. The balance between positive and negative plant interactions and its relationship to environmental gradients: a model. *Oikos* 81:196–207.
- Bruno, J. F., J. J. Stachowicz, and M. D. Bertness. 2003. Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution* 18:119–125.
- Callaway, R. M. 1995. Positive interactions among plants. *Botanical Review* 61:306–349.
- Cintron, G., A. E. Lugo, D. J. Pool, and G. Morris. 1978. Mangroves of arid environments in Puerto Rico and adjacent islands. *Biotropica* 10:110–121.
- Connell, J. H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *American Naturalist* 122:661–696.
- Cook, S. J., and D. Ratcliff. 1984. A study of the effects of root and shoot competition on the growth of green panic (*Panicum maximum* Var. *trichoglume*) seedlings in an existing grassland using root exclusion tubes. *Journal of Applied Ecology* 21:971–982.
- Day, S., W. J. Streever, and J. J. Watts. 1999. An experimental assessment of slag as a substrate for mangrove rehabilitation. *Restoration Ecology* 7:139–144.
- Day, T. A., and R. G. Wright. 1989. Positive plant spatial association with *Eriogonum ovalifolium* in primary succession on cinder cones—seed-trapping nurse plants. *Vegetatio* 80:37–45.
- Dobson, A. P., A. D. Bradshaw, and A. J. M. Baker. 1997. Hopes for the future: restoration ecology and conservation biology. *Science* 277:515–522.
- Egerova, J., C. E. Proffitt, and S. E. Travis. 2003. Facilitation of survival and growth of *Baccharis halimifolia* L. by *Spartina alterniflora* Loisel. in a created Louisiana salt marsh. *Wetlands* 23:250–256.
- Elster, C. 2000. Reasons for reforestation success and failure with three mangrove species in Colombia. *Forest Ecology and Management* 131:201–214.
- Elster, C., L. Perdomo, and M. L. Schnetter. 1999. Impact of ecological factors on the regeneration of mangroves in the Ciénaga Grande de Santa Marta, Colombia. *Hydrobiologia* 413:35–46.
- Feller, I. C. 1995. Effects of nutrient enrichment on growth and herbivory of dwarf red mangrove (*Rhizophora mangle*). *Ecological Monographs* 65:477–505.
- Feller, I. C., D. F. Whigham, K. L. McKee, and C. E. Lovelock. 2003. Nitrogen limitation of growth and nutrient dynamics in a disturbed mangrove forest, Indian River Lagoon, Florida. *Oecologia* 134:405–414.
- Field, C. D. 1996. Restoration of mangrove ecosystems. International Society for Mangrove Ecosystems, Okinawa, Japan.
- Flower, J. M. 2004. Experimental seedling at two decaying mangrove sites: advantage for the protected areas of Guadeloupe. *Revue d'Ecologie—La Terre et La Vie* 59:171–180.
- Goldberg, D. E., and A. M. Barton. 1992. Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. *American Naturalist* 139:771–801.
- Gomez-Aparicio, L., R. Zamora, J. M. Gomez, J. A. Hodar, J. Castro, and E. Baraza. 2004. Applying plant facilitation to forest restoration: a meta-analysis of the use of shrubs as nurse plants. *Ecological Applications* 14:1128–1138.

- Gurevitch, J., and L. V. Hedges. 1993. Meta-analysis: combining the results of independent experiments. Pages 378–398 in S. M. Scheiner and J. Gurevitch, editors. Design and analysis of ecological experiments. Chapman and Hall, New York, New York, USA.
- Holmgren, M., M. Scheffer, and M. A. Huston. 1997. The interplay of facilitation and competition in plant communities. *Ecology* 78:1966–1975.
- Holzappel, C., and B. E. Mahall. 1999. Bidirectional facilitation and interference between shrubs and annuals in the Mojave Desert. *Ecology* 80:1747–1761.
- Hunter, A. F., and L. W. Aarssen. 1988. Plants helping plants: new evidence indicates that beneficence is important in vegetation. *BioScience* 38:34–40.
- Imbert, D., A. Rousteau, and P. Scherrer. 2000. Ecology of mangrove growth and recovery in the Lesser Antilles: state of knowledge and basis for restoration projects. *Restoration Ecology* 8:230–236.
- Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. *Oikos* 69:373–389.
- Kaly, U. L., and G. P. Jones. 1998. Mangrove restoration: a potential tool for coastal management in tropical developing countries. *Ambio* 27:656–661.
- Lewis, R. R. 2005. Ecological engineering for successful management and restoration of mangrove forests. *Ecological Engineering* 24:403–418.
- Lindquist, E. S., and C. R. Carroll. 2004. Differential seed and seedling predation by crabs: impacts on tropical coastal forest composition. *Oecologia* 141:661–671.
- Macintyre, I. G., M. A. Toscano, R. G. Lighty, and G. B. Bond. 2004. Holocene history of the mangrove islands of Twin Cays, Belize, Central America. *Atoll Research Bulletin* 510:1–16.
- Maestre, F. T., S. Bautista, J. Cortina, and J. Bellot. 2001. Potential for using facilitation by grasses to establish shrubs on a semiarid degraded steppe. *Ecological Applications* 11:1641–1655.
- Mahall, B. E., and R. M. Callaway. 1992. Root communication mechanisms and intracommunity distributions of two Mojave desert scrubs. *Ecology* 73:2145–2151.
- Martinez, M. L. 2003. Facilitation of seedling establishment by an endemic shrub in tropical coastal sand dunes. *Plant Ecology* 168:333–345.
- McKee, K. L. 1993a. Determinants of mangrove species distribution in neotropical forests: biotic and abiotic factors affecting seedling survival and growth. Louisiana State University, Baton Rouge, Louisiana, USA.
- McKee, K. L. 1993b. Soil physicochemical patterns and mangrove species distribution—Reciprocal effects? *Journal of Ecology* 84:477–487.
- McKee, K. L. 1995a. Mangrove species distribution and propagule predation in Belize: an exception to the dominance-predation hypothesis. *Biotropica* 27:334–345.
- McKee, K. L. 1995b. Seedling recruitment patterns in a Belizean mangrove forest: effects of establishment and physico-chemical factors. *Oecologia* 101:448–460.
- McKee, K. L., D. R. Cahoon, and I. C. Feller. 2007. Caribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation. *Global Ecology and Biogeography*, in press.
- McKee, K. L., and P. L. Faulkner. 2000. Mangrove peat analysis and reconstruction of vegetation history at the Pelican Cays, Belize. *Atoll Research Bulletin* 468:46–58.
- McKee, K. L., I. A. Mendelssohn, and M. W. Hester. 1988. Reexamination of pore water sulfide concentrations and redox potentials near the aerial roots of *Rhizophora mangle* and *Avicennia germinans*. *American Journal of Botany* 75:1352–1359.
- Mendelssohn, I. H., and J. T. Morris. 2000. Eco-physiological controls on the productivity of *Spartina alterniflora* Loisel. Pages 59–80 in M. P. Weinstein and D. A. Kreeger, editors. Concepts and controversies in tidal marsh ecology. Kluwer Academic, Dordrecht, The Netherlands.
- Milbrandt, E. C., and M. N. Tinsley. 2006. The role of saltwort (*Batis maritima* L.) in regeneration of degraded mangrove forests. *Hydrobiologia* 568:369–377.
- Olofsson, J., J. Moen, and L. Oksanen. 1999. On the balance between positive and negative plant interactions in harsh environments. *Oikos* 86:539–543.
- Pugnaire, F. I., P. Haase, and J. Puigdefabregas. 1996. Facilitation between higher plant species in a semiarid environment. *Ecology* 77:1420–1426.
- Rivera-Monroy, V. H., R. R. Twilley, D. Bone, D. L. Childers, C. Coronado-Molina, I. C. Feller, J. Herrera-Silveira, R. Jaffe, E. Mancera, E. Rejmankova, J. Salisbury, and E. Weil. 2004. A conceptual framework to develop long-term ecological research and management objectives in the wider Caribbean Region. *BioScience* 54:843–856.
- Robinson, G. R., and S. N. Handel. 1993. Forest restoration on a closed landfill—rapid addition of new species by bird dispersal. *Conservation Biology* 7:271–278.
- Rützler, K., and I. C. Feller. 1996. Caribbean mangrove swamps. *Scientific American* 274:94–99.
- SAS. 2002. JMP statistics and graphics guide. Version 5. SAS Institute, Cary, North Carolina, USA.
- Sherman, R. E., T. J. Fahey, and J. J. Battles. 2000. Small-scale disturbance and regeneration dynamics in a neotropical mangrove forest. *Journal of Ecology* 88:165–178.
- Tomlinson, P. B. 1994. The botany of mangroves. Cambridge University Press, Cambridge, UK.
- Valiela, I., J. L. Bowen, and J. K. York. 2001. Mangrove forests: one of the world's threatened major tropical environments. *BioScience* 51:807–815.
- Woodroffe, C. D. 1995. Mangrove vegetation of Tobacco Range and nearby mangrove ranges, central Belize barrier reef. *Atoll Research Bulletin* 427:1–35.
- Wright, R. M., D. W. Urish, and I. Runge. 1991. The hydrology of a Caribbean mangrove island. Pages 170–184 in G. Cambers, editor. Coastlines of the Caribbean. American Society of Civil Engineers, New York, New York, USA.