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Long-term growth and succession in restored and natural mangrove forests in southwestern Florida

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Abstract

We compared colonization, growth and succession from 1989 to 2000 in a restored mangrove site and in gap and closed canopy sites in a natural mangrove forest. The restored site was created in 1982 and planted with *Rhizophora mangle* ($\approx 2\ \mathrm{m}^{-2}$) propagules. By 1989, *Laguncularia racemosa*, with densities up to 12.9 tree m^{-2}, was a dominant in all plots, although densities were greater at edge plots relative to inner plots, and near open water (west plots) relative to further inland (east plots), and in tall mangrove plots relative to scrub plots. *Rhizophora mangle* (1989 tree densities about 2 m^{-2}) was a codominant in inner and scrub plots, while *Avicennia germinans* had the lowest densities (<1 tree m^{-2}) in all plots. From 1989 to 2000 *L. racemosa* experienced reduced recruitment and apparent density-dependent mortality of canopy individuals in plots with high initial densities. Scrub plots experienced high rates of colonization by *R. mangle* and *L. racemosa*, rapid growth in height of all species (1989–1996), followed by a dieoff of *L. racemosa* in later years (1997–2000) as the canopy came to resemble that of tall mangrove plots. Colonization and growth rates were lower in gap and closed canopy regions of the natural forest relative to rates in the restored site. After 11 years, densities of *L. racemosa* were 10–20× lower and *R. mangle* slightly less in the gap relative to densities in tall mangrove plots in the restored site at the same age. Although the restored stand had converged with the natural forest by 2000 in terms of some factors such as species richness, vegetation cover, litterfall, and light penetration, trees were still much smaller and stem densities much higher. Full development of mature structure and ecological function will likely require decades more development.

Introduction

There is a clear need for long-term, quantitative ecological studies in restored mangrove forests, and for comparative studies in natural forests. Restoration and creation of intertidal mangrove forests is of critical importance to the continued ecological functioning of tropical estuaries because of the high rates of destruction of these ecosystems in many locales around the world (Crooks and Turner 1999; Hawkins et al. 2002). In the New World tropics, mangrove restoration often involves re-establishment of natural hydrologic and tidal regimes, planting mangrove propagules, or planting marsh plants as nurse species (Lewis 1990; Cintrón 1992). In the Indo-Pacific, both restoration of mangrove habitat *per se* and silvaculture are practiced (Field 1996). Although restoration projects are numerous, few have received quantitative study to ascertain success and almost none of these have been studied for more than a few years. Notable exceptions include the large number of mangrove silvaculture studies in the Indo-Pacific that have tracked growth and density in planted and sometimes artificially thinned settings (e.g., Chan 1996; Hong 1996; Siddiqi and Kahn 1996; Untawale 1996), and an evaluation of recruitment and growth over several years in an oil spill site in Panama (Duke 1996). The general lack of long-term study of growth and succession hampers our understanding of restoration processes and time scales because it may take decades for restored stands to develop the tree sizes, dominance regimes, and normal above-and-below ground biomass and productivity regimes, faunal populations, and soil-organic matter structure typical of a natural mangrove forest.

Many physical and biological factors influence the population dynamics, community structure, canopy dominance, and succession in natural and restored mangrove forests (see review by Smith 1992). Mangroves show species-specific differences to gradients in certain physical factors such as temperature (Lugo and Patterson-Zucca 1977; Markely et al. 1982), inundation and salinity (Clarke and Hannon, 1967, 1970; Ball 1988; Smith 1989; Ellison and Farnsworth 1993), water movement (Rabinowitz 1978a, b), nutrients (Feller 1995; McKee 1995a, b), and soil sulfide content (Thibodeau and Nickerson 1986; McKee 1993a, b). The formation of gaps or new habitat from delta formation, restoration activities, and mudbank accretion also influences mangrove recruitment and growth (Craighead and Gilbert 1962; Thom 1967; Alexander 1968; Thom et al. 1975; Smith 1987b, 1992). Lightening strikes and storm throw often create large (>500 m^2) gaps (Smith 1992), whereas small gaps (<1 m^2) can be created in *Rhizophora mangle* L. forests by boring insects (Feller and McKee 1999). Gaps can differ from closed canopy areas in physico-chemical parameters, and by serving as refuges from predators (Smith 1992; Feller and McKee 1999; Sousa et al. 2003; Devlin, 2004). Environmental regimes, colonization rates Rabinowitz (1978a, b, c), predation Onuf et al. 1977; Smith 1987a, b; Smith et al. 1989), and intra-and-interspecific interactions among seedlings and mature trees (Ball 1980; McKee 1995a, b) interact to determine the patterns of canopy dominance and succession. In addition, differences in response by different mangrove genotypes and maternal lineages is just now being explored (Devlin, 2004).

Here, we report long-term (1989–2000) colonization, growth, and succession in a restored mangrove site (created 1982), and provide comparisons with gap and closed canopy sites in a natural mangrove forest. We also compare our litterfall and long-term vegetation results to the findings of McKee and Faulkner (2000) who worked in this same site (Windstar in Naples, FL).

Site description

The natural mangrove forest at Windstar

The mangrove forest at the Windstar-on-Naples Bay golf course and housing development is approximately 1730 m in shoreline length and 328 m in maximum intertidal width. The forest is a mixed stand of *R. mangle*, *Laguncularia racemosa* (L.) Gaertn.f., and *Avicennia germinans* (L.) Stearn. with (*Conocarpus erectus* L.) also being an important member of the canopy in some locations. The natural forest was mature and well developed at least 40 years ago, based on our observations of aerial photographs, and unlike many mangrove stands in the region, did not experience extensive tree fall during hurricane Donna in 1960 (T. Below, Rookery Bay Audubon Warden, pers. comm.).

The restored mangrove sites at Windstar

Sediment from Naples Bay was pumped in the natural mangrove forest at Windstar in the1940s and 1950s killing the mangroves in three sites (1–4 ha each). In August and September of 1982, as mitigation for the additional loss of mangrove wetlands resulting from construction, the dredged sediment was removed and natural elevations restored (+0.22 to +0.58 m National Geodetic

Vertical Datum). This elevation range ensured regular tidal flooding, although variance existed in micro-topography within the sites. A low berm remained on the western (Naples Bay) side at the boundary between the natural forest and the restored site. A flushing channel, approximately a half meter wide and a few centimeters deep at low tide was cut through the berm during site construction. Pairs of unrooted *R. mangle* propagules were planted every 1 m throughout the restoration sites (Stephen 1984). The present authors had no part in creation of the sites.

Eight months after planting, survival of the *R. mangle* seedlings was estimated visually to be 97%, and some colonization by *A. germinans* was noted (Stephen 1984). At 3.5 years, Bradow (1986) reported 85% survival of *R. mangle* with many of the young trees reaching 1–1.5 m in height. He noted that much of the area had been colonized by *L. racemosa* and to a lesser extent by *A. germinans*. Some of the white mangroves were reported to be in excess of 2 m tall, although quantitative measurements were not taken (Bradow 1986).

Our study was conducted in the northernmost of the three restored sites and in both closed canopy and gap sites of the natural forest that surrounds the restored site. The roughly circular restored site (diameter ≈ 130 m) is completely surrounded by a natural mangrove forest. The fringe area of the natural forest immediately to the west (seaward side) of the restored site is a strip ranging from approximately 15–38 m wide. The basin portion of the natural forest immediately east of the restored site is about 71 m deep, measured from edge of the restored site to the edge of the uplands. All three mangrove species were abundant in the natural forest.

Our initial field observations in 1989 suggested that (1) the white mangrove, *L. racemosa*, a volunteer colonizer of the site, was the numerical dominant in most areas of the restored site but was less abundant in the site's interior; (2) the planted *R. mangle* survived and grew well, but there appeared to have been little further colonization of the site by this species based on the visual evidence of pairs of young trees (saplings) that had resulted from the planted pairs of propagules; (3) the black mangrove, *A. germinans*, had colonized throughout the site although the relative abundance of this species was low; (4) all three species contributed to the canopy, which was about 2 m tall in most of the site; (5) elevations were slightly higher in some areas, and the higher sites (termed "scrub mangrove sites") were dominated by short (<1 m), highly branched mangroves and the herbaceous succulent plant *Batis maritima*.

Research topics addressed

From our initial observations we posed four problems for study. These are phrased below as *a priori* predictions and were analyzed by observing changes over time in permanent plots and comparing changes in the restoration site with those in closed canopy and gap plots in the natural mangrove forest.

(1) Abundance and dominance of *L. racemosa* will decline over time in "tall mangrove" plots in the restored site in a density-dependent manner. This species is considered to be an opportunistic colonizer and poor competitor for light (Ball 1980) and we reasoned that the 3–4× differences in total tree densities existing at different locations within the site would lead to different thinning regimes.

(2) Density and dominance of *L. racemosa* will persist in scrub plots in the restored site, although over very long time frames it may be replaced by *A. germinans*. We suspected that the slightly higher elevations, possibly leading to high summer soil salinities and less frequent flooding, might be responsible for the existence of the so-called scrub plots. *Avicennia germinans* can tolerate high soil salinities and might be expected to dominate the scrub plots, but in 1989 this species had not colonized in high numbers. Thus, if the premise was correct that stress conditions produced the scrub vegetation and if future colonization by *A. germinans* remained low, we expected that dominance by *L. racemosa* would be maintained in these plots for some time, although with eventual replacement by *A. germinans* in the very long term.

(3) Colonization and succession in the natural forest gap will proceed in a similar pattern to that observed in the restored site, although rates will be slower because of shading by surrounding canopy trees. We expected that the natural canopy gap created by lightening in 1989 would be rapidly colonized by the opportunistic *L. racemosa*, and that this species would eventually be displaced by one or both of the other two mangrove species since they tended to be codominants in this region

of the forest. A propagule source existed for all three mangrove species in the forest, and since tides flood the gap several times per month, all species had an opportunity to colonize and recruit, and thus eventual dominance likely would be determined by environmental conditions and biotic interactions among the colonists.

(4) The trees of the restored forest would converge over time in terms of dominance structure, tree size, and leaf litterfall, with the natural forest. One goal of mangrove restoration is the eventual establishment of a forest that is similar to the one removed by disturbance. In the absence of previous data on growth and succession in restored mangrove forests in this region, we arbitrarily predicted that a restored stand would be similar in architecture and structure after 15–20 years. We tested this prediction by comparing our observational data on growth, tree size, and density in the restored and natural forests, since by the end of our study the restored stand was 18 years old. Also, we compared our litterfall and community structure data with those of McKee and Faulkner (2000) collected in these same natural and restored sites.

Methods

Definitions

"Canopy trees" were canopy-height individuals that had produced more than one set of lateral branches. All such were also sexually mature, and all three species in all plots in the restored site were reproducing in 1989 when trees were at most 6 years old. "Subcanopy trees" occurred only in the natural forest and were those trees in which the crown did not reach the bottom of the canopy layer. "Sapling" was defined in the restored sites as plants having produced only one set of lateral branches, and in the natural forest, as any branched individual <0.61 m tall. This artificial distinction was necessitated by the large difference in the size of sexually mature trees in the natural and restored sites. We broke with the usual convention of using 2.5 cm diameter at breast height (DBH) as an arbitrary cutoff to separate saplings from trees because the small trees of the restored site were, and had been for years, flowering and producing propagules, and were the dominant members of the canopy in the restored site. We defined "seedlings" as unbranched, rooted plants. "Stressed trees" we defined as those having <10 leaves, with many of those appearing chlorotic.

Height was measured to the top of the tallest foliage using a telescoping rod. Trunk diameter in the natural forest was measured 0.41 m above ground as DBH. Trees in the restored site were too small for typical DBH measures from 1989 to 1995. Thus, trunk diameter of *R. mangle* in the restored stand was measured at one-half the distance between where the lowest branch and the highest prop root came off the trunk. This point on the trunk was marked with paint and subsequent measurements recorded at the mark. *Rhizophora mangle* was re-marked at least annually, which was found to be adequate to ensure that the same spot on the trunk was measured in all years. For *L. racemosa* and *A. germinans* in the restored site, trunk diameter was defined as the diameter at the base of the plant, immediately above the soil. From 1996, both typical DBH and the diameter measurements listed above were taken in the restored site and the two measures of trunk diameter compared by linear regression. Basal area was calculated using equations given by Cintrón and Schaeffer-Novelli (1984).

Sampling the restored site

Our initial field observations suggested that the site had three distinct "zones" possibly arising from environmental and distance gradients (elevation, distance from site edge, and distance from Naples Bay). The locations of our permanent plots were sited to evaluate differences along these three zones: (a) Tall mangrove versus scrub plots (elevation gradient), (b) increasing distance from site edge (inner plots versus east and west edge plots) and (c) increasing distance from Naples Bay (west versus east plots). Sampling occurred from 1989 to 2000, with the restored site being 6.5 years old at the start of the study.

We established twelve 5×5 m plots in a stratified random fashion in the restored site (Figure 1). Three *scrub* plots were designated in areas where trees appeared stunted, were generally <1 m tall, and where tree densities were so low that large gaps existed in the canopy. Nine *tall mangrove* (having a canopy >2 m tall in 1989) plots were established such that there were three plots in the

Figure 1. Approximate locations of scrub (stars), east (squares), west (triangles), and inner (circles) plots in the restored site. Also, approximate locations of closed canopy plots in the natural forest west (W) and east (E) of the restored site, and the dead vegetation of the gap (open circle). The approximate path of the flushing channel is illustrated by the line. The slightly oblique photograph was taken by the authors from a helicopter December 1989, a few months after the gap in the natural forest was formed by a lightening strike. The box on the map of Florida indicates the location of the Naples Bay study area.

east, west, and inner sections of the study site. *East* and *west* tall plots were located relatively near the outer edge of the restored mangrove site (distances from site edge range 2–17 m), with east plots located more on the inland side of the site, and west plots located near the open water of Naples Bay and the flushing channel. *Inner* tall plots were located nearer the center of the site (distances from site edge range 37–51 m). Distances from the continually flooded flushing channel probably provide the best measure of the relative accessibility of tall mangrove plots to tidal waters. Distances from the flushing channel ranged as follows: west plots (2–29 m), inner plots (25–33 m), east plots (58–66 m), and scrub plots (42–75 m). Relative topographic elevation measurements indicated that east, inner, and west tall plots were all within approximately 5 cm elevation of one another and were similar in elevations to the surrounding natural forest, whereas elevations in scrub plots were 15–22 cm higher than the tall plots and thus tidal flooding was less frequent.

In each 5 × 5 m plot, we randomly selected and marked five trees of each mangrove species (*R. mangle*, *A. germinans*, and *L. racemosa* and collected data on survival, reproduction, stress condition, height, and trunk diameter. In a few plots, there were fewer than five (minimum $n = 3$) *A. germinans* trees marked because of the sparseness of this species. During each sampling, we also haphazardly placed five 1 m^2 quadrats in each plot in which we measured numbers of live and dead mature trees, saplings, rooted seedlings, and unrooted propagules. Data on survival of tagged tress were collected at least annually from 1989 to 2000 except for 1994. Data on growth in height and trunk diameter and density patterns were gathered in 1989, 1991, 1993, 1995, 1996, 1997, and 2000. Basal areas were calculated from DBH using equations reported by Cintrón and Shaeffer-Novelli (1984). In 1989 and 1996, we measured the percent cover of scrub and tall mangroves from low altitude aerial photographs taken from a hovering helicopter and ground truthing. Litterfall was collected monthly in both the restored and natural forests in three replicate 0.5 × 0.5 m traps per location during 1990 and compared with litterfall data collected in 1997 by McKee and Faulkner (2000) in this same site. Leaf litter was separated by component and species, dried to constant weight at 70 °C, and weighed in the laboratory.

Sampling the natural mangrove forest: closed canopy areas

In the natural forest 12, 5 × 5 m study plots were located near (within 10–30 m) the restored mangrove site. Approximately half of these plots were located west of the restored site (nearer Naples Bay) near a fringe forest and half on the eastern side (nearer the uplands) in a basin forest. These plots were completely censused in June of 1989 and 2000 for densities of canopy trees, subcanopy trees, saplings, seedlings, and unrooted propagules of all species. We recorded the DBH for all canopy and subcanopy trees.

Sampling the natural mangrove forest: gap site

Lightening struck a large *A. germinans* in 1989 creating a gap in the natural forest near the upland edge. In December 1989, we surveyed the gap recording the size of the gap, numbers and DBH of dead and live trees. The patch was re-surveyed in April and July of 1990 for short-term colonization, and then surveyed in July of 2000 to evaluate longer term recovery. Seedling and young tree densities and heights were collected in three replicate 3×3 m plots.

Environmental variables

In 1997, we recorded light penetration in the restored and natural stands both as photosynthetically active radiation (PAR, recorded with a Decagon Devices, Inc. light wand) and as total illuminance (foot candles, as used by Lugo and Snedaker (1975) in nearby Rookery Bay, FL). From 1989 to 1996, only illuminance data were collected. In 1989, maximum standing water depths at high tide and salinities of standing and ground water were recorded. Ground water was squeezed from sediment taken from 10 cm below soil surface. Rainfall data were obtained from NOAA for a location in Naples near Windstar. We estimated the number of tides flooding the restored site using relative elevations of pvc corner poles at plots, field measurements of water depth at these poles, and tide charts. Salinity was measured using a hand-held refractometer.

Statistical analyses

Survival of tagged trees in the restored site was analyzed by repeated-measures ANOVA (1989–2000) excluding 1994 when no data were gathered. Initial (1989) sizes (height and trunk diameter) were analyzed by species and plot via two-way ANOVA. Growth in height of marked trees was assessed by repeated-measures ANOVA (species and plot as main effects) for years when there were no missing data points (1989, 1995, 1996, 1997, and 2000). Where further analyses were suggested by repeated-measures ANOVAs, the actual growth in height and DBH (calculated as year 2000 minus 1989 values) were subjected to ANOVA and multiple comparisons.

Densities (numbers m^{-2}) in the restored site were analyzed first by separate repeated-measures ANOVA for each species, with adult trees, saplings, rooted seedlings, and numbers of standing dead adult trees as dependent variables, and plot and time as independent variables. This analysis provides by-species tests of the combined density vectors for the life history stages as well as separate univariate tests of significance for each life history stage. Where significant differences were detected with repeated measures ANOVA, further analyses by one-way ANOVA were conducted. Densities for each species in the restored site were analyzed for 1989 and 2000 using one-way ANOVA and Tukey multiple comparisons to detect differences among plots for the various dependent variables. In addition, the change in density from 1989 to 2000 was analyzed by one-way ANOVA for live adult trees, saplings, seedlings, unrooted propagules, and dead adult trees. Basal area was analyzed by repeated-measures ANOVA using 1989 and 2000 data, with plot type and species as main effects.

Analyses of growth in DBH of trees in the natural mangrove forest was conducted separately by species and by region of the forest (eastern near the uplands, or western near Naples Bay). The mean 1989 and 2000 DBH values of a species in a specific region of the forest were compared by a *t*-test. If differences were significant, then estimated growth for that species was calculated as the difference of the 2000 and 1989 means values.

A $p < 0.05$ threshold was used for determining significance in all analyses. When necessary, size and density data were $\text{Log}_{10}(X + 1)$ transformed to alleviate heterogeneity of variances or deviations from normality. Percent survival data were arcsin (square root) transformed prior to application of inferential statistics. For among-zone tests in the restored sites, the unit of replication was the 5×5 m plot and subsamples (tagged trees and quadrats) were combined to give average values for a replicate plot. Mean and 1 SE values are reported throughout unless otherwise indicated.

Results

Field observations, environmental conditions, and litterfall

Our field observations from 1989 through 2000 indicated that in the restored mangrove site there was no mortality or obvious effects on growth or reproduction resulting from the several freezes that occurred during that period. Mean salinities of standing water during tidal flooding in the restored site ranged from 5 to 45 Mg ml^{-1} in 1989 and values recorded from Naples Bay ranged from 10 to 38.6 Mg ml^{-1}. Salinities of standing water in summer were significantly greater in inner plots (35 Mg ml^{-1}) than in other tall mangrove and scrub plots (30 Mg ml^{-1}) (one-way ANOVA $p < 0.012$). In late fall, standing water salinities did not vary significantly among plots (39–41 Mg ml^{-1}, one-way ANOVA $p = 0.219$).

Highest ground pore water salinities (65.0 ± 4.71 Mg ml^{-1}) were found in Scrub plots in summer 1989 and this mean was significantly greater than groundwater salinities in other plots (28–30 Mg ml^{-1}) ($p < 0.012$). There was no difference in ground water salinity among plots in late fall 1989 (38–40 Mg ml^{-1}) ($p = 0.114$).

The tall mangrove areas of the site (east, inner, and west plots) were flooded by 54.1 ± 6.1 tides mo^{-1}, while scrub plots were flooded by 32.5 ± 12.4 tides mo^{-1}. Depths of standing water ranged from 0 to 29 cm. Analysis of rainfall from a nearby NOAA station indicated that there was no difference ($t = 0.040$, df $= 13$, $p = 0.968$) in annual totals between the period prior to our study initiation (1982–1988) and during our study (1989–2000).

In 1990, leaf litterfall was significantly lower (Student's *t*-test, $p < 0.05$) in the restored site (0.71 ± 0.14 g dry mass m^{-2} day^{-1}) compared to natural forest values (1.11 ± 0.29 g dry mass m^{-2} day^{-1}). The percent of ambient light penetrating the canopy in the restored forest declined from 42% in 1991 to 7% in 1997. Percent light penetration in 1997 was not significantly different among restored site plots but was greater in the restored site than in the closed canopy natural forest (ANOVA, $F = 3.349$, $p < 0.015$).

Percent cover in the restored stand

At study initiation in 1989, 73.8% of the restored site area was covered by tall mangrove habitat, and 21.7% of the site contained scrub mangroves or bare ground. Portions of the bare ground and scrub areas also had a ground cover of the halophyte *Batis maritima*. The remaining area of the site was open water during most tidal stages. By 1996, the category of "tall mangroves" had expanded to encompass 94.5% of the site and very little bare ground and *B. maritima* remained.

Survival of marked trees

Survival from 1989 to 2000 of permanently marked trees was high in most plots (Figure 2). At 2000 however, percent survival of *R. mangle* and *A. germinans* was not significantly different among plots (one-way ANOVAs $p = 0.384$ and 0.487 respectively), but survival of *L. racemosa* was significantly ($p < 0.018$) lower in west plots (Figure 2). Field notes indicated that a number of tagged *L. racemosa* trees in west plots appeared stressed beginning in 1995. From 1996 to 2000 an increasing number of these trees died, and others appeared highly stressed. In 2000, $>50\%$ of the marked *L. racemosa* trees in west plots were dead (Figure 2), all of which had been healthy members of the canopy in 1989.

The mortality shown in Figure 2 for *R. mangle* in west plots between 1995 and 2000 was the result of a gall-inducing fungus that became widespread in one of the 5×5 m plots. When first tagged for further study in 1989, only a few *R. mangle* trees were noted as having numerous galls on the trunks and main branches in this west plot. These trees did not appear stressed at that time; however, by 1993 many *R. mangle* trees in this plot had apparently been infected and appeared more and more stressed as numerous galls were noted on the trunks and branches of the trees. Nearly all of these infected trees were dead by 1995 and one

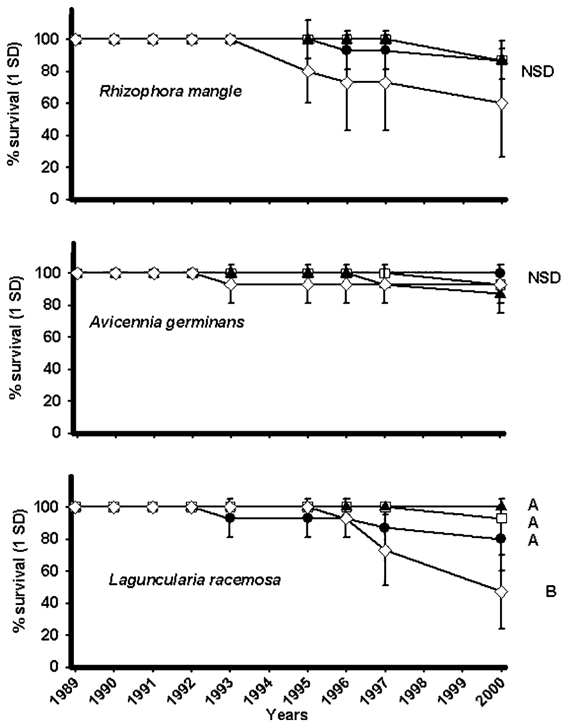

Figure 2. Mean percent survival (1 SD) of surviving tagged trees for each plot type (circles = scrub, squares = east, triangles = inner, and diamonds = west). One-way ANOVA of survival in 1997 and 2000 showed no significant differences among plots for *R. mangle* and *A. germinans*, but *L. racemosa* survival was significantly lower in west plots in 1997 ($p < 0.045$) and 2000 ($p < 0.018$). Survival in years prior to 1997 was not different among plots for any species. The same letter after 2000 data points indicates no significant difference.

additional individual was dead in 2000. We have seen no evidence of any further spread of this virulent fungal infestation outside the vicinity of this one west plot, and there has been no mortality of *R. mangle* in the other two west plots.

Growth in height and diameter of marked trees

Height and DBH were positively and linearly related for each species ($p < 0.05$). Regression equations for year 2000 values, with DBH in cm and height in m, were:

R. mangle: DBH = 0.807 × height − 0.290, $R^2 = 0.746$, $n = 50$

A. germinans: DBH = 1.091 × height − 0.529, $R^2 = 0.738$, $n = 44$

L. racemosa: DBH = 0.721 × height + 0.056, $R^2 = 0.652$, $n = 47$

Patterns of growth in height and trunk diameter were similar, and consequently only height is discussed in the text although both are presented in tables. At the beginning of the study in 1989, marked trees of all three mangrove species were significantly shorter in scrub plots than in other plots (Table 1). *Avicennia germinans* was also significantly shorter in east plots than other tall mangrove plots (Figure 3).

Repeated-measures ANOVA showed significant main effects of time on height for all three species, indicating that there was significant growth over the 1989–2000 period, a significant plot effect showing a difference in growth among plots, and a significant species effect demonstrating differences in growth among species (Table 2). There were also significant height × plot and height × plot × species interactions showing the complexity in the patterns of growth of species in different locations. One-way ANOVAs of total growth from 1989 to 2000 showed greatest growth in *R. mangle* and *A. germinans*, and generally greater growth for these species in scrub rather than tall mangrove plots (Table 2). For *L. racemosa*, there was no difference among plots in growth in height over the 11 year period. Growth of *L. racemosa* was less than that of *R. mangle* and *A. germinans* in scrub plots but growth of the three species was not different in tall (east, west, and inner) mangrove plots (Table 2).

This growth culminated in 2000 in a change relative to 1989 in distribution of tree heights in the various plots (Figure 3). Whereas the only significant difference in height in 1989 for *R. mangle* was that trees were shorter in scrub plots, in 2000 *R. mangle* was taller in west plots than in any other plots and heights of scrub trees had converged with those of tall mangrove plots (Figure 3). In 1989 *A. germinans* had been significantly shorter in scrub and east plots, but in 2000, following the rapid growth especially in scrub plots, there was no significant difference in height among any plots (Figure 3). *Laguncularia racemosa* height in 1989 and 2000 was not different among tall mangrove plots but this species remained significantly shorter in scrub plots relative to tall mangrove plots (Figure 3).

Table 1. Two-way ANOVA and a summary of Tukey multiple contrasts are presented for tree heights (A) and trunk diameter (B) in the first year of the study (1989).

Source	SS	df	MS	*F*	*p*
(A) Tree height in the restored site in 1989					
Plot	61.137	3	20.379	63.928	0.0005
Species	8.441	2	4.220	13.239	0.0005
Plot × species	4.612	6	0.769	2.411	0.030
Error	47.818	150	0.319		
	Means	Summary of Tukey comparisons			
Plot					
Scrub	0.98	A			
East	2.02	B			
West	2.50	B			
Inner	2.60	B			
Species					
R. mangle	2.29	A			
L. racemosa	2.00	A			
A. germinans	1.71	B			
	SS	df	MS	*F*	*p*
(B) Tree trunk diameter in the restored site in 1989					
Plot	19.438	3	6.479	4.511	0.005
Species	137.396	2	68.698	47.829	0.0005
Plot × species	22.990	6	3.832	2.668	0.017
Error	214.013	149	1.436		
	Means	Summary of Tukey comparisons			
Plot					
Scrub	4.433	A			
East	3.919	A,B			
West	3.728	A,B			
Inner	3.513	B			
Species					
R. mangle	3.173	A			
L. racemosa	3.341	A			
A. germinans	5.181	B			

Main effects are plot and species. ANOVA $R^2 = 0.610$ for height and 0.547 for trunk diameter. Values of least square means are in m for height and cm for trunk diameter. The same letter in Tukey comparisons indicate no significant difference between means.

1989–2000 changes in density and basal area in the restored site

Two-way ANOVA of tree densities in the restored site at the beginning of the study (1989) indicated significant variation by plot, species, and their interaction (Table 3). Tree densities were lowest in scrub and inner plots and highest in east and west plots. Averaged over the entire restoration site, *A. germinans* densities in 1989 were significantly and substantially lower than those of *R. mangle* and *L. racemosa* (Table 3). In 1989, densities of all three species varied significantly by plot (Figure 4). *Rhizophora mangle* densities in 1989 were much lower in scrub plots, while *L. racemosa* and *A. germinans* densities were highest in west plots nearer Naples Bay (Figure 4).

Repeated-measures ANOVA showed significant changes in density of all species during the study period, and significant interactions indicating species-specific and location-specific differences in the degree of density change (Table 4). Densities of *R. mangle* trees increased significantly in scrub plots from 1989 to 2000 through recruitment, but there was no significant change in density of this species in tall mangrove plots. This increased colonization and survival resulted in *R. mangle* tree densities in scrub plots in the year 2000 that were

Table 2. Repeated measures ANOVAs for heights and DBH of tagged trees in the restored site in 1989–2000.

	F	*p*	Huynh-Feldt *p*
Height			
Between subjects source			
Species	12.60	0.005	
Plot	5.83	0.005	
Species × plot	3.77	0.005	
Within subjects source			
Height	222.07	0.005	0.005
Height × species	1.95	0.05	0.11
Height × plot	10.99	0.005	0.005
Height × species × plot	2.99	0.005	0.005

Summary of one-way ANOVAs and Tukey multiple comparisons for 1989–2000 growth in height

	p	Scrub	Inner	West	East
Summary of differences among plots					
R. mangle	0.012	A	A,B	A,B	B
A. germinans	0.0005	A	B	B	B
L. racemosa	0.14	No sig. diff.			
		Rm	Ag	Lr	
Summary of ANOVA of differences among species					
Scrub	0.013	A	A,B	A,C	
East	0.391	No sig. diff.			
Inner	0.067	No sig. diff.			
West	0.074	No sig. diff.			

	F	*p*	Huynh-Feldt *p*
DBH			
Between subjects source			
Species	2.36	0.10	
Plot	0.78	0.51	
Species × plot	7.72	0.005	
Within subjects source			
Height	116.41	0.005	0.005
Height × species	8.52	0.005	0.005
Height × plot	2.43	0.03	0.03
Height × species × plot	9.81	0.005	0.005

Summary of one-way ANOVAs and Tukey multiple comparisons for 1989–2000 growth in DBH

	p	Scrub	Inner	West	East
Summary of differences among plots					
R. mangle	0.218	No sig. diff.			
A. germinans	0.0005	A	B	A,B	B
L. racemosa	0.010	A	B	A,B	A,B
		Rm	Ag	Lr	
Summary of ANOVA of differences among species					
Scrub	0.005	A	B	A	
East	0.460	No sig. diff.			
Inner	0.167	No sig. diff.			
West	0.018	A	A,B	B,C	

Main factors are species and plot. For within-subject analyses, Huynh-Feldt corrected *p* values less than 0.05 are considered significant. Below repeated-measures analyses are individual one-way ANOVAs for elucidation of specific differences among plots and among species in total growth from 1989 to 2000.

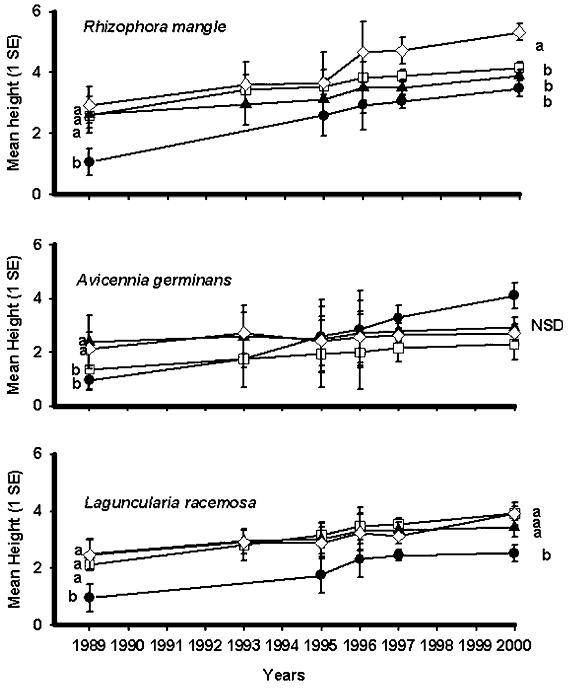

Figure 3. Mean (1 SE) of height in m of marked trees. Circle = scrub, squares = east, triangle = inner, and diamond = west plots. The same letter by 1989 and 2000 means indicates no significant difference (ANOVA, $p < 0.05$) among plots in those years, and NSD indicates that the ANOVA was not significant.

significantly higher than those of west plots (Figure 4). There was also a significant, but much smaller in absolute numbers, increase in standing dead *R. mangle* trees in west and east plots.

Laguncularia racemosa tree densities also differed significantly among plots over time (Table 4), and tree numbers in scrub plots increased over time while tree densities in east and west tall mangrove plots decreased significantly and substantially over time (Figure 4). At the beginning of the study in 1989, tree densities were greatest in east and west plots, and significantly lower in scrub and inner plots (Figure 4). *Laguncularia racemosa* densities declined from 37% (east plots) and 83% (west plots) from 1989 to 2000. Associated with the overall decreasing numbers of live trees, was an increase in the numbers of standing dead *L. racemosa* to a high in 1997 of $> 5\ \text{m}^{-2}$ in west plots (Figure 4). *Avicenniua germinans* also experienced a 46% density decline in west plots, although because densities of this species were very low throughout the restored site, this decline did not seem to change the appearance of the canopy (Figure 4).

Growth and density changes combined to produce changes in stand basal area. Repeated-measures ANOVA (using 1989 and 2000 values) indicated no significant differences in basal area among plots ($F = 1.42$, $p = 0.26$) or species ($F = 1.36$, $p = 0.28$), although there was a significant plot × species interaction term ($F = 4.75$, $p < 0.005$). The interaction was produced by a very large increase in *A. germinans* basal area in scrub plots, that was a result of extremely high growth rates of a few individual trees. All plots

Table 3. Two-way ANOVA ($R^2 = 0.580$) and a summary of Tukey multiple contrasts are presented for starting (1989) tree densities.

Source	SS	df	MS	*F*	*p*
Plot	583.16	3	194.39	18.98	0.005
Species	1238.14	2	619.07	60.46	0.005
Plot × species	567.01	6	94.50	9.23	0.005
Error	1720.27	168	10.24		
	Means	Summary of Tukey comparisons			
Plot					
Scrub	3.00	A			
Inner	5.60	A,B			
East	11.47	B,C			
West	16.93	C			
Species					
R. mangle	2.02	A			
L. racemosa	6.70	A			
A. germinans	0.55	B			

Main effects are plot and species. Values of least square means are in m for height and cm for trunk diameter. The same letter in Tukey comparisons indicate no significant difference between means.

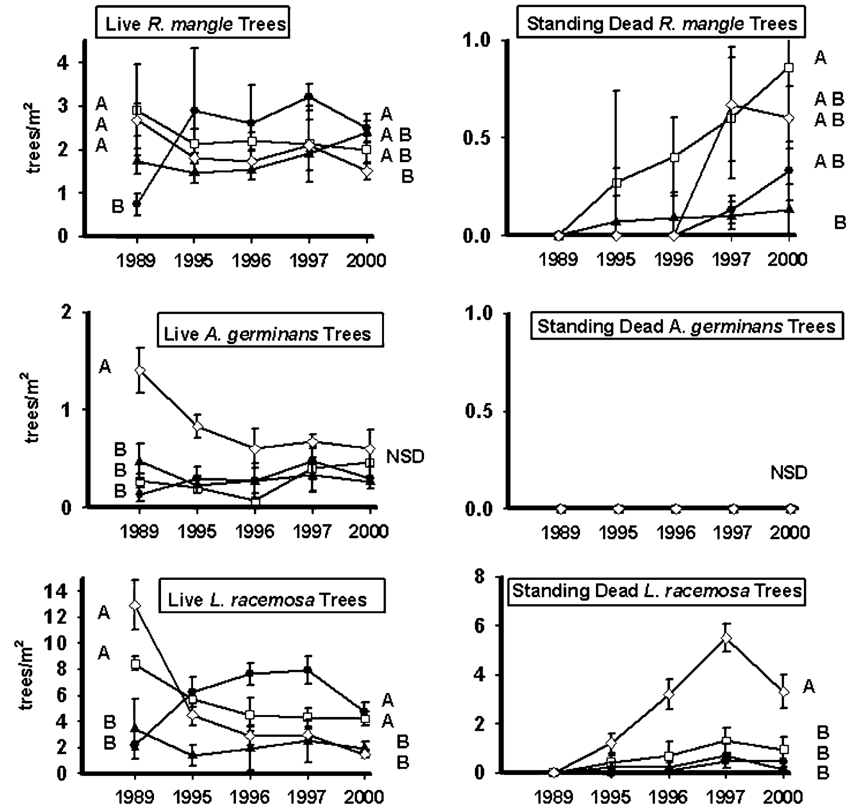

Figure 4. Live and standing dead tree densities in the restored for each plot. Values are means and 1 SE. Circles = scrub, squares = east, diamond = west, and triangle = inner plots. NSD means no significant difference (one-way ANOVA) of densities, while different letters indicate significant differences among plots for that date (1989 or 2000). Results of repeated-measures ANOVA for each species are presented in Table 4. Note differences in y-axis scales.

had increases in stand basal area from 1989 to 2000, but the increase was by far the greatest in scrub plots (1.7–2.2x that of the other plots). The different plots did not follow significantly different patterns of change over time ($F = 2.16$, $p = 0.12$), but there were differences in the rates of change in basal area of different species ($F = 3.46$, $p < 0.05$) and over time, a significant plot × species interaction ($F = 6.73$, $p < 0.005$). Over all plots, the increase in basal area from 1989 to 2000 of *R. mangle* and *A. germinans* was similar, and was much greater than that of *L. racemosa*. *Laguncularia racemosa* actually declined in overall basal area in scrub plots over the study period.

Sapling, seedling, and unrooted propagule densities in the restored site

Numbers of sapling and seedling *L. racemosa* and *A. germinans* declined in all plots over the study period (Figure 5). Numbers of sapling *R. mangle* were relatively low but were present at all plots at all years, while numbers of seedlings were higher in later years of the study (Figure 5).

Rhizophora mangle sapling densities (Figure 5) were not significanly different among plots ($F = 1.28$, $p = 0.290$) or over time ($F = 1.395$, $p = 0.246$), although there was a significant plot × time interaction ($F = 2.693$, $p < 0.008$). *Avicennia germinans* sapling densities were not different among plots ($F = 0.153$, $p = 0.928$), but did differ over time ($F = 9.975$, $p < 0.0005$), and there was no plot × time interaction ($F = 1.161$, $p = 0.331$). *Laguncularia racemosa* sapling densities were different among plots in the restored site ($F = 3.448$, $p < 0.022$) and over time ($F = 12.841$, $p < 0.0005$), but there was no plot × time interaction ($F = 0.504$, $p = 0.696$).

Seedling densities of *R. mangle* (Figure 5) were different among plots ($F = 3.942$, $p < 0.013$) and

Table 4. Repeated measures ANOVAs for densities of trees in the restored site in 1989–2000.

Source	F	p	Huynh-Feldt p
Between subjects			
Species	159.57	0.005	
Plot	9.22	0.005	
Species × plot	6.00	0.005	
Within subjects			
Tree densities	11.45	0.005	0.005
Densities × species	10.92	0.005	0.005
Densities × plot	18.64	0.005	0.005
Densities × species × plot	9.1	0.005	0.005

Summary of one-way ANOVAs and Tukey multiple comparisons for density change (2000 minus 1989 densities)

	p	Scrub	Inner	West	East
Summary of differences among plots					
R. mangle	0.005	A	A,B	B	B
A. germinans	0.005	A	A,B	B	C
L. racemosa	0.02	A,B	A,B	B	A

		Rm	Ag	Lr
Summary of differences among species				
Scrub	0.05	A,B	B	A
East	0.005	A	A,B	B
Inner	0.060	No sig. diff.		
West	0.005	A	A	B

Main factors are species and plot. For within-subject analyses, Huynh-Feldt corrected p values less than 0.05 are considered significant. Below repeated-measures analyses are individual one-way ANOVAs for elucidation of specific differences among plots and among species in the change in density (2000 minus 1989 values).

over time ($F = 37.615, p < 0.0005$), but there was no difference in the pattern of change over time for the different plots (interaction $F = 1.933$, $p = 0.085$). *Avicennia germinans* seedlings did not differ significantly among plots ($F = 1.321$, $p = 0.277$), but did vary over time ($F = 5.319$, $p < 0.007$), and there was no plot × time interaction ($F = 1.127$, $p = 0.351$). Densities of the various life history stages of *A. germinans* were not correlated. *Laguncularia racemosa* seedlings varied significantly among plots ($F = 3.944, p < 0.013$), over time ($F = 21.909$, $p < 0.0005$), and there was a significant interaction ($F = 4.066$, $p < 0.009$) of the main effects. Sapling and seedling densities were significantly correlated ($r = 0.50$, $p < 0.0005$), but other life history stages were not correlated with one another.

Unrooted propagule densities (Figure 5) were recorded only for *R. mangle*. Densities did not vary among plots ($F = 0.806$, $p = 0.496$) but did vary over time ($F = 57.791$, $p < 0.0005$), and there was no plot × time interaction ($F = 1.103$, $p = 0.365$). Tree and sapling densities of *R. mangle* were significantly correlated ($r = 0.35$, $p < 0.04$), but other life history stages were not correlated with one another. Unrooted *A. germinans* propagules were seldom seen at any plot in the restored site during the 11 years of the study.

The natural forest: closed canopy plots

In 1989, the eastern (basin) natural forest was co-dominated by *L. racemosa* and *A. germinans* (Table 5). *Rhizophora mangle* trees were typically smaller in DBH and, in terms of basal area, comprised only 15.6% relative dominance. There was a significant (t-test, $p < 0.005$, $n = 39$) growth in *L. racemosa* DBH from 1989 at a rate of 0.29 cm yr^{-1}; however, *A. germinans* did not exhibit significant growth over this period (t-test, $p = 0.26$, $n = 13$). Growth of *R. mangle* trees was slow but significant (t-test, $p < 0.005$, $n = 52$) over this time period. Saplings of all three species were present at low densities in 1989, but none were recorded in 2000 (Figure 6). Seedling densities were low for all species at both times, although greatest densities were recorded for *R. mangle* in 2000 (Figure 6).

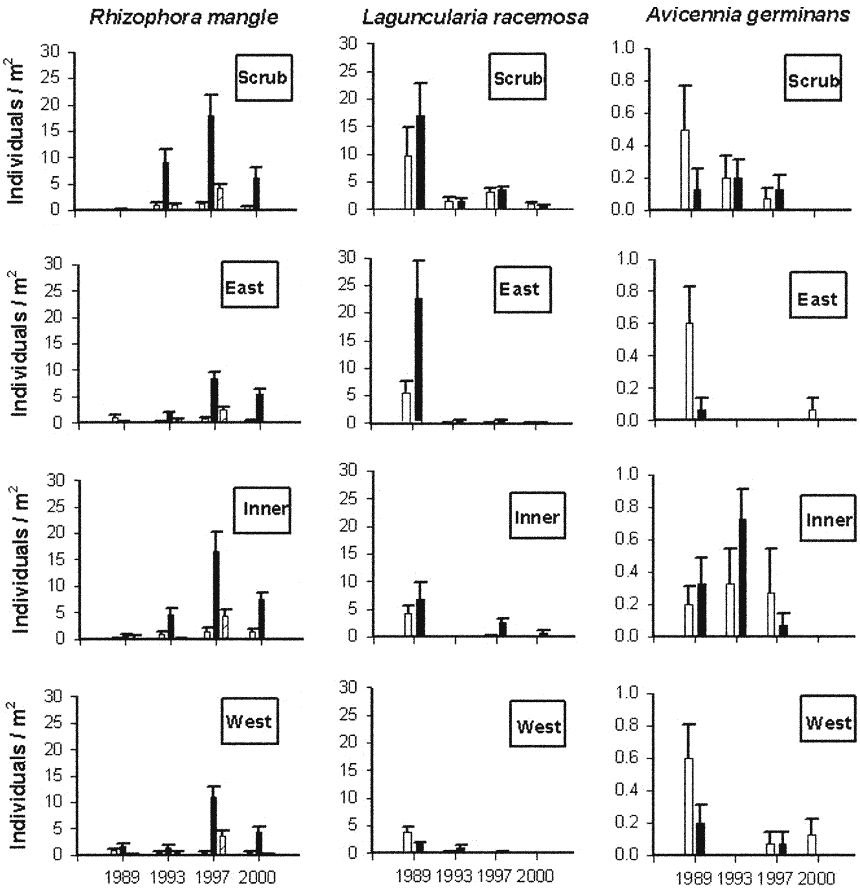

Figure 5. Densities of saplings and seedlings for all three mangrove species, and unrooted propagules of *R. mangle*, for each plot type (scrub, east, inner, and west) for 1989, 1993, 1997, and 2000. Values are means (1 SE). Unfilled bars are saplings, solid black bars are seedlings, and cross-hatched bars are unrooted propagules. Note different scales for *A. germinans*.

Table 5. The east (landward) and west (seaward) regions of the natural forest are compared for 1989 and 2000 collections of DBH (cm) and numbers of trunks in 5 × 5 m quadrats (1989 $n = 6$; 2000 $n = 3$).

	1989				2000				DBH growth (cm yr^{-1})
	DBH (cm)	Trunk density	Basal area	Relative dom.	DBH (cm)	Trunk density	Basal area	Relative dom.	
Natural forest east									
R. mangle	7.0 (0.52)	3.0 (1.0)	1.5 (0.51)	15.6	7.5 (0.30)	5.3 (0.9)	1.8 (0.14)	11.0	0.05
L. racemosa	11.5 (1.46)	3.2 (1.1)	4.5 (0.97)	46.9	14.8 (1.62)	3.3 (0.7)	7.0 (1.4)	41.7	0.29
A. germinans	10.0 (1.71)	1.5 (0.3)	3.6 (1.22)	37.5	15.5 (1.25)	1.7 (0.9)	7.5 (1.21)	44.6	NS
Total		7.7	9.6			10.3	16.3		
Natural forest west									
R. mangle	6.5 (0.52)	2.0 (0.8)	1.3 (0.20)	11.0	8.6 (0.44)	3.3 (0.3)	2.4 (0.25)	12.3	0.20
L. racemosa	9.6 (1.77)	5.2 (0.8)	3.4 (1.32)	28.9	12.8 (0.38)	2.7 (0.9)	5.2 (0.30)	26.7	0.29
A. germinans	12.9 (2.40)	0.3 (0.2)	5.4 (1.95)	45.8	16.3 (1.55)	1.3 (0.3)	8.5 (1.58)	43.6	0.31
C. erectus	7.3 (0.30)	2.5 (1.5)	1.7 (0.14)	14.4	10.3 (0)	1.0 (0)	3.3 (0)	16.9	NS
Total		10.0	11.8			8.3	19.4		

In addition, annual growth (cm yr^{-1}) in DBH is calculated omitting quadrats in which a species was absent. Basal area is presented in m^2 ha^{-1}. Density is in stems m^{-2}. Values are means (1 SE). Growth in DBH was tested via Student's *t*-tests (see text for details), and NS indicates no significant growth.

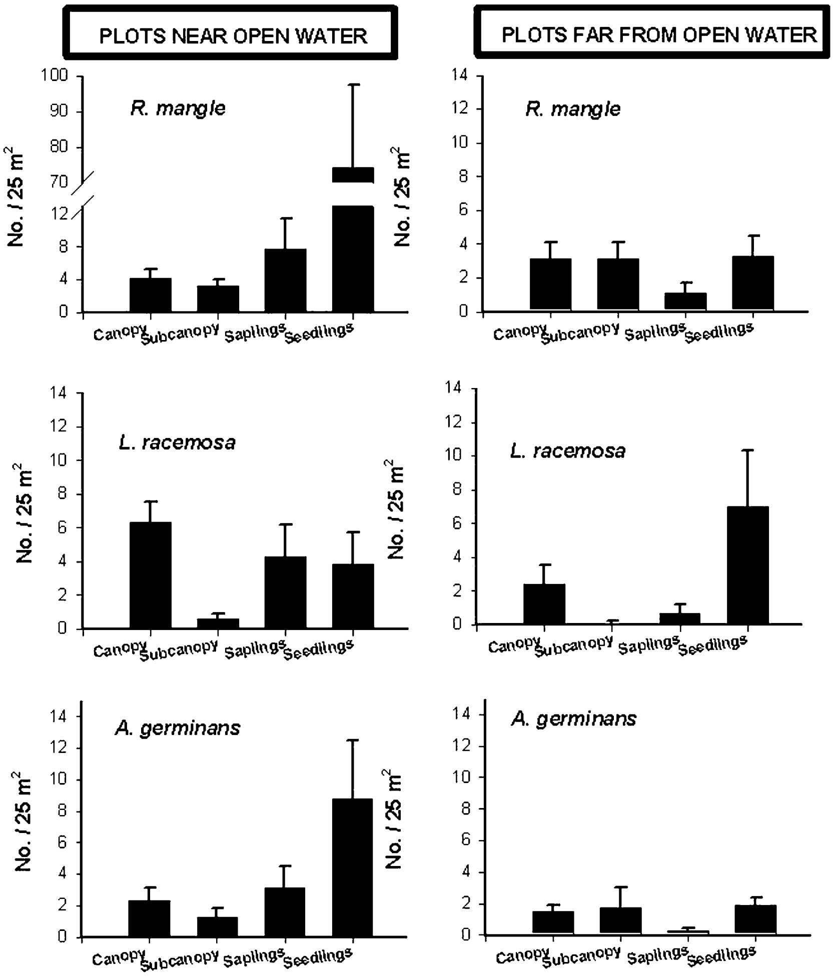

Figure 6. Numbers per 25 m^2 of canopy trees, subcanopy trees, saplings, and seedlings in the closed canopy plots in the natural forest. Plots are grouped by proximity to the open water of Naples Bay. Values are means (1 SE). Note the different scale on the y-axis for *R. mangle* near open water that was necessary to show very high densities of seedlings.

The western natural forest was dominated by *A. germinans* with secondary dominance by *L. racemosa* near the restored site (Table 5). Our quadrats were specifically selected to be very close (within 10 m) of the restoration site, and *R. mangle* was only a minor component of the canopy in that region (11.0% relative dominance). However, it is clear from field observations that *R. mangle* is a primary dominant in the western natural forest region in locations closer to open water. Growth in DBH of canopy trees was significant (Student's t-tests, at $p < 0.05$) for all three species and rates were somewhat similar among species, ranging from 0.20 to 0.31 cm yr^{-1}. Relative dominance did not change substantially over the 11 year study period (Table 5). Numbers of saplings declined from 1989 to 2000 for all three species (Figure 6). *Rhizophora mangle* seedling densities in both 1989 and 2000 were much higher than those recorded in the eastern adjacent forest (Figure 6).

The natural forest: lightning-created gap site

The gap was approximately 15 m in diameter. Prior to the strike, the gap site was populated by *Avicennia germinans* (9 individual trees, 16 total trunks, 5.71 ± 1.82 cm DBH) and *Rhizophora mangle* (10 individual trees with 1 trunk each, 2.28 ± 0.85 cm DBH). These data were gathered by measuring dead and dying trees in December 1989. Of the *A. germinans* with new or some sur-

Table 6. Year 2000 densities per square meter and heights (mean ± 1 SD) are presented for $n = 3$, 5×5 m quadrats in the gap created by lightening in 1989.

	R. mangle	*L. racemosa*	*A. germinans*
Densities			
Young tree	1.52 ± 0.65	0.59 ± 0.42	0
Seedling	2.96 ± 2.55	0.26 ± 0.36	0.07 ± 0.13
Young tree heights (m)			
Mean	0.91 ± 0.31	1.60 ± 0.53	NA
Max	2.06	2.56	

What we refer to as "young tree" here is done so for consistency with designation of trees in the restored site and to facilitate comparisons.

viving growth, all except one were dead by 1991. The one survivor had one dead trunk, and another trunk that was dead for about half of its circumference but with surviving vascular tissue over the other half. This trunk survived in this same form through 2000 and produced sufficient new growth to be a contributor to the regeneration of the canopy. No *R. mangle* survived the lightening strike.

By July1990, 10 *L. racemosa* seedlings had colonized the gap. Field observations indicated that *R. mangle* colonized during the next several years. Light readings were not taken in the early years following gap formation, but the gap was open and light penetration was mostly unblocked at mid-day. In December 1997, during field sampling for light penetration, the canopy appeared to be closing via vegetative growth from surrounding canopy trees, and a number of saplings and seedlings were noted but not quantified. Mid-day light penetration (PAR) in 1997 ranged from 837 ± 291 μmol m^{-2} s^{-1} near the center of the 8-year-old gap to 47 ± 3 μmol m^{-2} s^{-1} near the edge. Light penetration under adjacent closed canopy areas was 21 ± 3 μmol m^{-2} s^{-1} while readings from adjacent non-forested open areas was 1097 ± 19 μmol m^{-2} s^{-1}. In July 2000, about 11 years after the lightening strike, the gap was essentially closed in through vegetative growth from surrounding trees (field observations), and was populated by numerous sapling and seedling *R. mangle* and *L. racemosa* (Table 6). Gap "saplings" were shorter than the "young trees" of similar age in the restored site.

Discussion

Growth and succession in the restored site

Our results are consistent with other studies of colonization, growth, and succession that indicate that environmental conditions and distance from source populations affect seedling colonization (see review in Middleton 1999). After colonization, however, plants exhibit species-specific growth responses to site conditions, experience predation, and compete with neighbors for light, nutrients, space, pollinators, etc. (Gurevitch et al. 2002). Tolerance to stress, growth and life history characters, disturbance regime, and competitive ability are combined in some general models to predict development of assemblages (Grime 1977; Kautsky 1988). Our data are consistent with these ideas. Colonization, tree growth, and succession in the restored mangrove site occurred steadily throughout the 18 year history of the site. In our restored site, environmental conditions, such as differences in elevation, and distances from site edge and Naples Bay, affected recruitment; and, competitive thinning apparently affected stand development in the long run.

Various models have been proposed to explain zonation and dominance in mangrove forests and our long-term data on colonization and succession can help differentiate among some of these. Our data do not support the predictions of the propagule sorting hypothesis (Rabinowitz 1978a, b). If most colonization is from off-site, the propagule sorting model would predict higher densities of *R. mangle* (the species with the largest propagules) in west plots because these plots are situated near Naples Bay and the flushing channel. Alternatively, if the surrounding natural forest was the main source of propagules, the model would predict higher densities in edge (west and/or east plots) relative to inner plots. Neither of these were the case since densities of *R. mangle* did not differ among plots until later in the study when colonization, probably from within-site, resulted in a small increase in density of *R. mangle* in scrub plots. Since scrub plots were higher in elevation, this increase in density also runs counter to the propagule sorting hypothesis. The converse argument could be made for *L. racemosa* the species with the smallest propagules. Highest relative densities of this species could be predicted in either scrub (highest elevation), or inner or east plots (greatest distances from edge or Naples Bay respectively) by the propagule sorting hypothesis. However, highest densities actually occurred in west plots nearest the flushing channel and waters of Naples Bay.

Our data support portions of, or some combination of, hypotheses suggesting control by physio-chemical conditions (Watson 1928; MacNae 1968) and biotic interactions such as competition (Ball 1980). Scrub areas within the restored site that had higher elevations appeared to have somewhat more stressful growth conditions in the years prior to our study (1982–1989), as indicated by the existence of shorter, more highly branched trees, including obvious planted pairs of *Rhizophora mangle*. Interestingly, however, it was the trees in these scrub plots that experienced the most rapid growth from 1989 to 2000, and it was only in these plots where tree densities increased, although this was followed in later years by density declines as the canopy became more closed. We had no data from the 1982 to 1989 period and did not regularly gather data on edaphic conditions or physiological state during our study period. We speculate in order to stimulate future research that conditions in scrub plots changed as a function of the growth of the vegetation, because we found no evidence from rainfall data of differences in environmental conditions in pre (1982–1989) or study (1989–2000) periods.

In many forests in Florida, *L. racemosa* is a dominant species at higher elevations. Thus, from the hypothesis of differing competitive regimes along gradients (Keddy 1990; Keddy et al. 1998) one might expect that *L. racemosa* would be more competitive at higher elevations. However, our observational data suggest that *L. racemosa* was an inferior competitor under both lower elevation (tall mangrove plots) and higher elevation (scrub plots) conditions. In tall mangrove plots stress in the pre-study period appeared to not have been an issue, since these areas experienced high colonization rates by *L. racemosa* and rapid initial tree growth (1982–1989), followed by density dependent thinning from the early 1990s to 2000. The apparent competitive inferior, *L. racemosa*, had growth rates that were only half those of the apparent competitive dominant, *R. mangle*, in tall plots where thinning was occurring. However, since canopy closure was more a function of the very abundant *L. racemosa* than the other two species and because thinning did not occur in plots where *L. racemosa* was not in great abundance, it seems likely that much of the decline in *L. racemosa* density and dominance is from self-thinning rather than direct competition with other species. In tall mangrove areas (east, inner, and west plots), there was a strong negative relationship between the annual rate of change in density of *L. racemosa* and the 1989 starting densities per m^2 ($r = 0.90$, change in density per year $= -0.09 \times$ [1989 densities] $+ 0.28$). This lends further support to the idea that the dieoff was density dependent. At the highest starting densities (12.8 m^{-2}), this equation predicts the average death of about 1 tree yr^{-1}, however at low starting densities of scrub plots (2.13 m^{-2}) there is a predicted small annual density gain through recruitment, just as was recorded in the field in scrub plots.

It is possible that differences in competitive abilities along the intertidal gradient may influence the distribution and dominance by *R. mangle* and *A. germinans*, but we cannot address this issue since competitive thinning of these species did not occur during our study, with the possible exception of some reductions in density of this species in west plots (where *R. mangle* was very tall in 2000). Data collections in future years may help resolve this point.

Thus, our first prediction was supported by the data. *Laguncularia racemosa* declined in density-dependent fashion in tall mangrove plots relative to the other species. Our second prediction, that *L. racemosa* would increase in dominance compared to the other species in scrub plots, but would be replaced in later years by *A. germinans*, was not supported. In the early-to-middle years of the study (1989–1996), *L. racemosa* and *R. mangle* both increased in size and numbers in scrub plots, but in later years (1997–2000) *L. racemosa* underwent an apparent density-dependent decline similar to that recorded earlier in tall mangrove plots. *Avicennia germinans* did not increase in density in scrub plots as we had expected that it might.

Comparisons with the natural forest: gap plots

Our third *a priori* prediction, that colonization and growth in the gap would resemble that in the restored site was only partially supported, because colonization and plant growth rates were less than in the restored site. The forest gap site was recolonized by *L. racemosa* and *R. mangle* seedlings, and through vegetative growth of the canopy of the one surviving trunk of the lightening-struck *A. germinans* and by trees surrounding the gap. Although the gap had begun to close by 1997, still at mid-day, 76% of ambient PAR penetrated to the forest floor. This level of light penetration is similar to the 63% mean value recorded in small gaps by Feller and McKee (1999). Consistent with results of Feller and McKee (1999) and Sherman et al. (2000), survival was higher in gaps and resulted in densities of young sapling trees in the gap that were much greater than those recorded in closed canopy areas. Young trees (saplings) of *R. mangle* and *L. racemosa* were codominant in the gap after 11 years. However, while *R. mangle* densities were slightly less but similar to those encountered in the restored site, *L. racemosa* densities in the gap were 10–20× lower than those in the restored site at the same site age. Colonization may have been limited by the long distance between the gap and Naples Bay.

Growth in height of these young trees was slower in the natural forest gap than in the restored site probably because of increased shading from the surrounding canopy. *Rhizophora mangle* and *L. racemosa* trees in the restored site at 11 years were typically 2–3 m in height in tall mangrove plots, while in the gap mean plant height at 11 years was 1.6 m and only three *L. racemosa* saplings were over 2 m tall. Interestingly, there was no recruitment of *A. germinans* into the gap despite a number of large *A. germinans* trees in the undisturbed forest near the gap. This pattern of recruitment is consistent with the results of McKee (1995a) who did not find distance to adult trees to be important for *A. germinans*, although it was a major factor explaining colonization by *L. racemosa* and *R. mangle*. Our results for *A. germinans* are in contrast with those of Sherman et al. (2000) who reported *A. germinans* seedlings and saplings in some gaps in *Rhizophora* and *Rhizophora–Laguncularia* dominated sectors of the forest. They, however, found no difference between gaps and closed canopy sites in terms of densities of *L. racemosa* and *A. germinans* saplings, and attribute this to small numbers of saplings of these species found in their sites (Sherman et al. 2000). Crab predation has been shown to be important in limiting recruitment by *A. germinans* in some locales (Smith et al. 1989) but not others (McKee 1995c; Sousa and Mitchell 1999). However, since crab seedling predators are not abundant in our study area (field observations) we speculate that failure of *A. germinans* to colonize the gap was because of low numbers of propagules (i.e., none in our litterfall traps; few observed on the ground) in this forest possibly because of low reproductive output, low rates of transport from off-site by tides, or both.

Comparisons with the natural forest: closed canopy plots

Our prediction 4, that dominance and forest structure in the restored site would become similar to that of the natural forest was only partially supported. Eighteen years of colonization, growth, and succession did not produce a mangrove stand that was comparable in terms of tree size to the canopy individuals of natural forest surrounding the site. The reduction in relative abundance of *L. racemosa* in the restored plots is consistent with succession towards stand characteristics that resemble the closed canopy parts of the natural forest. However, the data show that tree size was still much smaller in 2000 in the restored forest (mean DBH 2.8 cm) relative to the natural forest (mean DBH 12.6 cm) and densities much greater. Even though the trees in the restored site are smaller, in total they had a greater basal area (42.7 m^2 ha^{-1}) than the natural forest (Table 5) because of their very high tree densities. McKee and Faulkner (2000) reported much lower basal areas for this restored site, but their values are not directly comparable to ours because they only included individuals >2 cm DBH in their calculations whereas we included all sexually mature individuals forming the canopy.

In the New World tropics, there are few sites with long-term growth data with which to compare our results from the natural forest at Windstar. Annual growth rates in our natural mangrove forest (DBH changes from 0.05 to 0.31 cm yr^{-1}) were considerably less than those reported by Day et al. (1987) and Day (1990) (DBH changes from 0.1 to >2 cm yr^{-1}) in Caribbean Mexico. Forests of the two locations are considerably different in latitude and environmental conditions, which makes generalizations regarding growth difficult.

Synthesis

Restored and created stands of mangroves quickly develop species richness and cover that may be similar to natural "target" forests nearby. Other ecological functions, such as leaf production per unit area and development of soil structural components, may take 15 or more years, to reach levels found in natural forests (McKee and Faulkner 2000). We found that litterfall after 7 years of colonization and growth was 36% less in the restored site relative to the natural site, but McKee and Faulkner (2000) for this same site reported that after 14 years litterfall rates were the same in restored and natural forests. Also, maturation in terms of tree size, density, and dominance may require several decades. Development of mangrove stand structure at the Windstar restoration site was reported (for the 1996–1997 year) to be slower than at another restored site at Henderson Creek, because of somewhat stressful conditions possibly resulting from impaired flushing and circulation (McKee and Faulkner 2000). However, our data suggest that growth rates have not fluctuated much since 1989 in tall mangrove plots, and the flushing channel did not begin to fill in until the mid-1990s (personal observations). Thus, it seems likely that other factors, such as possible competition among the young trees, may be contributing to the overall slower growth at the Windstar site.

Many questions remain regarding the best ways to define the degrees of success of restoration along a variety of ecological dimensions, and the appropriate time frames over which to gage restoration success (Hawkins et al. 2002). Similarly, questions still remain as to the degree of impact of biological factors (e.g., competition, predation, parasitism, etc.) and physical factors (e.g., nutrients, tides, salinity, desiccation, etc.) in the long-term development of structure and function of restored sites. Questions remain as to why *R. mangle*, with its huge population in southwest Florida and abundant propagule production, did not colonize the restored site in substantial numbers. It may be that the small size of the flushing channel and a low berm on the seaward side of the restored site may have reduced accessibility of the site to floating propagules. Another question is why *A. germinans*, very abundant and robust in forests of the region, colonized and recruited to the restored and gap sites in such low numbers. Some questions should be resolvable by field experiments. Long-term studies, such as this one, provide some of the observations necessary to formulate hypotheses for experimental testing and data for validating predictive models.

The restored mangrove stand has developed some ecological functions that are equivalent to those in the natural forest. However, it appears that full development of mature forest structure and tree size may not occur for decades.

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