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EFFECTS OF NEIGHBORS ON GROWTH AND MORTALITY OF MANGROVE SEEDLINGS IN FLORIDA, U.S.A.[1]

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Abstract: Changes in height and mortality rates of red mangrove (*Rhizophora mangle*), black mangrove (*Avicennia germinans*), and white mangrove (*Laguncularia racemosa*) seedlings were measured in three field stands for 45 months. Differences between stands and the effects of size and distance of neighboring trees on individual growth rates were examined. Trees in a ditchside stand demonstrated higher growth rates than those near the upland edge, which in turn, grew faster than those in the high marsh proper. Mortality rates for red, black, and white mangroves were 9.6%, 4.6%, and 3.2% per year, respectively, whereas height increment rates ranged from 28.5–131.3 cm per year. Moderate salinities and lack of interference from mature trees are considered partially responsible for the relatively low mortality and high growth rates observed. The only consistent effects of neighbors on changes in height of subject trees were positive. This result is attributed to shared environmental conditions between neighboring trees.

Key Words: *Avicennia*, Florida, growth, *Laguncularia*, mangroves, *Rhizophora*

INTRODUCTION

Studies on the establishment, survival, and growth of mangroves within coastal wetlands have focused on factors responsible for zonation patterns sometimes evident in mangals worldwide (Ball 1980, Rodríguez 1987, Smith 1987). These studies often involve experimental plantings of mangrove seedlings (e.g., Rabinowitz 1978a, b, Smith 1987), or growth experiments under various laboratory conditions (Patterson *et al.* 1993). Growth studies have also been conducted in commercial mangrove forests or plantations to determine optimum harvest rates and thinning dynamics (Putz and Chan 1986).

Results of these studies show considerable variation regardless of the geographic range covered. Growth rates vary widely even within species. Some have found that mangrove seedlings grow best under conditions like those existing in the zones were they are usually found in the field (e.g., Smith 1987), whereas others report maximum growth under conditions more typical of other species (Rabinowitz 1978a, Smith 1987). Likewise, the relative importance of physical, biological, and stochastic factors in the control of mangrove growth has been found to exhibit considerable variation.

The objective of this study was to determine the effects of neighboring trees on growth in height and on mortality of mangrove seedlings established in a newly colonized site and to examine possible growth differences between seedlings growing in three different marsh zones. Over 45 months, I examined changes in height and mortality of seedlings of red mangrove (*Rhizophora mangle* L.), black mangrove (*Avicennia germinans* L.) and white mangrove (*Laguncularia racemosa* Gaertn.) in stands near a ditch, in the upper marsh, and near the upland edge of the marsh.

STUDY SITE

The study was conducted in a coastal wetland located on the barrier island side of the Indian River Lagoon (Florida, U.S.A.) between the cities of Ft. Pierce and Vero Beach (Figure 1). In 1965, the site was impounded for mosquito control by building an earthen dike around the marsh so that it could be artificially flooded during the mosquito-producing season (May to October). Because of the restricted connection with the lagoon, salinity at the site tends to be lower than in more open marshes nearby (mean surface salinity = 20.4 ppt, S.E. = 0.61). A complete description of the site, including data on management history, water chemistry, and vegetation dynamics can be found in Rey *et al.* (1990a, b).

The original vegetation of the marsh consisted of a mixture of herbaceous halophytes (*Salicornia virginica*

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L., *S. bigelovii* Torr., and *Batis maritima* L.) and red and black mangroves. Initial mosquito control efforts at the site resulted in considerable damage to the vegetation and almost complete elimination of mangroves from the site. This was attributed to excessively high and prolonged flooding (Harrington and Harrington 1982, Rey *et al.* 1990b). After reduction of flooding levels, herbaceous halophytes started a slow recovery, but mangrove recovery was not evident until 1982, when mangrove seedlings began to proliferate and grow at several locations within the impoundment.

METHODS

One hundred mangrove seedlings were haphazardly selected from three stands on the north end of the marsh (Figure 1). The NW stand is adjacent to a ditch that runs parallel with the Indian River Lagoon, the NE stand is in the upper marsh with no ditches or creeks in its vicinity, and the SO stand is near the upland edge of the marsh. The seedlings were selected by throwing a tennis ball over the back in randomly chosen directions (N, NE, E, SE, etc.) and selecting the seedling closest to the ball. The process was repeated until all sections of the stand were covered. Because the NW stand was long and narrow, the stand was divided into two approximately equal sections and the selection process conducted separately in each to ensure proper coverage.

The height of each seedling was measured at quarterly intervals from April 1982 to December 1985. Change in tree height has been shown to be an appropriate index of mangrove growth (Rabinowitz 1978a, Burns and Ogden 1985, Smith 1987) and was chosen because the seedlings were initially too small for consistent trunk-diameter measurement and biomass measurement would have required destructive harvesting.

During January 1986, the diameter at breast height (DBH, 1.2–1.4m from base) of each tree was measured, as well as the DBH of the ten closest neighbors and their distance to the center tree. DBH of trees with multiple trunks was taken as the sum of the individual trunk DBHs. Only 16 out of 690 neighbors measured had to be included in two "neighborhoods" and none in three or more. None of the center trees were in other center tree's neighborhoods.

To examine the effects of potential competitors on changes in height of the original trees, the following variables were computed (Lorimer 1983):

$$Ci = \Sigma(DC_i/DS)/D_i \tag{1}$$

$$Ce = \Sigma\, DC_i/D_i \tag{2}$$

$$Ec = \Sigma\, DC_i \tag{3}$$

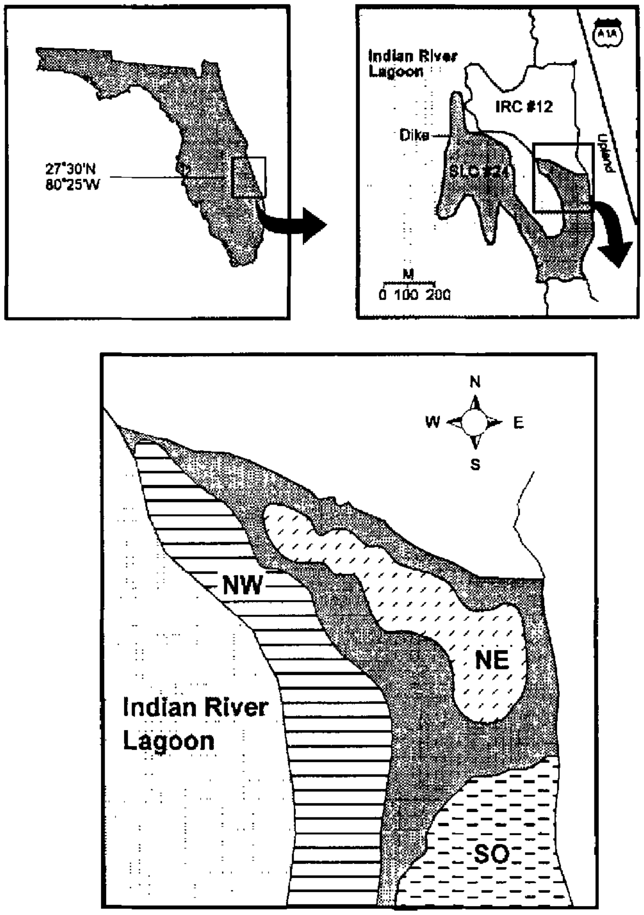

Figure 1. Map of the study area showing the general location of the site and the three mangrove stands (NE, NW, SO).

where DC_i is the DBH of the ith neighbor, DS is the DBH of the subject (center) tree, and D_i is the distance between the center tree and the ith neighbor. The first two indices measure potential competion as a function of the diameter of competing trees weighed by their distance from the subject tree; *Ci* also takes into account the diameter of the subject tree whereas *Ce* does not. *Ec* is only an index of competitor sizes and does not account for competitor distance or subject diameter. Linear regression analyses where computed between these variables and growth in height to examine the relationship, if any, between the nearest neighbor measures and individual tree growth.

The Wilk-Shapiro Test (WST, Shapiro and Wilk 1965) was applied to the tree size distributions to test for deviations from normality. Two-way analyses of variance or covariance were used to examine the effects of tree species and stand upon the overall variance in mangrove height changes, and the Waller-Duncan test (Waller and Duncan 1969) was used for *a posteriori* comparison of means.

Table 1. Growth statistics (cm) by species and stand. The first two columns indicate all possible combinations of stands (NE, NW, SO) and mangrove species (RED, BLACK, WHITE). ALL indicates all stands and/or species combined; N = sample sizes.

Stand	Species	N	Total Growth	S.E.	Mean Growth Per Yr.
NE	RED	2	222.50	27.7	59.7
NE	BLACK	4	106.17	12.9	28.5
NE	WHITE	5	196.59	51.4	52.7
NE	ALL	11	168.42	27.2	45.2
NW	RED	11	489.60	25.4	131.3
NW	BLACK	20	314.76	24.5	84.4
NW	WHITE	12	359.62	38.5	96.4
NW	ALL	43	372.00	19.9	99.7
SO	RED	4	303.08	47.6	81.3
SO	BLACK	8	238.89	46.4	64.0
SO	WHITE	3	184.23	37.0	49.4
SO	ALL	15	245.07	29.4	65.7
ALL	RED	17	414.29	32.4	111.1
ALL	BLACK	32	269.72	22.6	72.3
ALL	WHITE	20	292.56	32.1	78.4
ALL	ALL	69	311.96	17.4	83.6

Table 2. Results of analysis of variance for the effects of stand and species on the log of total growth. WALLER indicates rankings resulting from the Waller-Duncan *a posteriori* test; all inequalities are significant at the 0.05 level. RM = *Rhizophora mangle*, LR = *Laguncularia racemosa*, AG = *Avicennia germinans*.

Source	DF[1]	F	$p \leq$	WALLER
Stand	2	26.45	0.0001	NW > SO > NE
Species	2	9.46	0.0003	RM > LR = AG
Interaction	4	1.00	0.4135	–

[1] Total DF = 68.

Appropriate transformations were applied to the data when necessary. Tests for unequal spread based upon the interquartile range of residuals from bisquare regressions (Hoaglin *et al.* 1983, Huber 1981) did not indicate a need for variance-adjusting weighing after transformations.

RESULTS

Mortality

A total of 21 trees died during this study. Of these, 10 were red mangroves, 8 were black, and 3 were white. This translates to mortality rates of 9.6%, 4.6%, and 3.2% per year for red, black, and white mangroves, respectively. Tree death, however, was not uniform in time, as 11 of the 21 deaths were recorded during the September 1985 sampling. If those 11 trees are excluded, the mortality rates are 1.9%, 3.5%, and 3.2% per year for red, black, and white mangroves, respectively. The dead specimens did not appear to be smaller than the surviving individuals, but there was a tendency for their last height increment (growth during their last live sampling interval) to be somewhat lower than the others, particularly for the red mangroves.

Ten trees (1 red, 7 black, and 2 white) could not be located again after the start of the study, possibly because their tags fell off, but could not be confirmed to be dead. These were excluded from the analyses.

Growth

Overall height increment rates for red, black, and white mangroves were 111.1, 72.3, and 78.4 cm/yr, respectively (Table 1). The rates ranged from 28.5 cm/yr for black mangroves at the NE stand to 131.3 cm/yr for reds at the NW stand. All species exhibited similar seasonal growth patterns, with peaks occurring during summer and fall, and lows during winter. Total growth in height was highly correlated with final height (Spearman rank correlation $p \leq 0.001$) but not with initial height ($p > 0.05$).

Two way analysis of variance revealed significant effects of species and stand on height increment rates but no significant species by stand interaction (Table 2). *A posteriori* comparison of means via the Waller-Duncan test indicates that *R. mangle* had higher height growth rates than *L. racemosa* and *A. germinans* and that trees in the NW stand had higher growth rates than those in the SO stand, which in turn had higher rates than those in the NE stand (Table 2). The model accounted for approximately 55% of the variance in growth.

Neighbor Effects

No differences in average neighbor distances were evident between stands (ANOVA: $F_{2/60} = 0.20$, $p = 0.820$) or species ($F_{2/60} = 0.54$, $p = 0.586$. Likewise, there were no differences in DBH between center trees and neighbors ($F_{2/15} = 1.129$, $p = 0.3493$).

Ec was the only variable with consistent significant regressions on growth for each species and for all species combined (Figure 2). In all cases, the slopes of the regressions of growth on *Ec* were positive and significantly different from 0 (Figure 2). *Ce* was significant only for black mangroves, whereas *Ci* had significant positive slopes for black and white mangroves, negative for reds, and not-significant for all species combined. R^2 values for log-growth vs *Ec* regressions ranged from 0.459 for white mangroves to 0.258 for reds, with intermediate values of 0.281 and 0.302 for all species and black mangroves, respectively.

Analysis of covariance for the effects of stand and *Ec* on mangrove growth in height corroborate the above results with significant effects of stand after adjusting for *Ec* ($F_{2,59} = 9.12$, $p \leq 0.001$), and of *Ec* after adjusting for stand ($F_{1,59} = 5.70$, $p \leq 0.02$).

DISCUSSION

Growth

The growth in height measured during the study, particularly at the NE stand, is at the high end of the range previously reported for these and other species of mangroves (Burns and Ogden 1985, Clarke and Myerscough 1993, Ellison and Farnsworth 1993, Patterson *et al.* 1993). Moderate salinity (e.g., Soto and Jiménez 1983) and lack of interference from mature trees (e.g., Smith 1987, Ellison and Farnsworth 1993) probably contributed to the high growth. Note that, although change in height estimates tree growth (Rabinowitz 1978a, Burns and Ogden 1985, Smith 1987), it is unclear how accurate this variable is as an overall estimator of biomass accumulation in this experimental situation.

The hierarchy in height changes of trees in the different stands (NW > SO > NE, Table 2) is related to the location of the stands within the marsh. Many previous studies document the fact that marsh substrates near ditches and tidal creeks (e.g., NW stand) are flushed more often (Mendelsshon and Seneca 1980, King *et al.* 1982, Rey *et al.* 1990c), have higher nutrient (Gallagher 1975, Valiela *et al.* 1978, Agosta 1985) and oxygen (Linthurst 1979, Howes *et al.* 1981) contents, and lower salinity (Chalmers 1982, Rey *et al.* 1989), organic matter content (Rey *et al.* 1989), and sulfide concentrations (Gardner *et al.* 1988, Rey *et al.* 1992,) than upper marsh areas, such as the NE stand, that are distant from such influences. Likewise, locations near the upland edge (such as the SO stand) characteristically have lower salinities than those in the upper marsh proper (Rey *et al.* 1991, Rey and Kain 1993). Differences in salinity (Hicks and Burns 1975, Soto and Jiménez 1983, Tomlinson 1986), nutrient:salinity ratios (Pool *et al.* 1977, Boto and Wellington 1984), flushing rates (McNae 1968) and sulfide concentrations (King *et al.* 1982, Nickerson and Thibodeau 1985, Gardner *et al.* 1988, Koch and Mendelssohn 1989) are known to influence mangrove growth and probably contributed to the observed differences. Interactions among these factors are extremely important and very complex, and carefully controlled manipulative experiments are necessary to unravel specific effects upon mangrove establishment and growth (McKee 1993).

Although there certainly are inherent differences in growth rates among species, the fact that red mangrove height increments were significantly higher than those of black and white mangroves may also reflect the fact that conditions in the impounded marsh favor the former species. In particular, prolonged flooding and moderate salinities, such as found at the study site, favor the growth of *Rhizophora* over *Avicennia* and *Laguncularia* (Soto and Jiménez 1983, Naidoo 1985, López-Portillo and Ezcurra 1989, Ellison and Farnsworth 1993, McKee 1993; however, see Rabinowitz 1978a and Patterson *et al.* 1993 for contrasting results).

Mortality

Mortality rates at the study sites were relatively low compared to those reported for newly established mangroves elsewhere (e.g., Lugo and Snedaker, 1974, Burns and Ogden 1985, Jiménez and Sauter 1991, Clarke and Myerscough 1993, Ellison and Farnsworth 1993, Patterson *et al.* 1993). In the present study, seedlings were already established when the study was started and were past the high mortality rates observed immediately after propagule colonization (Lugo and Snedaker 1974). Additionally, the seedlings were established in areas free of competing adults and were not subject to shading and other stresses to which seedlings invading an established stand are normally exposed (Lugo and Snedaker 1975, Lugo 1986). For example, Lahman (1988), working in similar impoundments nearby, reported mortality rates for red mangrove trees comparable to those reported here (1.6–2.9%/yr.), but seedling mortality in established stands was much higher (80–90%/yr.). The deaths recorded during the September 1985 sampling were probably caused by severe storms during late summer of that year that caused excessive and prolonged flooding of the marsh (Rey *et al.* 1990b) and stressed the growing seedlings, which are particularly vulnerable to overflooding (McKee 1993).

The fact that the dead individuals were not initially smaller than the surviving ones is in contrast to the findings of Rabinowitz (1978b), who reported a direct relationship between survival and initial propagule size (see also Burns and Ogden 1985). This result, however, is probably an artifact caused by the very similar initial sizes of the subject trees. The observation that white and black mangroves did not show any tendency towards decreased growth in height prior to their death also contrasts with the results for red mangroves, where growth rates during the last live period were all below the average for all conspecifics. Perhaps shorter intersample intervals would have led to more consistent

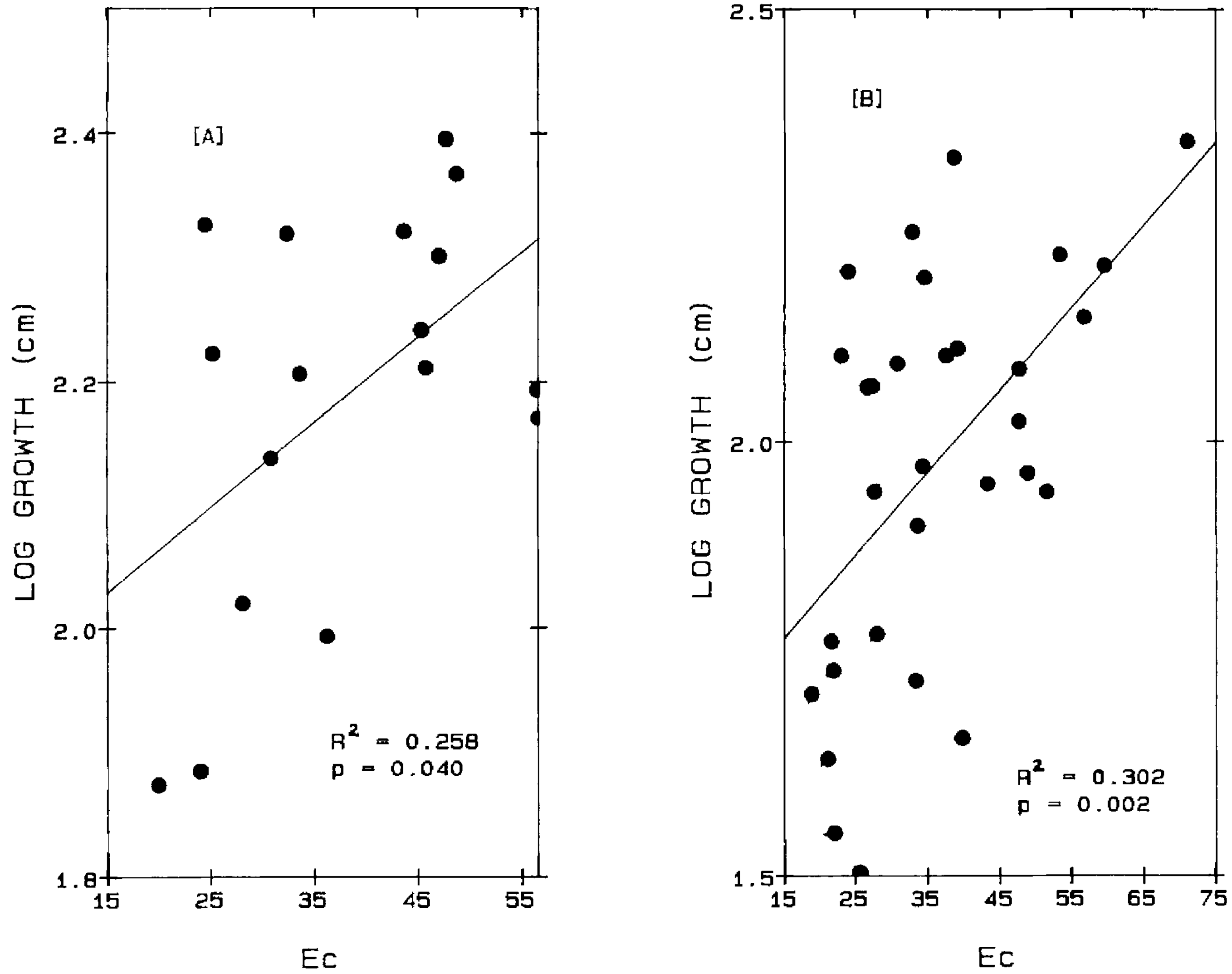

Figure 2. Linear regressions of (log) total growth vs *Ec*. [A] *Rhizophora mangle*, [B] = *Avicennia germinans*, [C] = *Laguncularia racemosa*, [D] = all trees.

results. Lahman (1988) also observed decreased growth in red mangroves prior to their death but did not examine black or white mangroves.

Neighbor Effects

It is apparent from the results of the regression analyses that growth increment rates of trees with larger and/or closer neighbors were not negatively affected in relation to those with smaller and/or farther ones; the fact that all regression slopes were positive indicates the opposite. This observation may be due to interneighbor facilitation but is more likely a result of small-scale variation in physical-chemical conditions that allow all trees sharing more favorable patches to grow faster than those in less favorable ones. Such patchiness is characteristic of coastal marshes and mangals worldwide (Chapman 1977, Steers, 1977, Phleger, 1977, McKee 1993) and has been documented in the study site and similar nearby marshes (Carlson *et al.* 1983, Rey 1991, Rey and Kain 1993). This phenomenon often causes problems with nearest neighbor analyses of plant competition because the analyses cannot detect negative relationships resulting from neighborhood competition if they are offset by shared local environmental effects that cause positive relationships (Mitchell-Olds 1987). The range of the percent variance in tree growth accounted for by *Ec* (25.8–45.9%) is typical of analyses using nearest neighbor measures for predicting tree growth (Firbank and Watkinson 1985).

In addition, other factors are probably responsible for the lack of obvious negative impacts of neighbors on the growth increment rates of center trees: (1) the trees were growing in a newly-colonized location with plenty of open space, (2) they were the largest trees in

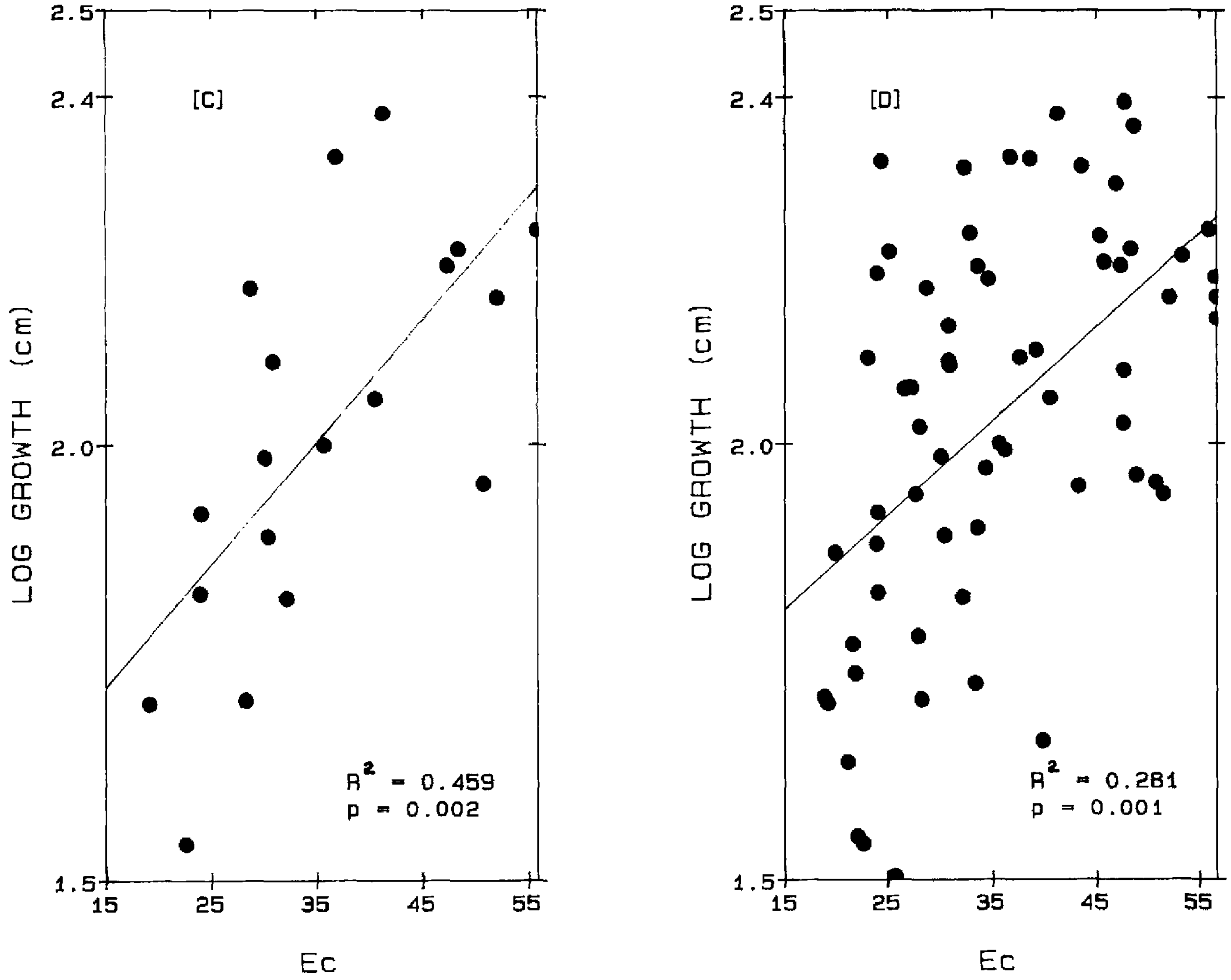

Figure 2. Continued.

their respective stands, and (3) the trees were still relatively small. It may be that, as Ball (1980) determined for Biscayne Bay (Florida) mangroves, inter-tree competition will be manifested only after the stand matures, or that neighbor effects in mangroves are expressed as a boundary constraint on maximum potential size rather than as determinants of actual size (Waller 1981, Liddle *et al.* 1982, Goldberg 1987). Conversely, other factors (physical-chemical, disturbance, environmental stress, etc.) may continue to be of primary importance in determining growth rates and stand structure.

CONCLUSION

There was no evidence for relative negative effects of neighbors on growth in height of mangrove seedlings at the experimental sites, probably because the experimental stands were still relatively young. At this early stage of stand development, local conditions, both within and between stands seem to be more important in determining growth and survival of the young plants.

Between-stand differences in physical conditions were important in determining relative growth increment rates of the trees resident in each. Likewise, shared conditions between neighbors and centers in patches within stands likely influenced the observed relationships between growth of center trees and neighbor size and proximity.

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