Effects of Season, Rainfall, and Hydrogeomorphic Setting on Mangrove Tree Growth in Micronesia

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ABSTRACT

Seasonal patterns of tree growth are often related to rainfall, temperature, and relative moisture regimes. We asked whether diameter growth of mangrove trees in Micronesia, where seasonal changes are minimal, is continuous throughout a year or conforms to an annual cycle. We installed dendrometer bands on Sonneratia alba and Bruguiera gymnorrhiza trees growing naturally within mangrove swamps on the islands of Kosrae, Federated States of Micronesia (FSM), Pohnpei, FSM, and Butaritari, Republic of Kiribati, in the eastern Caroline Islands of the western Pacific Ocean. Trees were remeasured monthly or quarterly for as long as 6 yr. Annual mean individual tree basal area increments ranged from 7.0 to 79.6 cm²/yr for all S. alba trees and from 4.8 to 27.4 cm²/yr for all B. gymnorrhiza trees from Micronesian high islands. Diameter increment for S. alba on Butaritari Atoll was lower at 7.8 cm²/yr for the one year measured. Growth rates differed significantly by hydrogeomorphic zone. Riverine and interior zones maintained up to seven times the annual diameter growth rate of fringe forests, though not on Pohnpei, where basal area increments for both S. alba and B. gymnorrhiza were approximately 1.5 times greater in the fringe zone than in the interior zone. Time-series modeling indicated that there were no consistent and statistically significant annual diameter growth patterns. Although rainfall has some seasonality in some years on Kosrae and Pohnpei and overall growth of mangroves was sometimes related positively to quarterly rainfall depths, seasonal diameter growth patterns were not distinctive. A reduced chance of moisture-related stress in high-rainfall, wetland environments may serve to buffer growth of Micronesian mangroves from climatic extremes.

Key words: Bruguiera gymnorrhiza; Butaritari Atoll; coastal forests; dendrometry; ENSO; Kiribati; Kosrae; Pohnpei; rainfall dependence; Sonneratia alba.

PROTECTING THE MANY SERVICES PROVIDED BY COASTAL ECOSYSTEMS FROM anthropogenic change requires understanding the basic function of these ecosystems. In mangrove forests, which provide valuable ecosystem services along tropical and subtropical coastlines, tree growth rates may be a useful indicator of site conditions resulting from change, but little is known about the natural rates and patterns of growth for most mangrove species and geomorphic settings. In addition to universal environmental factors such as day length, sun angle, and air temperature, wetland tree growth can also be affected by site geomorphology, wetland size, soil fertility, salinity, andhydroperiod (Day 1985, Ewel & Wickenheiser 1988, Conner & Day 1992, Keeland et al. 1997, Krauss et al. 2006). Because hydrological cycles regulate wetlands and because El Niño/Southern Oscillation (ENSO) events create variation in hydrological cycles in the Pacific islands, we decided to explore relationships among diameter growth rates, rainfall, and hydrogeomorphic zone of Pacific island mangroves.

Long-term diameter growth increments have been calculated for some Pacific island mangrove forests (Devoe & Cole 1998, Cole et al. 1999), but the lack of seasonal data, primarily due to the difficulty of reading and interpreting tree rings, remains a major reason for our poor understanding of natural and anthropogenic controls over tropical forest growth. Mangroves in many tropical locales exhibit seasonal diameter growth patterns, often as a consequence of distinctive wet and dry seasons. In Laguna de Términos, Mexico, for example, mangroves have their greatest annual diameter increment during the “Norte” season in which large portions of the region’s 1680 mm of annual rainfall are deposited in short time periods (Day 1990). There, mangrove growth is correlated with the presence of a seasonally available supply of fresh water. Accordingly, diameter increment of Bruguiera and Rhizophora species appeared to be greater during some months in tropical Thailand (Jintana et al. 1985). Subtropical mangroves also grow seasonally; however, it was more difficult to link diameter growth increment to rainfall, temperature, or hydroperiod without considering site fertility and salinity in south Florida (Lahmann 1988, Krauss et al. 2006). Nutrient and salinity controls may be reduced on high-rainfall Pacific islands. We predict, therefore, that since rainfall and temperature vary little seasonally on some Pacific islands, diameter growth rates will be fairly constant throughout the year.

Sensitivity in our measure of diameter growth, hence, is very important, leading to use of dendrometer bands. Dendrometer bands, which can measure small (millimeters) increments in circumference growth, offer an alternative to tree-ring analysis for documenting fine-scale growth increments. The goals of this project were threefold. First, we asked whether variation in growth rates followed annual patterns indicative of seasonality. Second, we questioned whether mangroves in different hydrogeomorphic zones, receiving equivalent rainfall, displayed different patterns of growth and seasonality. Finally, we determined whether fine-scale diameter growth patterns of adult mangroves are linked to large-scale
climate fluctuations on remote Pacific islands. These questions are particularly important given the extreme fluctuations in rainfall produced by ENSO events.

METHODS

STUDY SITES.—This project was conducted on two high islands (maximum altitude > 500 m) in the Federated States of Micronesia (Kosrae: 5°19' N; 163°00' E; Pohnpei: 6°51' N; 158°19' E) and on one atoll in the Republic of Kiribati (Butaritari Atoll: 3°04' N; 172°47' E). All islands are located in an area of the Pacific Ocean known as Micronesia (Fig. 1). Three mangrove forests located in different river basins were selected on the high islands (Yela and Utwe on Kosrae, Enipoas on Pohnpei), and one beach strand was selected on Butaritari. Both high islands support a large mangrove area (approximately 14% of land area): Kosrae has an estimated 1500 ha of mangroves, while Pohnpei contains approximately 5300 ha (MacLean et al. 1988). Few atolls have extensive mangrove forests. Only four of the 33 atolls in Kiribati support significant mangrove stands, which cover 258 ha of a combined land area of 811 km² in the entire country (Metz 1996).

Mangroves on these Pacific islands can usually be divided into fringe, riverine, and interior hydrogeomorphic settings (Ewel et al. 1998a,b). In Kosrae and Pohnpei, *Sonneratia alba* J. Smith, *Bruguiera gymnorhiza* (L.) Lamk., and *Rhizophora apiculata* BL...
share codominance in all zones. Many mangrove forests on Butaritari are fringe, dominated by S. alba and Rhizophora stylosa Griff., although small areas of interior forests, dominated by R. stylosa and Lumnitzera littorea (Jack) Voigt., can also be found (K. Krauss, pers. obs.).

Diameter Increment.—The first trees selected for measurement in Kosrae and Pohnpei were located in permanent measurement plots established in 1995 or later, and were selected from among B. gymnorrhiza and S. alba growing in fringe, riverine, and interior hydrogeomorphic zones. Additional trees were added around the perimeter of these plots to attain 15 per species per zone; presence of a single trunk at band height and a codominant crown class were the principal factors in tree selection. A few trees, especially for S. alba, had forked boles below the band height. Since our crown-class requirement prevented selection of all trees within a given area, we were very careful to select codominant trees from the range of diameters present on each site. We thus present diameter increment on an individual tree basis.

A total of 90 trees were banded from each river basin in Kosrae and Pohnpei. The circumference of each tree was scraped lightly at a height of approximately 1.8 m for S. alba and 1.6 m for B. gymnorrhiza, measured for diameter, and fitted with a metal dendrometer band according to methods described by others (Cattelino et al. 1986, Keeland & Sharitz 1993). Since these bands were first introduced (Hall 1944), they have been applied widely, but only a few studies have used them to quantify mangrove tree growth (Day et al. 1982, Jintana et al. 1985) or to relate mangrove growth to natural or anthropogenic factors (Lahmann 1988, Day 1990, Krauss et al. 2006). Our dendrometers were constructed of 1.3-cm-wide by 0.025-cm-thick stainless steel (300 Series, Keyes Davis Company, Battle Creek, MI, U.S.A.) and 7.6-cm-long stainless steel springs (LE-026C-11 SS, Lee Spring Company, Brooklyn, NY, U.S.A.).

In Kiribati, only S. alba trees in a fringe forest were present in sufficient quantities to include in the study; 53 codominant trees were selected from a specified area and banded at a height of approximately 1.6 m using the same methods described above. Over all sites on Kosrae, Pohnpei, and Butaritari, mean initial tree diameter where the band was affixed ranged from 21 to 78 cm for S. alba and from 22 to 42 cm for B. gymnorrhiza (Table 1).

Bands were installed in Kosrae and Pohnpei from February 1997 to January 1998, and trees were monitored until November 2002 to February 2003, depending on the individual site. Measurement frequency varied from monthly to quarterly on Kosrae. Measurements on Pohnpei were limited to quarterly intervals at best, with the three final years representing annual increments only. Dendrometer bands were installed on trees in Kiribati in January 2001 and remeasured quarterly for one year, with the last measurement in February 2002.

Rainfall Record.—Long-term records (1961–1990) from Kosrae suggest that rainfall averages 4.8 m in the lowlands, reaching as much as 6 m in the uplands in some years (Merlin et al. 1993). To document short-term rainfall variation, we installed a tipping-bucket rain gage and data logger (HOBO Event, Onset Computer Corp., Bourne, MA, U.S.A.) in a large canopy gap in the Yela River basin to obtain rainfall for 1999 and 2000. In Pohnpei, the Ponape Agriculture and Trade School maintains a rain gage in a lowland location near the Enipoa River basin. Continuous data are available from 1980 to 2000, including full documentation of the 1997–1998 ENSO drought on Pohnpei (Fig. 2).

Statistical Analysis.—Band losses and irregular measurement periods made statistical analyses challenging, especially for determining whether growth followed an annual pattern. We used two principal techniques to explore these relationships: time-series modeling and regression analysis.

Time-series modeling was used to account for bias associated with periodic band losses or data gaps (Chatfield 1989). For Yela, Utwe, and Enipoa, we tested for repetitive growth patterns while comparing differences in growth rates among zones within a basin for each species (between fringe and interior, fringe and riverine, interior and riverine) and between species (B. gymnorrhiza and S. alba) for each zone, for a total of 27 difference combinations.

Data were autocorrelated throughout, so time-series analysis (ARIMA Statement: SAS Institute 1999) was used to account for the correlation among measurements and initial tree size, with alpha set conservatively at 0.01. Measurements were taken or averaged for 2-mo (t) intervals, providing fairly continuous records throughout. A cubic spline was used to fit polynomial data piecewise from each time series; splines were also used to estimate any missing points from unequally spaced or missing measurements (Chatfield 1989). For Utwe and Yela, only 1 of 26 and 2 of 31 points were estimated, respectively. However, estimation was necessary for 6 of the 17 points collected from the Enipoa River basin; estimation here was associated principally with missing quarterly intervals from 2000 to 2002.

When comparing tree growth increments, differences between growth means for two time series were graphed over time. If a linear trend was evident, we took the difference of the series, i.e., \(X_{Z(i)} - X_{Z(i-1)}\). We tested both raw data and differences for stationarity, which can be defined as systematic changes in either means or variances over time (Chatfield 1989). When stationarity was attained, we checked the autocorrelation function and the partial autocorrelation function to determine the kind of model that fit the data. Four models were fit to the data (see Results, Table 2), where \(X_{Z(i)}\) is the basal area growth time series for treatment \(x - z\) (e.g., fringe – interior); \(X_{b(i)}\) is the basal area growth time series for treatment \(x\); \(Z_{g(i)}\) is the basal area growth time series for treatment \(x\); \(Z_{g(i)}\) is the basal area growth time series for treatment \(x\); \(\beta\) is the \(\gamma\)-intercept; \(\phi_1, \phi_2, \phi_3\) are constant parameters, and \(\epsilon\) is random error or white noise (cf. Gotelli & Ellison 2004).

Univariate regression analyses were then used to detect linear trends by species between quarterly circumference increments and quarterly rainfall depths. Only the Yela and Enipoa Rivers had functional rainfall gages nearby for the period of dendrometer record. These analyses were restricted to 2 yr for Yela and 4 yr for Enipoa. No statistical analyses were performed on Kiribati data, but data were included for an understanding of relative growth potential for S. alba from an entirely different environment.
TABLE 1. *Initial individual tree diameter (±1 SE) and basal area increment (±1 SE) for Sonneratia alba and Bruguiera gymnorrhiza growing in Kosrae and Pohnpei (Federated States of Micronesia) and on Butaritari Atoll (Republic of Kiribati).*

<table>
<thead>
<tr>
<th>Island</th>
<th>Basin/site</th>
<th>Record duration (yr)</th>
<th>Zone</th>
<th>Mean initial tree diameter (cm)</th>
<th>Mean basal area increment (cm²/yr)</th>
<th>Mean initial tree diameter (cm)</th>
<th>Mean basal area increment (cm²/yr)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kosrae</td>
<td>Yela</td>
<td>5.8</td>
<td>Fringe</td>
<td>35.6 ± 3.6</td>
<td>14.1 ± 3.3</td>
<td>30.8 ± 1.3</td>
<td>4.8 ± 0.6</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Riverine</td>
<td>68.4 ± 8.9</td>
<td>76.0 ± 12.9</td>
<td>41.6 ± 3.3</td>
<td>27.4 ± 3.0</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Interior</td>
<td>78.0 ± 9.0</td>
<td>79.6 ± 12.7</td>
<td>35.8 ± 1.7</td>
<td>22.2 ± 2.7</td>
</tr>
<tr>
<td>Kosrae</td>
<td>Utwe</td>
<td>4.8</td>
<td>Fringe</td>
<td>47.4 ± 5.0</td>
<td>26.6 ± 3.5</td>
<td>21.9 ± 1.0</td>
<td>5.3 ± 0.8</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Riverine</td>
<td>39.6 ± 6.3</td>
<td>26.2 ± 5.0</td>
<td>30.1 ± 1.8</td>
<td>11.0 ± 1.5</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Interior</td>
<td>48.8 ± 6.2</td>
<td>40.2 ± 7.1</td>
<td>30.8 ± 1.6</td>
<td>18.9 ± 1.7</td>
</tr>
<tr>
<td>Pohnpei</td>
<td>Enipoas</td>
<td>5.1</td>
<td>Fringe</td>
<td>36.6 ± 1.8</td>
<td>13.5 ± 2.4</td>
<td>23.9 ± 1.0</td>
<td>7.6 ± 0.9</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Riverine</td>
<td>48.7 ± 3.5</td>
<td>29.1 ± 3.7</td>
<td>32.4 ± 1.3</td>
<td>9.2 ± 1.6</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Interior</td>
<td>32.1 ± 2.2</td>
<td>7.0 ± 1.0</td>
<td>24.3 ± 1.0</td>
<td>6.3 ± 0.8</td>
</tr>
<tr>
<td>Kiribati</td>
<td>Butaritari</td>
<td>1.1</td>
<td>Fringe</td>
<td>20.7 ± 0.7</td>
<td>7.8 ± 0.9</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>

RESULTS

RAINFALL RECORD.—Records of rainfall between 1961 and 1990 on Kosrae and between 1980 and 2000 on Pohnpei indicate variable monthly precipitation patterns, with slightly less rainfall in February and October (Fig. 2A). Rainfall in the Yela River basin on Kosrae ranged from 5322 to 5473 mm/yr for the two monitoring years. Rainfall in a lowland location near the Enipoas River basin on Pohnpei ranged from 3404 to 5105 mm/yr for a 4-yr monitoring period. Rainfall for individual months during this study were also variable, and ranged from 259 mm to 683 mm for a 2-yr duration on Kosrae and from 25 mm to 813 mm for a 4-yr duration on Pohnpei (Fig. 2B). Butaritari, likewise, is a relatively wet atoll for Kiribati and receives 3114 mm of rainfall annually, approximately double the average of all atolls in Kiribati combined (Levy 1996).

FIGURE 2. (A) Average monthly rainfall (mm) for Kosrae and Pohnpei, Federated States of Micronesia. Data from Kosrae are from WRCC (2004), while data from Pohnpei are from a manual rain gage located at the Ponape Agriculture and Trade School (Miklos Szentkiralyi, pers. comm.). Annual mean rainfall during this extended period for Kosrae was 4842 mm/yr; annual mean rainfall for Pohnpei was 4181 mm/yr. (B) Insert graphs show monthly rainfall for the 4-yr record on Pohnpei (lower) and approximate rainfall for the 2-yr record on Kosrae (upper). An ENSO drought year is depicted in 1998.
TABLE 2. Parameter estimate ($\phi$, $\beta$) for statistically significant comparisons ($\alpha = 0.01$) of individual tree basal area growth increment by island and basin for time-series models. Only 18 of 27 overall comparisons are shown.¹

<table>
<thead>
<tr>
<th>Island</th>
<th>Basin</th>
<th>$S. alba$ Result of zone comparison</th>
<th>$B. gymnorrhiza$ Result of zone comparison</th>
<th>$\phi$</th>
<th>$\beta$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kosrae</td>
<td>Yela</td>
<td>Fringe &lt; interior</td>
<td>Fringe &lt; interior</td>
<td>8.97²</td>
<td>2.79²</td>
</tr>
<tr>
<td>Kosrae</td>
<td>Utwe</td>
<td>Fringe &lt; interior</td>
<td>Fringe &lt; riverine</td>
<td>8.03²</td>
<td>3.92²</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Interior &gt; riverine</td>
<td>Interior = riverine</td>
<td>22.8³</td>
<td>n.s.⁴</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Fringe &lt; interior</td>
<td>Fringe &lt; riverine</td>
<td>2.46²</td>
<td>2.54²</td>
</tr>
<tr>
<td>Pohnpei</td>
<td>Enipoas</td>
<td>Fringe ≠ riverine</td>
<td>Fringe &lt; riverine</td>
<td>n.s.⁴</td>
<td>0.87²</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Interior &gt; riverine</td>
<td>Interior &gt; riverine</td>
<td>2.55¹</td>
<td>1.67²</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Fringe &gt; interior</td>
<td>Fringe &gt; interior</td>
<td>1.51¹</td>
<td>3.92²</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Fringe &lt; riverine</td>
<td>Fringe = riverine</td>
<td>2.57²</td>
<td>n.s.⁴</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Interior &lt; riverine</td>
<td>Interior &lt; riverine</td>
<td>4.07²</td>
<td>0.50²</td>
</tr>
</tbody>
</table>

¹Overall, 27 comparisons were made (3 basins × 3 zones × 3 species comparisons per zone). For simplicity, the 9 species comparisons are not shown in this table.
²The interpretation is that the change of slope over one unit of time for treatment X is $\phi_1$ growth units different than treatment Z. Difference detected for $\phi_1$ (fit for 20 of 27 comparisons)

$$XZ_{i(t)} - XZ_{i(t-1)} = [X_{i(t)} - X_{i(t-1)}] - [Z_{i(t)} - Z_{i(t-1)}] = \varepsilon + \phi_1.$$  

³Difference detected for $\phi_1$, but with a better correlation to an earlier time point than to the current (fit for 3 of 27 comparisons)

$$XZ_{i(t)} = \beta + \phi_{i(1)}X_{i(t-1)} + \phi_{i(2)}X_{i(t-2)} + \phi_{i(3)}X_{i(t-3)} + \varepsilon.$$  

⁴No differences detected for $\phi_1$ (i.e., $\phi_1 = 0$) (fit for 3 of 27 comparisons)

$$XZ_{i(t)} - XZ_{i(t-1)} = [(X_{i(t)} - X_{i(t-1)})] - [(Z_{i(t)} - Z_{i(t-1)})] = \varepsilon.$$  

⁵Differences detected for $\beta$ only, $\phi_1$ constant (fit for 1 of 27 comparisons)

$$X_{i(t)} - Z_{i(t)} = \phi_1 + \varepsilon.$$  

Variation in rainfall associated with ENSO events can influence long-term means (Fig. 2). The rainfall record for Pohnpei, for example, includes five ENSO-related droughts since 1980. Rainfall on Butaritari is commensurate with that for Micronesian high islands during ENSO drought years; the rainfall for Pohnpei for the past five ENSO years since 1980 ranged from 2769 mm (in 1983) to 3861 mm (in 1995; M. Szentkiralyi, pers. comm.).

Diameter Growth Patterns.—Mangrove diameter increment on Micronesian high islands did not exhibit repetitive, annual patterns (Figs. 3 and 4). For all comparisons ($N = 27$), only three indicated that data were more correlated to an earlier time point than to the current time point. Only one was for comparisons associated with hydrogeomorphic zone (Table 2). In two cases, correlations were shifted by 2 mo ($t - 1$) while in one case correlations were shifted by 6 mo ($t - 3$); it is difficult to determine whether this latter shift is due to annual rainfall variation. None were shifted by a time period indicative of a seasonal growth effect (i.e., $t - 6$).

Individual tree basal area increment ranged from 7.0 to 79.6 cm²/yr for all measured $S. alba$ trees and from 4.8 to 27.4 cm²/yr for all measured $B. gymnorrhiza$ trees from Micronesian high islands (Table 1; Figs. 3 and 4). Annual increment was significantly greater in $S. alba$ than in $B. gymnorrhiza$ for nearly all of the applicable time-series combinations tested, with the change in slope for one unit of time between 0 and 7.19 units less in $B. gymnorrhiza$ than in $S. alba$ among all three river basins. Likewise, $S. alba$ trees were also uniformly larger than $B. gymnorrhiza$ trees (Table 1). Even though $S. alba$ outgrew $B. gymnorrhiza$ in nearly all river basins and zones, hydrogeomorphic setting significantly influenced growth (Table 2). Growth rates were faster in riverine and interior zones than in fringe forests in the Yela and Utwe River basins. This was not the case in the Enipoas River basin, where basal area increment for both $S. alba$ and $B. gymnorrhiza$ was significantly greater in the fringe zone than in the interior zone (Table 2). The comparisons between interior
zone and riverine zone basal area increments were variable among study sites. *Sonneratia alba* in Butaritari experienced a slow basal area increment of 7.8 cm²/yr relative to the growth registered on most high island sites for the one year measured (Table 1; Fig. 4). Within-year growth depressions were evident for *S. alba* in riverine and interior forests in the Yela River basin (Fig. 3). These depressions were related to either the loss of tree bands from extremely large trees, which were accounted for in the analysis, or lag effects of an ENSO-related drought. For riverine plots in the Yela River basin, for example, only 9 of an initial 15 trees were still being measured at the end of the February 1999 growth depression, while interior plots in the same basin experienced a loss of one large *S. alba* tree (115.7 cm diameter) in November 1999 (Fig. 3). Result significance was unaffected, however, when those trees were excluded from the analysis.

Growth, normalized for tree size (*i.e.*, circumference increment), was related significantly to quarterly rainfall amount for *S. alba* in fringe and riverine hydrogeomorphic zones (Fig. 5). Such patterns were not evident for either *S. alba* growing in interior zones or *B. gymnorrhiza* growing in any zone. This analysis is restricted to the Yela and Enipoas River basins, where data from nearby rain gages could be linked directly to a local growth response.

**DISCUSSION**

**ANNUAL GROWTH RESPONSE.**—In forests where rainfall or temperature varies seasonally, growth is often concentrated during certain months and may be linked to rainfall, or to factors other than rainfall (Njoku 1963). Diameter growth in mangroves has certainly been linked to rainfall in past studies (Day 1990, Krauss et al. 2006). However, we found little evidence for statistically significant, repetitive seasonal patterns of diameter growth for the two mangrove tree species studied in Micronesia. Mangrove soils in Micronesia often remain wet throughout the year and are rarely subjected to the physicochemical stresses found in mangrove swamps with periodic
drying (Ewel et al. 1998a). Continuously wet environments may moderate or even mask seasonal growth responses (Breitsprecher & Bethel 1990).

Forest wetlands in general may not respond to short-term phenomena such as year-to-year variation in rainfall where saturated soils reduce the probability of water deficit. Costly physiological and morphological adaptations to wet soils may consequently “pay off” by ameliorating water deficits during dry seasons or droughts. Permanently flooded baldcypress (Taxodium distichum [L.] Rich.) trees had fewer false rings, for example, than did periodically flooded trees (Young et al. 1993). Yet, even with nearly continuous soil saturation, some mangrove forests do exhibit seasonal growth patterns in some regions. Subtropical mangroves in south Florida, for example, can register 75 to 90 percent of their annual diameter growth during the wet season (Lahmann 1988, Krauss et al. 2006) as a response to wider seasonal temperature and rainfall changes than are experienced in Micronesia. In some tropical forests, tree stems shrink during the dry season (Daubenmire 1972), perhaps responding to lack of moisture rather than higher temperature. Conversely, some trees experience growth spurts during dry spells (Hazlett 1987). Neither response was registered consistently for Micronesian mangroves.

Although diameter growth of mangrove trees on Kosrae did not vary seasonally, there is some evidence that litterfall might. Peak rates of litterfall were observed during March of one year, when B. gymnorrhiza leaves made up most of the litter mass (R.D. Hauff & K.C. Ewel, pers. obs). High rates of litterfall were observed again from September to November. Peak production of leaves and propagules for B. gymnorrhiza and S. alba corresponded to high rainfall in March and April of that year; however, flower and stipule production was, like stem diameter increment, aperiodic. It is uncertain whether these litterfall patterns repeat themselves annually.

Overall rainfall regime can influence growth of Pacific island mangroves; faster growth rates were observed for S. alba trees in fringe and riverine zones as rainfall increased, whereas B. gymnorrhiza growth rates were unresponsive to the rainfall depths measured (Fig. 5). Accordingly, S. alba grew faster.
than \textit{B. gymnorrhiza} on many other high islands in Micronesia (Devoe & Cole 1998), indicating that trends observed in our study may be long-term and wide-scale in effect. Island-specific rainfall for Micronesia also track mean annual increment for \textit{S. alba} and \textit{B. gymnorrhiza} closely along a rainfall gradient (Cole et al. 1999), with the lowest mean annual increment being recorded on Yap (rainfall = 3086 mm/yr) and the highest on Kosrae (rainfall = 5250 mm/yr, Devoe & Cole 1998, slightly higher than the 4842 mm/yr rainfall that we report in Fig. 2).

**HYDROGEOMORPHIC SETTING.**—Individual tree basal area increment was highest in interior zones in the Yela and Utwe River basins on Kosrae. This was especially true for the interior versus fringe zone comparison (Table 2). Similar differences were not evident for standing plot-level basal area or volume of wood from some of the same locations on Kosrae (Ewel et al. 1998a); however, trees were shorter in fringe locations than in either riverine or interior locations, perhaps because of higher salinities, lower nutrients (esp. phosphorus; see McKee et al. 2002), and greater tidal amplitude (Odum et al. 1982). A mean salinity of 39.6 g/L for fringe zones, on the other hand, did not differ statistically from a mean salinity of 23.5 g/L for interior and riverine zones on Kosrae (Ewel et al. 1998a). In fact, Gleason et al. (2003) found an opposite trend for relative elevation (akin to zone) and salinity when additional areas in some of the same Kosraean river basins were surveyed, indicating highly variable relationships in high rainfall environments between location and salinity.

Growth regulators (cf., Twilley & Rivera-Monroy 2005), hence, are likely to be variable but low on Kosrae and may not explain differences among hydrogeomorphic zones effectively in years with a normal climate. Globally, this is not the case for many other mangrove forests, where distinct and consistent productivity patterns often result from contrasting hydroperiod, nutrient, and salinity regimes among fringe, riverine, and interior hydrogeomorphic zones (Odum et al. 1982, Twilley et al. 1986). In contrast to results from Kosrae, trees did grow faster in fringe zones of the Enipoas River basin than in interior zones (Table 2). These results suggest that ground water influences may confound the surface water relationship to vegetation on Pohnpei. Land-use history and natural disturbances (e.g., cyclones) may also play an important role on Pohnpei (H. Anson, pers. comm.).

Rapid initial growth rates in both the riverine and interior zones of Yela were followed by immediate depressions in the year following the 1997–1998 ENSO drought. Growth rates returned to normal in 2000 when rainfall would have restored normal ground water flow between upslope freshwater wetlands and mangroves (cf., Drexler & Ewel 2001). We suspect that growth depressions may have been real effects of the ENSO drought for two reasons. First, the effects only occurred in riverine and interior zones where salinities are kept low not only by rainfall but also by ground water (to a greater degree at Yela than at Enipoas; Drexler & DeCarlo 2002) and overland flows. We also found a short-term decrease in soil elevation in these same zones, indicating that soils may have dewatered over the ENSO time interval (D.R. Cahoon, J.A. Allen, K.W. Krauss, pers. comm.; see Whelan et al. 2005). Second, growth did not lag in zones where daily tides inundated mangrove soils consistently throughout the ENSO drought (e.g., Yela River fringe). The positive relationship between rainfall and \textit{S. alba} growth increment in Yela and Enipoas fringe and riverine zones demonstrates how responsive Micronesian
mangroves can be to variation in periodic rainfall amounts (Fig. 5).

This study demonstrates that growth rates of mangrove trees, like most species, vary at different ecological settings. Accordingly, hydrogeomorphic location often provides constraints to mangrove growth potential (Odum et al. 1982, Smith 1987, Kitaya et al. 2002). In addition, on sites where there is little annual variation in temperature or rainfall, diameter growth rates were seasonally aperiodic. Response to ENSO-induced drought conditions indicates that location with respect to normal inputs of surface water (fringe, interior, and riverine hydrogeomorphic zones) may not be the only way in which hydrology affects growth. A reduced chance of moisture-related stress in permanently wet, high-rainfall mangrove forests may serve to buffer growth against climatic variation.

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