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# SUN–SHADE ADAPTABILITY OF THE RED MANGROVE, *RHIZOPHORA MANGLE* (RHIZOPHORACEAE): CHANGES THROUGH ONTOGENY AT SEVERAL LEVELS OF BIOLOGICAL ORGANIZATION[1]

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*Rhizophora mangle* L., the predominant neotropical mangrove species, occupies a gradient from low intertidal swamp margins with high insolation, to shaded sites at highest high water. Across a light gradient, *R. mangle* shows properties of both "light-demanding" and "shade-tolerant" species, and defies designation according to existing successional paradigms for rain forest trees. The mode and magnitude of its adaptability to light also change through ontogeny as it grows into the canopy. We characterized and compared phenotypic flexibility of *R. mangle* seedlings, saplings, and tree modules across changing light environments, from the level of leaf anatomy and photosynthesis, through stem and whole-plant architecture. We also examined growth and mortality differences among sun and shade populations of seedlings over 3 yr. Sun and shade seedling populations diverged in terms of four of six leaf anatomy traits (relative thickness of tissue layers and stomatal density), as well as leaf size and shape, specific leaf area (SLA), leaf internode distances, disparity in blade–petiole angles, canopy spread : height ratios, standing leaf numbers, summer (July) photosynthetic light curve shapes, and growth rates. Saplings showed significant sun/shade differences in fewer characters: leaf thickness, SLA, leaf overlap, disparity in blade–petiole angles, standing leaf numbers, stem volume and branching angle (first-order branches only), and summer photosynthesis. In trees, leaf anatomy was insensitive to light environment, but leaf length, width, and SLA, disparities in blade–petiole angles, and summer maximal photosynthetic rates varied among sun and shade leaf populations. Seedling and sapling photosynthetic rates were significantly depressed in winter (December), while photosynthetic rates in tree leaves did not differ in winter and summer. Seasonal and ontogenetic changes in response to light environment are apparent at several levels of biological organization in *R. mangle*, within constraints of its architectural baüplan. Such variation has implications for models of stand carbon gain, and suggest that response flexibility may change with plant age.

**Key words:** anatomy; architecture; Belize; flexibility; light; ontogeny; photosynthesis; *Rhizophora*.

The red mangrove, *Rhizophora mangle* L., dominates neotropical mangrove forests, while globally, the genus *Rhizophora* comprises the majority of species, number and density of stems, net primary productivity and litter export from mangal (Hutchings and Saenger, 1985; Tomlinson, 1986; Saenger and Snedaker, 1993; Ricklefs and Latham, 1993; E. J. Farnsworth and A. M. Ellison, unpublished data). Uniquely among neotropical mangroves, *R. mangle* occupies a broad tidal gradient, from lowest low water (LLW), where it receives daily tidal inundation and high insolation, to highest high water (HHW), where shadier, dry, stagnant and/or occasionally hypersaline conditions may prevail. Mangroves such as *R. mangle* adjust their leaf morphology, photosynthetic rates, plant stature, and nutrient uptake in response to changing resource availability (Camilleri and Ribi, 1983; Tomlinson, 1986; Choong et al., 1992; Feller, 1995; Ball, 1996). The varied physiognomy of mangrove trees and forests, from tall riverine to dwarf scrub (Lugo and Snedaker, 1974; Lugo, 1980; Feller, 1995), reflects significant morphological and physiological flexibility across a range of coastal conditions, a flexibility that likely contributes to the predominance of this species. Because *R. mangle* embodies a broad continuum of responses across light, tidal, and nutrient environments, it is a promising model organism for studying trade-offs and functional links among modes of plasticity. Here, we comprehensively profile phenotypic flexibility of *R. mangle,* from the level of leaf anatomy through stem and whole-plant architecture, across changing light levels associated with a tidal gradient. We examine photosynthetic, growth, and mortality differences among populations. We quantify differences in the magnitude and type of flexibility shown by seedlings, saplings, and mature trees, asking which facets of plasticity change over ontogeny.

*Rhizophora mangle* defies heuristic categorization as "early or late-successional," "pioneer or mature-phase," or "light-demanding or shade-tolerant" (Tomlinson, 1986), designations that have been applied widely to other forest species (e.g., Bazzaz, 1979; Denslow, 1980; Brokaw, 1987; Canham, 1988; Swaine and Whitmore, 1988; King, 1994; Sipe and Bazzaz, 1994; Ackerly, 1996). In contrast to other neotropical mangrove species, *Rhizophora mangle* seedlings both can persist in a man-

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grove understory at low growth rates, and can grow rapidly when canopy gaps form (Ellison and Farnsworth, 1993). While the majority of studies have focused on differential mangrove responses to edaphic stressors, salinity, and nutrient availability (reviewed in Ball, 1996) to explain mangrove growth, and community zonation and dynamics, field light environments rarely have been explored as factors in mangrove performance (Smith, 1987, 1992; Ellison and Farnsworth, 1993; McKee, 1995).

The carbon costs to growth of increasing salt tolerance in mangroves (via conservative water use and high allocation to root biomass) have been well documented (Ball, 1988a, b; Ball, Cowan, and Farquhar, 1988). Hence, one might expect that mangroves would be constrained in their allocational, allometric, or growth responses to changing light resource environments, and might be more able to make leaf-level adjustments to light than to alter whole-plant architecture. Data are unavailable on how these carbon costs change through ontogeny, as plants accommodate changing water relations as they increase in stature and enter a high-light canopy, although an untested conceptual model of source–sink dynamics during mangrove growth exists (Gill and Tomlinson, 1971). We hypothesize that mangroves may become increasingly constrained in the breadth of their light responses as they mature.

Structure, display, and photosynthetic physiology of leaves vary within and among plants over integrated gradients of light, temperature, and water availability in functionally significant ways (Hanson, 1917; Björkman and Holmgren, 1963; Horn, 1971; Boardman, 1977; Mooney and Gulmon, 1979; Givnish, 1987, 1988; Reich, Walters, and Ellsworth, 1992), and change as leaves themselves age (Chabot and Hicks, 1982). Much less is known about characterstics of leaves, and larger modules change as whole plants mature. Distinctions are made between "seedling" and "adult" leaves mainly when dimorphism between seedlings and adults is obvious or dramatic (e.g., Stein and Fosket, 1969; Jones, 1995; Lawson and Poethig, 1995; Rich, Holbrook, and Luttinger, 1995). These phase changes are of interest from taxonomic and life history standpoints, and must be accounted for in developing models of carbon gain, leaf turnover, growth, and stand development. Studies from annuals demonstrate that both the nature and plasticity of characters may change over plant ontogeny (e.g., Parrish and Bazzaz, 1985; Coleman, McConnaughay, and Ackerly, 1994; Schmid and Bazzaz, 1994). However, most studies that quantify plasticity in woody plants focus on a single growing season (e.g., Comstock, Cooper, and Ehleringer, 1988; Harrington, Brown, and Reich, 1989) or age class (usually the critical seedling stage for mangroves, e.g., Naidoo, 1987; Ball, 1988a; Lin and Sternberg, 1992; McKee, 1995). Field studies have tended to quantify responses of mangrove *trees* to nutrients (Onuf, Teal and Valiela, 1977; Feller, 1995) or differences in sun–shade morphology of *saplings* (Turner et al., 1995) or shade tolerance of *seedlings* (Smith, 1987). Mature *Rhizophora* species are noted to exhibit high fidelity to Attim's architectural model (Tomlinson, 1986; Turner et al., 1995); are they capable of ontogenetic variations on a theme?

Clark and Clark (1992) point out that accurate classification of life history strategies of tropical trees demands an understanding of long-term tree development in a variety of microsites. Subtle differences in resource response breadth among seedlings, saplings, and trees can yield insight into the question of how a shaded juvenile can accommodate life as a canopy adult (Lei and Lechowicz, 1990), and how modular organisms age and senesce (Watkinson, 1992). Likewise, an understanding of the commonalities and disparities among life stages is prerequisite to extrapolating from experiments on seedlings to predict responses of adults or mixed-age stands to variables such as nutrient loading or climate change.

## MATERIALS AND METHODS

***Site description***—The study took place from 1 January 1992 until 1 June 1995. Observation of seedlings, saplings, and trees was centered on Wee Wee Cay, Belize, Central America (16°45′N, 88°08′W), a 2-ha mangrove-dominated island <1.5 m above sea level at its highest interior point. The island overlies a carbonate platform in the barrier reef lagoon complex of Belize; the mangal is primarily oligotrophic with no riverine nutrient input, and occupies tidal inundation class 1, a microtide (sensu J. G. Watson, in Tomlinson, 1986). The prevailing climate is tropical–subtropical transitional (Hartshorn et al., 1984), with a rainy, cool season October–January and hot, dry weather with intermittent storms prevailing the rest of the year. Typical of most cays in this lagoon (Fosberg et al., 1982; Stoddart, Fosberg, and Spellman, 1982), *R. mangle* predominates on both the fringe and interior of Wee Wee Cay.

At LLW, >100 scattered seedlings, saplings, and islets of trees occur on the shallow seaward seagrass bed. These individuals (hereafter referred to as the "sun" population) grow in full sun (summer PAR at noon exceeding 2300 $\mu mol \cdot m^{-2} \cdot s^{-1}$), and are inundated to ≈30 cm twice daily by tides. The substrate is Holocene peat overlain by sands and loose carbonate silts. The mangrove stand on the cay itself (at HHW) is a relatively even-aged canopy of ≈40-yr-old *R. mangle* trees, interspersed with less common *A germinans*, *L. racemosa*, and *Conocarpus erectus* L. (the stand is known to postdate hurricane Hazel, which cleared much of the island in October 1954; P. Shave, personal communication, Wee Wee Cay Marine Lab). "Shade" seedlings and saplings growing under the island canopy receive mean maximum noon PAR levels of 398 ± 14 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (SD, $N = 27$ measurements), and are inundated tidally to ≈15 cm twice daily. The substrate is a continuous layer of ≈5000 to 7000-yr-old to present-day organic peat, overlain by <5 cm deep layer of autochthonous sands and carbonate particles as in the LLW site.

Although tidal inundation levels vary between 15 and 30 cm, frequency of inundation, interstitial soil water salinities, and soil types do not change significantly across the 50-m lateral extent of this gradient. At this site, sun and shade populations overlap along presumptive tidal gradients, and no species transition indicative of major edaphic variation occurs within the boundaries of the study site. Because we focus on flexibility of aboveground architecture in this study, for conceptual simplicity we refer to the apparent environmental heterogeneity of this tidal gradient under the rubric of a "light" gradient. Our stated assumption is that PAR varies most in magnitude (ranging two orders of magnitude from shaded to sunny sites) of all abiotic parameters over this area. The objective of our mensurative study was to characterize, at a fine scale of resolution, mangrove flexibility across this small-scale gradient.

***Distinctions among ontogenetic stages***—Phenotypic criteria based on size and reproductive activity were used to classify individuals for study, as aging mangroves beyond the seedling phase is problematic (Duke and Pinzón, 1992). Naturally established cohorts of shaded *Rhizophora mangle* seedlings were distinguished by a lack of aerial roots and branching, and a visible hypocotyl showing no secondary lignification. Sun seedlings had been planted as leafless propagules in common gardens on the seaward fringe of Wee Wee Cay in July 1993 (see *Seedling growth,* below). Sun and shade seedling heights ranged between 15 and 70 cm. "Saplings" were defined as individuals >1 m tall, possessing at least one branch, one aerial root, and a lignified hypocotyl, and being not yet reproductive. Sun saplings were selected at random from a group that was monitored over 3 yr for growth and production (A. M. Ellison and E. J. Farnsworth, unpublished data). Shade saplings were found on the island fringe under adult trees. Trees were by definition >5 m tall, and had reproduced at least once.

Within seedling and sapling stages, comparisons of leaf anatomy, morphology, architecture, and growth were made between sun and shade individuals. Due to the even-aged nature of the Wee Wee stand, all mature trees identified had some portion of their branches in the canopy, or facing to seaward. Thus, a distinction between sun and shade environments was plausible only for modules, not for whole trees.

***Leaf anatomy***—One young (first leaf pair) and one old (third leaf pair) leaf from each of three seedlings, saplings, and trees in sun and shade ($N$ = 36 leaves total) were collected in May 1995, for anatomical analysis. Specimens were fixed immediately in formalin-glacial acetic acid-alcohol (FAA). Five-millimetre long freehand cross sections were taken from each leaf midsection, beginning >3 mm from the midvein and extending toward the leaf margin. Unstained sections in which leaf anatomy was clearly visible were placed on slides with a layer of Cargill Type B immersion oil, and photographed at 100× magnification using a Nikon F-35 mm camera (Nikon, New York, NY) mounted on a Nikon inverted compound microscope. We measured total leaf thickness, and relative thicknesses of the cuticle, upper epidermal layer, hypodermal layer, palisade layer, and spongy mesophyll (including two-cell-layer lower epidermis; Tomlinson, 1986; Feller, 1996). We also counted the number of stomata in a 1-mm$^2$ grid placed on the ventral side of the leaf.

***Macroscopic leaf characters***—Leaves were collected from sun and shade seedlings, saplings, and tree branches in July 1993. Sample sizes were contingent on the numbers of leaves on individuals or branches destructively harvested for cluster architecture measurements (see below). Leaves were promptly measured in situ for length (±1 mm), width (±1 mm), thickness (±0.1 mm), petiole length (±1 mm), two orthogonal petiole widths (±0.1 mm), leaf wet mass (±0.01 g), and petiole wet mass (±0.01 g). Leaf-pair number was noted, as an index of age, for each leaf. The absence of drying facilities at this remote field site precluded direct wet-to-dry mass conversions on this leaf material. In order to derive estimates of dry biomass from wet masses, separate samples of 100 leaves in each of six categories, sun/shade seedling/sapling/tree leaves, were collected in March 1994. These leaves were weighed immediately after collection, then transported within 24 h to the United States, where they were oven-dried to constant mass at 70°C for 1 wk, and subsequently weighed. Linear regressions of dry mass on wet mass were then derived separately for the six types of leaves. Slopes ranged from 0.193 to 0.361, and $0.762 \leq r^2 \leq 0.985$. Leaf area was measured using a LI-COR 3100 leaf area meter (LI-COR, Lincoln, NE), and regressions made of actual leaf area on an elliptical area estimated from length and width measurements of leaves ($r^2$ = 0.738).

***Leaf display and cluster architecture***—*Rhizophora mangle* seedlings and main stems of saplings and trees produce orthotropic (vertical axis) shoots with terminal clusters of opposite leaves with a radial phyllotaxy; leaf scars are easily counted as an index of leaf turnover. Side branches of trees can assume a horizontal (plagiotropic) position. Seedlings by definition possessed a single cluster. During summer 1993, 20 sun and 20 shade seedlings were randomly chosen and examined nondestructively; all leaf lengths, widths, petiole lengths, and leaf angles with respect to horizontal were measured. Internode distances between leaf pairs were also quantified, with internodes numbered consecutively from the hypocotyl (seedlings) or beginning of twig (saplings and trees), distally to the cluster tip. The same data were taken on two canopy margin ("outer") and two interior ("inner") clusters on each of ten sun saplings, as well as two outer clusters of ten shade saplings (inner clusters did not exist on shade saplings). Likewise, on eight trees, four clusters per tree were characterized. one inner and one outer each from two heights: 2.5 m and <0.5 m above the ground. Cardinal orientation of each twig (degrees from north) was also noted. Overhead photographs were taken (using a 55-mm micro lens) of six total clusters on each of six seedlings, saplings, and trees, in shade and sun. Photographs were later digitized with a PC-Vision+ frame-grabber (Imaging Technologies, Cambridge, MA), and analyzed using IMAGE (Rich, Ranken, and George, 1989), to measure leaf overlap as an index of leaf display efficiency.

***Branch architecture***—Five sun seedlings, five sun saplings, and five tree branches were harvested to determine fresh masses of tissues. Fine roots could not be reliably excavated during this harvest, so only aboveground prop roots were taken along with shoots. Five shade saplings and five shade seedlings similarly were measured nondestructively, but could not be harvested. Order (beginning with main stem as order 0), angle with respect to vertical, orientation, length, top and basal orthogonal diameters, number of leaves per branch, leaf mass per branch, and stem mass of each branch were recorded on each branch as the individuals were dismantled. For each prop root encountered (saplings only) root length, basal and top orthogonal diameters, angle with respect to vertical, and mass were measured. The bifurcation ratio of saplings and tree branches, an index of branching frequency known to vary intraspecifically across light environments (Steingraeber, Kascht, and Franck, 1979; Turner et al., 1995), were calculated according to Motomura (1947).

***Canopy display and height relationships***—The widths of the canopy (±1 cm) in N–S and E–W positions were measured on five sun and shade seedlings and saplings, and projected ground area estimated for five trees. Heights of these seedlings and saplings (in metres) were measured with a metre tape; tree heights were calculated trigonometrically using a clinometer.

***Photosynthesis***—Light-assimilation curves were assembled over a series of cloudless days in June 1993, for leaves on sun and shade seedlings ($N$ = 4 each), saplings ($N$ = 4), and tree branches ($N$ = 3). One young (first pair) and one old (third pair) fully expanded leaf were chosen per plant, except on trees, where young and old leaves from both high and low clusters (as defined above) were measured. A LICOR 6200 photosynthesis system (LI-COR, Lincoln, NE) fitted with a 1-L cuvette was used to measure photosynthesis. To construct the light curve in the field, photosynthetic rate at full sun was first measured on each seedling, sapling, and tree leaf. A 1.5 × 1.5 × 1.5 m PVC frame covered with neutral-shade mesh was then placed over each seedling or sapling. We remeasured photosynthesis on the same leaf after the plant had acclimated under the shade frame for 10 min. This procedure was repeated six times, with six successive layers of shade cloth placed over the frame. Each layer reduced light to the whole plant by ≈300 $\mu mol \cdot m^{-2} \cdot s^{-1}$, and photosynthetically active radiation (PAR) under full shading was <50 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Because whole trees could not fit under the frame, tree leaves were shaded using a 0.5 × 0.5 m PVC quadrat fitted with successive layers of shade cloth, which we held over the leaf to achieve the same incident light attenuation as we had with seedlings and saplings. Leaves were marked with a numbered plastic parakeet band (National Band and Tag Company, Lexington, KY) around the petiole.

In January 1994 (6 mo later), previously tagged leaves were relocated in the field (reported sample sizes reflect some intervening leaf abscission). Because of winter overcast, we used a portable lamp to provide PAR well above saturating levels (>1 000 $\mu mol \cdot m^{-2} \cdot s^{-1}$) to the leaf,

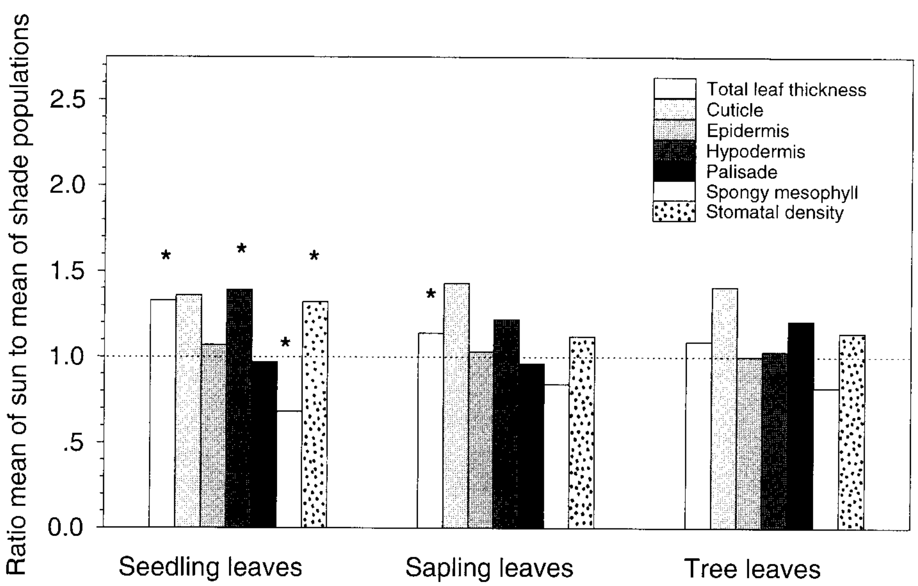

Fig. 1. Leaf anatomy differences across life forms, in sun and shade, determined from inspection of freehand sections. Bars are the ratios of the mean value of sun populations over the mean of the shade population. Ratios of total leaf thickness; percentage of total leaf thickness in cuticle, upper epidermis, hypodermis, palisade layer, and spongy mesophyll; and stomata (no./mm$^2$) are shown.

which was allowed to acclimate for ≥10 min. Maximum net photosynthesis was then measured using the LI-COR 6200.

***Seedling growth***—A comparative study of whole-organism growth in sun and shade was possible only for *R. mangle* seedlings during the study period. Strictly shade trees, as mentioned before, were unavailable. Unlike sun saplings, which were abundant, shade saplings were rare in the understory at Wee Wee Cay; sample sizes were adequate for architectural surveys, but were insufficient, given mortality, for long-term monitoring. Thus, seedlings planted in full sun and found growing in understory shade were selected for study.

In June 1992, 540 mature, undamaged propagules of *R. mangle* were collected from trees at several nearby cays. These propagules were weighed, their lengths were measured, and the sample divided into six subsamples to equalize mean initial sizes. The same day, we planted the propagules by inserting the base of the hypocotyl 4 cm deep into the substrate. Three common gardens of 90 *R. mangle* propagules each were established on the northwest side of Wee Wee Cay, in full sun. Three replicate gardens were established in similar wind, water depth, and insolation conditions at Norvall Cay (16°43′N, 88°10′W), 5 km south of Wee Wee Cay. Gardens were fenced with 0.5 m high, 2-cm mesh hardware cloth, which protected the stands from floating debris but did not exclude crabs or other herbivores. At 10 dates over 722 d, height (to base of terminal growing tip), number of leaves and leaf scars were measured on all seedlings.

In December 1992, 50 *R. mangle* seedlings growing naturally in the understory at Wee Wee Cay were located and labelled with numbered plastic bird bands. The Wee Wee cohort consisted of newly recruited seedlings with ≥1 leaf pair but no leaf scars. Three additional populations of shade seedlings, one at Spruce Cay (16°43′N, 88°09′W) and two at Twin Cays (16°48′N, 88°05′W), similarly had been under observation since January 1992. These populations contained seedlings of comparable age, but differed from each other in mean seedling age (estimated as proportional to leaf scars; Duke and Pinzón, 1992). At 11 dates over 867 d (and seven dates over 507 d for the Wee Wee cohort), growth and survivorship were measured as above on all seedlings.

## RESULTS

***Leaf anatomy***—Sun and shade leaves differed in absolute thickness, and in relative allocation to cuticle, epidermal, hypodermal, palisade, and spongy mesophyll tissues. The magnitude of these differences varied among mangrove life stages (Fig. 1). Only the relative (percentage of total leaf) thickness of the palisade layer was insensitive to light environment among seedlings, saplings, and trees. Leaf pair, as an index of leaf age, was used as a covariate in analysis of covariance (ANCOVA) models comparing sun and shade populations at each ontogenetic stage. Sun seedlings had significantly thicker leaves ($F_{1,9}$ = 16.218 (for sun/shade factor), $P$ = 0.003), as well as thicker hypodermal layers ($F_{1,9}$ = 11.420, $P$ = 0.008), but thinner spongy mesophyll layers ($F_{1,9}$ = 15.435, $P$ = 0.003). Stomatal density was also significantly greater among sun seedlings ($F_{1,9}$ = 16.266, $P$ = 0.003). ANCOVA models with light level (sun/shade) as a main effect and leaf pair as a covariate explained 65-90% of the variance in anatomical characters among seedling leaves. Leaf pair was a significant covariate only in explaining total leaf thickness of seedlings ($F_{1,9}$ = 63.876, $P$ < 0.0001) and saplings ($F_{1,9}$ = 83.718, $P$ < 0.0001). The only sun sapling leaf trait that differed significantly among light environments was overall thickness ($F_{1,9}$ = 11.500, $P$ = 0.008), and tree leaves showed no significant sun/shade differences.

***Macroscopic leaf characters***—Sun and shade mangrove leaves differed in length, area, petiole length, and estimated specific leaf area (Fig. 2). Many of these characters differed among leaf-pairs. For example, older leaves, among the first original leaves in new clusters (or the initial seedling leaves), were smaller than more recent sets of leaves, and often exhibited the lowest specific leaf areas. Shaded saplings and trees generally carried fewer standing leaf numbers (leaf pairs) per cluster than sun individuals (Fig. 2).

Sun/shade differences within a plant ontogenetic stage were investigated with ANCOVA, again using leaf pair as a covariate. Leaves of shade seedlings were signifi-

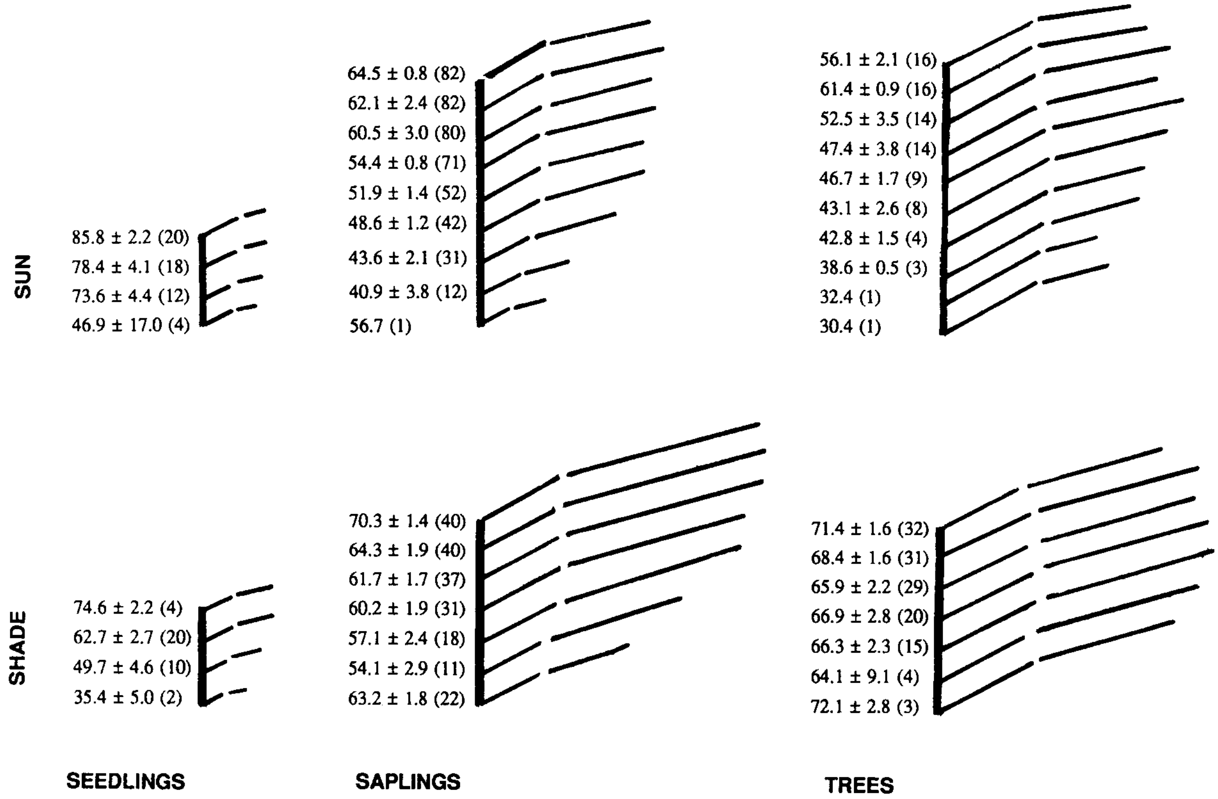

Fig. 2. Schematic diagram of macroscopic leaf characters, comparing sun (top row) and shade (bottom row) populations among age classes (columns). Vertical line represents cluster stem, with young (first pair) leaves at the top and progressively older leaf pairs to the bottom. Broken lines represent petioles (left, attached to stem) and leaves (right). Illustrated lengths of petioles are proportional (in mm) to mean petiole length (in cm). Illustrated lengths of leaves are proportional (in mm) to mean area (in cm$^2$) of leaves. Values to left of stem are mean (±1 SE) of specific leaf area (cm$^2$/g).

cantly heavier $(F_{1,105}) = 13.107$, $P < 0.0001$), longer ($F_{1,105} = 17.683$, $P < 0.0001$), but had shorter petioles ($F_{1,105} = 27.618$, $P < 0.0001$) than leaves of sun seedlings (Fig. 2). Shaded sapling leaves also were significantly longer ($F_{1,630} = 155{,}315$, $P < 0.0001$) and heavier ($F_{1,630} = 276.240$, $P < 0.0001$), but were borne on longer petioles ($F_{1,630} = 131.822$, $P < 0.0001$) than high-light sapling leaves. Shade leaves on trees were also significantly longer ($F_{2,309} = 28.688$, $P < 0.0001$) and heavier ($F_{2,309} = 9.449$, $P < 0.0001$), but petiole lengths of sun and shade leaves did not differ significantly.

Specific leaf area (SLA, ±0.1 cm$^2$/g) was the quotient of estimated leaf area and leaf dry mass based on wet mass/dry mass regressions. SLA of seedlings, saplings, and trees differed significantly between light environments ($8.591 \leq F \leq 163.124$, $P < 0.0001$, sun/shade comparisons within each ontogenetic stage [Fig. 2]). Shade leaves of saplings and trees showed larger areal spread per unit leaf mass than sun leaves, but leaves of shade seedlings had lower SLA values. Although leaf width scaled linearly with leaf length (Fig. 3), width did not vary as much as length. Thus, leaf elongation contributed most to differences in absolute leaf area between sun and shade populations.

Among plant stage classes, allometric changes in leaf characters were also apparent (Fig. 2). Leaves of sun seedlings were consistently the smallest in terms of

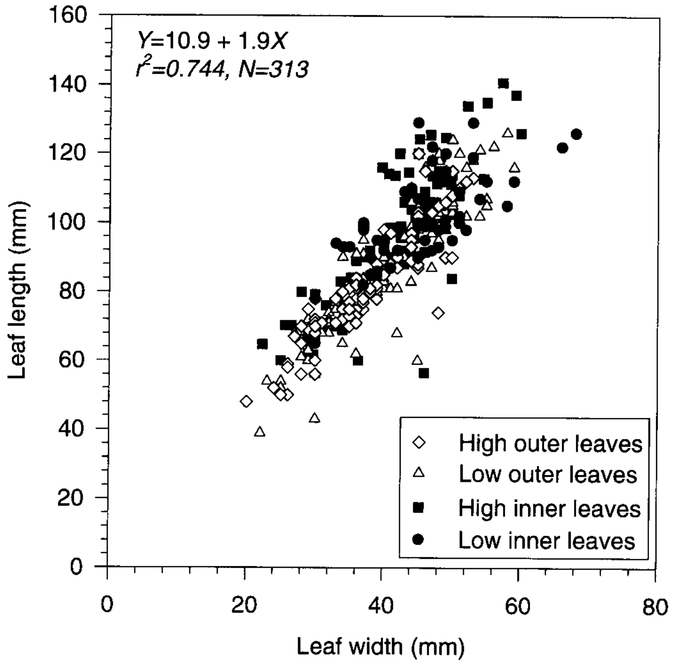

Fig. 3. Leaf length by width relationships among sun (clear symbols) and shade (filled symbols) leaves of trees, illustrating the wide range of leaf sizes within a single site.

TABLE 1. Comparisons of leaf display traits in sun and shade, across plant age groups. Blade–petiole angle is the mean difference between blade and petiole angle within a leaf, ± 1 SD (sample size in parentheses). *F* statistic and probabilities in column 3 are from ANCOVA performed on untransformed values, with light environment as main (fixed) factor and leaf pair as covariate, within a plant stage class. Leaf overlap is the percent of total potential leaf area lost due to area overlap. Values of *F* and *P* are from ANCOVA with light environment as main factor and total number of leaves in a cluster as a covariate.

| Leaf type | Blade–petiole angles | *F*, *P* | Leaf overlap (%) | *F*, *P* |
|---|---|---|---|---|
| Sun tree leaves | 9.6 ± 6.3 (65) | 13.11, 0.0001 | 12.5 ± 7.1 (6) | 0.034, 0.858 |
| Shade tree leaves | 15.9 ± 5.9 (51) | | 12.7 ± 3.7 (6) | |
| Sun sapling leaves | 9.5 ± 5.7 (142) | 7.68, 0.006 | 19.9 ± 10.8 (6) | 9.41, 0.01 |
| Shade sapling leaves | 12.2 ± 8.9 (77) | | 7.7 ± 4.7 (6) | |
| Sun seedling leaves | 6.3 ± 3.9 (62) | 17.47, 0.0001 | 8.3 ± 5.4 (6) | 0.19, 0.675 |
| Shade seedling leaves | 10.2 ± 6.7 (48) | | 4.0 ± 5.6 (6) | |

length, width, and petiole length and diameter when compared to sun leaves of saplings and trees (ANCOVAs with life stage and leaf pair as factors, followed by Tukey's HSD for posthoc multiple comparisons to distinguish life stage differences, $P < 0.0001$ all Bonferroni-adjusted pairwise comparison probabilities). Saplings showed the largest leaf length, width, petiole length, and leaf wet masses (shade leaves), and the highest magnitude differences in these characters between leaves on sun and shade individuals. Tree leaves were intermediate in these traits, but more closely resembled sapling leaves than seedling leaves (Fig. 2). Seedlings, saplings, and trees all differed significantly from each other within each light category with respect to leaf and petiole length and leaf mass. For sun populations, leaf age also explained a significant proportion of variance in these traits; shade leaves, however, varied less with leaf age.

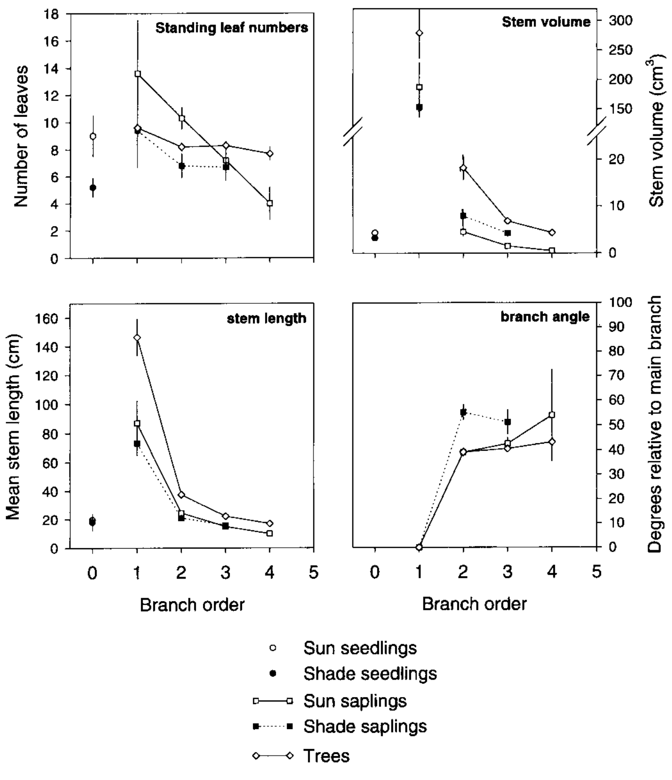

Fig. 4. Variation in branch-level architectural traits with branch order, comparing age classes. Circular symbols are seedling means (error bars are ±1 SD), with branch order = 0 only, by definition (see *Methods: Distinctions among age classes*). Squares are sapling means (to branch order = 2 in shade populations, branch order = 3 in sun populations). Only "sun" trees were available for harvesting (diamond symbols, to branching order = 4). Stem volume was calculated as the volume of a truncated cone. Branch angles are in degrees from absolute vertical.

***Leaf display and cluster architecture***—Leaf pair internode lengths converged acropetally on 0.5 cm in both low- and high-light sapling and tree clusters, and leaf pairs were equivalently spaced among the populations. The mean distance between the top of the hypocotyl and the first node (original leaf pair) was longer in shade seedlings (7.7 ± 2.2 cm [SD], $N = 20$) than in sun seedlings (5.5 ± 2.2 cm), indicating some etiolation early in growth. However, internodal growth thereafter declined more rapidly in shade seedlings (e.g., 1.3 ± 0.8 cm distance between nodes 2 and 3) than sun seedlings (4.5 ± 1.8 cm; *t* test, $P < 0.0001$, 34 df at this node).

Both seedling leaf blades and petioles were more horizontal in shade, and more vertical in sun. Sun/shade differences in mean absolute petiole and blade angles were significant only for seedlings (ANCOVA with light environment and leaf pair as factors, $F_{1,116} = 241.79$; $P < 0.0001$). Within a single leaf, however, blade angles tended to differ from petiole angles by 5° or more. The magnitude of this difference provided a measure of leaf horizontality relative to the petiole angle. In all plant stages, shaded leaf blades exhibited a higher blade/petiole angular disparity; that is, they were significantly more horizontal relative to petioles (Table 1).

Likewise, opposite leaves within a pair were asymmetric with respect to mean petiole and blade angles as well as blade lengths, indicating potential intracluster adjustments of leaf position. However, the magnitudes of blade angle and length asymmetries did not differ among light environments for any plant stage. Percentage leaf overlap was consistently lower in shaded clusters in all plant stages, but only significantly so in saplings (Table 1).

***Branching architecture***—Seedlings, saplings, and tree branches showed architectural differences among both light environments and ontogenic phases (Fig. 4). Comparing standing leaf numbers, stem length, and stem volume, seedlings resembled second- or third-order twigs of saplings and trees. Only a difference in standing leaf number attributable to light level was discernible among seedlings (ANOVA, light as main effect, $F_{1,8} = 19.514$; $P = 0.002$; cf. Figs. 2, 4). Sapling branches exhibited

TABLE 2. Canopy traits of sun/shade seedlings, saplings and trees ($N = 5$ for all classes surveyed). Spread was measured across two orthogonal diameters of the canopy using a meter tape, which were then averaged. Canopy area was estimated as the area of an ellipse from the two spread values. Shown are means ± SD for all variables. Values with different superscripted letters show significant sun/shade differences by ANOVA ($P < 0.008$, Bonferroni-adjusted probabilities for tablewide comparisons). Values with different superscripted roman numerals show significant differences among sun populations of age classes (seedlings, saplings, and trees); arabic numerals refer to differences among shade (seedlings and saplings only) populations. Different superscripted upper case letters indicate significant differences among sun and shade populations within the seedling stage class; different superscripted lowercase letters indicate significant differences among sun and shade populations within the sapling stage class.

| Plant type | Height (cm) | Spread (cm) | Spread : height | Area : height |
|---|---|---|---|---|
| Sun trees | 820.6 ± 154.1 | 392.0 ± 51.0 | $0.48 \pm 0.1^{\mathrm{I}}$ | $152.3 \pm 72.8^{\mathrm{I}}$ |
| Sun saplings | 85.2 ± 21.5 | 63.5 ± 13.3 | $0.75 \pm 0.1^{\mathrm{a,II}}$ | $36.3 \pm 10.4^{\mathrm{a,II}}$ |
| Shade saplings | 113.4 ± 15.4 | 87.7 ± 15.7 | $0.77 \pm 0.1^{\mathrm{a,1}}$ | $52.5 \pm 14.2^{\mathrm{a,1}}$ |
| Sun seedlings | 49.6 ± 3.9 | 10.4 ± 2.3 | $0.21 \pm 0.04^{\mathrm{A,III}}$ | $1.7 \pm 0.7^{\mathrm{A,III}}$ |
| Shade seedlings | 40.9 ± 6.4 | 15.6 ± 1.9 | $0.38 \pm 0.1^{\mathrm{B,2}}$ | $4.8 \pm 0.7^{\mathrm{B,2}}$ |

significant sun/shade differences for standing leaf numbers ($F_{1,47} = 7.614$, $P = 0.008$), stem volume ($F_{1,47} = 4.492$, $P = 0.039$), and mean branch angle ($F_{1,47} = 24.510$, $P < 0.0001$) only for first-order branches initiated directly off the main stem (Fig. 4). Higher order twigs converged on the same architecture regardless of light environment. Low-order tree branches originating off the main trunk occupied mosaics of sun and shade, and were not differentiated operationally into sun vs. shade categories. These large, main branches bore higher numbers of leaves than sapling or seedling main stems (Fig. 4). Stem length, volume, and branching angle of terminal twigs converged on those of sun saplings (Fig. 4).

Bifurcation ratios of sun and shade saplings and trees were 2.46 (±0.36 SD, $N = 5$), 2.50 (±0.20), and 2.26 (±0.25), respectively. These values did not differ among groups.

All five high-light saplings surveyed possessed prop roots, while only three of five shade saplings had prop roots. Mean numbers of prop roots per plant and mean total prop root mass per plant (estimated from regression of volume on mass for shade roots) were slightly, but not significantly higher in sun saplings than shade saplings (data not shown). Prop roots of shaded saplings tended to be longer ($F_{1,23} = 7.743$, $P = 0.011$) but not heavier, than roots of sun saplings.

***Canopy display and height relationships***—At the whole-organism level, canopy architecture varied among the three plant stages, and, among seedlings only, between light environments (Table 2). The area of canopy area supported by a given height of trunk increased 10- to 20-fold from the seedling to sapling stage. Trees had smaller than expected canopies for this level of expansion: canopy area to height ratios were only 3–5 times larger than sapling relative canopy areas. The ratio of average canopy width to stem height was similarly smallest for seedlings, largest for saplings, and intermediate in trees. Consequently, both spread-to-height and area-to-height ratios differed significantly among all stage classes, tested separately within sun and shade (Table 2). Seedlings growing in full sun showed significantly lower canopy spreads, canopy spread-to-height ratios, and canopy areas than shaded seedlings (Table 2). Saplings, in contrast, showed no significant canopy to height adjustments between light environments: both spread and height were slightly larger among high-light saplings.

***Photosynthesis***—Shade leaves showed consistently lower photosynthetic rates than sun leaves across all plant stages, but the magnitude of sun/shade differences varied among age classes (Fig. 5). The data for sun and shade leaves within each plant stage class were fitted to the monomolecular function of Causton and Dale (1990):

$$y = a(1-e^{(b-cx)}),$$

where $y$ is net assimilation rate (±0.1 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$), $x$ is the ambient photosynthetically active radiation incident on the leaf (±0.1 μmol photons$\cdot m^{-2} \cdot s^{-1}$), and $a$, $b$, and $c$ are constants. The rectangular hyperbolic function, $y = ax/(b + x)$, was also tested (Causton and Dale, 1990), but did not yield an improved fit. The NONLIN procedure of SYSTAT was employed to estimate constants, which were then used to calculate asymptotic maximal photosynthetic rate ($a$), light compensation point ($b/c$), and quantum efficiency ($ace^{b}$). Estimated maximal photosynthetic rates were highest in leaves of sun seedlings and lowest in leaves of shade seedlings (Table 3). Sapling leaves showed intermediate values of photosynthetic rates, with intermediate sun/shade differences between curves. Tree leaves showed the lowest photosynthetic rates overall, and the smallest sun/shade differences. Shade leaves of saplings and seedlings exhibited lower light compensation points, while shade leaves of trees and seedlings showed higher quantum efficiency values than their high-light counterparts (Table 3).

The effect of leaf age on photosynthetic rate ($a$) was explored for subpopulations of sun and shade leaves separately. Old (third leaf pair) leaves showed lower values of maximal photosynthesis than young (first leaf pair) leaves, across all plant stages, although differences were only significant, by nonoverlap of 95% confidence intervals, in sun seedlings and saplings. Seedlings showed greater disparities in photosynthesis attributable to leaf age than sapling (range 14.6–18.1 for young seedling leaves, 9.6–11.5 for old seedling leaves; range 11.3–13.7 for young sapling leaves, 9.1–10.7 for old sapling leaves). Shade leaves showed no discernible age-related differences in maximal photosynthesis.

Rates of $P_{\max}$ in December 1994 were substantially lower than in summer among seedlings and saplings, al-

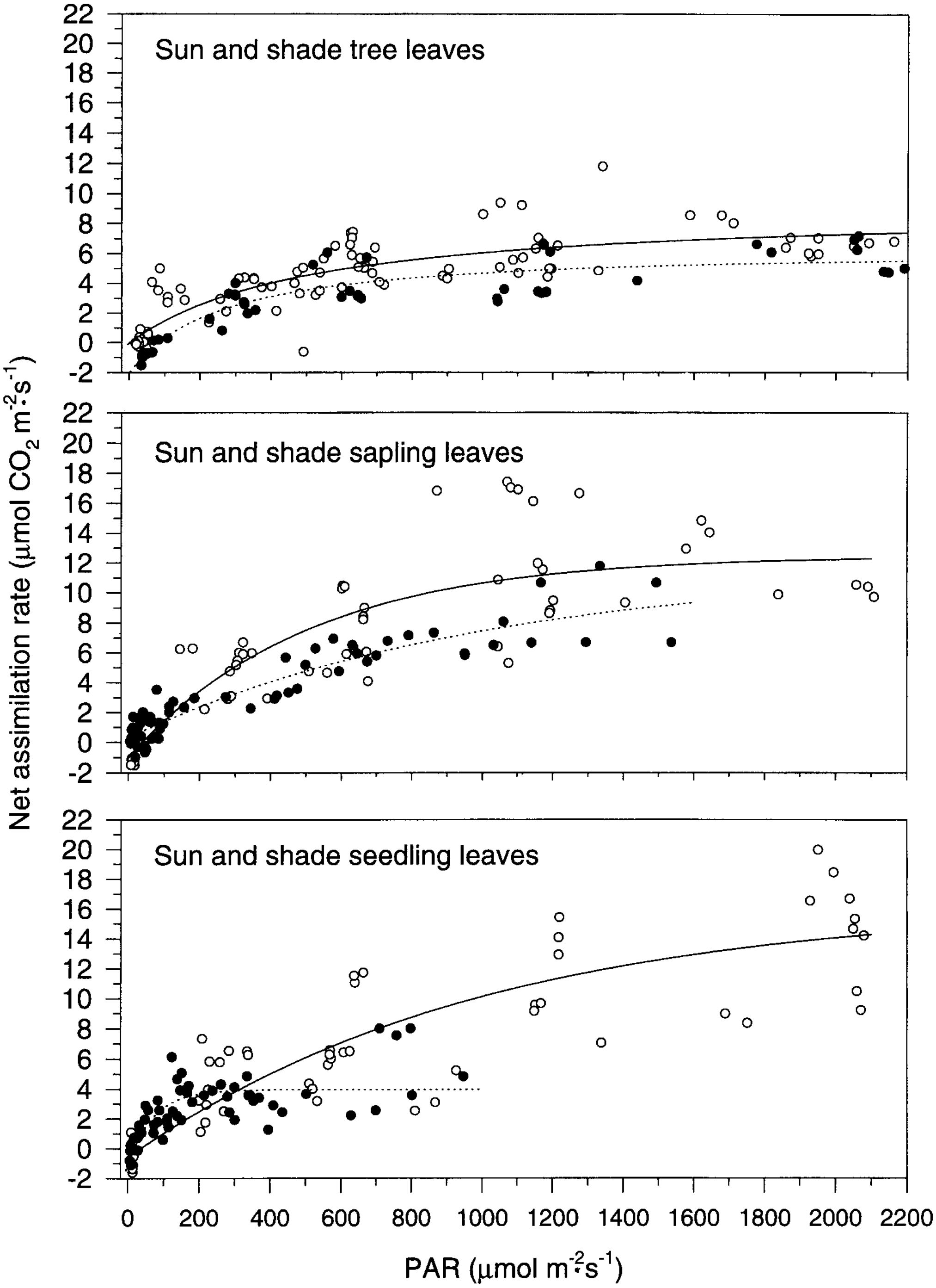

Fig. 5. Photosynthetic light curves determined in summer 1993 for seedlings, saplings, and trees, contrasting sun (open symbols) and shade (filled symbols) leaves; all leaf ages are shown. Solid lines are the best fit curve calculated from the monomolecular function of Causton and Dale (1990) for sun leaves; dashed lines were similarly calculated for shade leaves

though tree leaves maintained comparable rates between seasons (Table 3). No significant differences in $P_{max}$ were found among sun and shade leaves, or plant age cohorts (high-light leaves only considered).

***Seedling growth and mortality***—*Rhizophora mangle* seedlings growing in the full-sun gardens at Wee Wee Cay grew faster, were taller, and carried more standing leaves than the comparably aged, shaded Wee Wee cohort. The full-sun population showed spurts of stem elongation between August and December 1992 and 1993. These accelerations were not as apparent in terms of height growth in the shaded populations, although patterns of leaf flushing paralleled dynamics in sun (Fig. 6). Relative growth rates between August and December 1993 were calculated as:

TABLE 3. Estimates of mangrove photosynthetic parameters using the monomolecular function of Causton and Dale (1990). Estimates of constants are derived from light curves on field plants, pooling young (first pair) and old (third pair) leaves. The parameter "$a$" estimates the asymptotic maximal assimilation rate (equivalent to $P_{max}$); $b/c$ estimates the light compensation point (light level needed to boost photosynthetic rate above 0), and $ace^b$ estimates the photochemical efficiency of leaf light response (slope of curve at PAR = 0). All populations show significantly different $P_{max}$ by nonoverlap of 95% confidence intervals about "$a$." Winter maximal photosynthetic rates (Winter $P_{max}$) were measured on available leaves of sun/shade seedlings, saplings and trees in December 1994, with ambient PAR boosted to >1 100 μmol m²/sec with a hand-held lamp. Means (SE) are presented of three measurements per individual across $N$ individuals per light × age class.

| Leaf type | $a$ | $b$ | $c$ | $r^2$ | $b/c$ | $ace^b$ | Winter $P_{max}$ | SE | $N$ |
|---|---|---|---|---|---|---|---|---|---|
| Sun tree | 7.5 | 0.045 | 0.002 | 0.689 | 22.5 | 0.016 | 7.49 | 0.77 | 13 |
| Shade tree | 5.3 | 0.245 | 0.003 | 0.774 | 81.7 | 0.020 | 7.63 | 0.48 | 8 |
| Sun sapling | 12.5 | 0.076 | 0.002 | 0.711 | 38.0 | 0.027 | 6.79 | 0.65 | 18 |
| Shade sapling | 8.8 | 0.030 | 0.001 | 0.869 | 30.0 | 0.010 | 6.13 | 0.43 | 24 |
| Sun seedling | 16.4 | 0.036 | 0.001 | 0.759 | 36.0 | 0.017 | 7.05 | 1.49 | 6 |
| Shade seedling | 3.9 | 0.242 | 0.014 | 0.551 | 17.3 | 0.071 | N.A. | N.A. | 0 |

$$(\ln H_2 - \ln H_1)/(t_2 - t_1),$$

where $H_1$ and $H_2$ are the plant height at August ($t_1$) and December ($t_2$), respectively, and significantly differed between sun and shade populations ($F_{1,68} = 14.821$, $P < 0.0001$). Growth of sun seedlings at Norvall Cay showed the same dynamics as the Wee Wee gardens, and shaded populations at Twin and Spruce Cays paralleled those of the shaded Wee Wee set, despite different starting sizes and apparent ages of cohorts (Fig. 6).

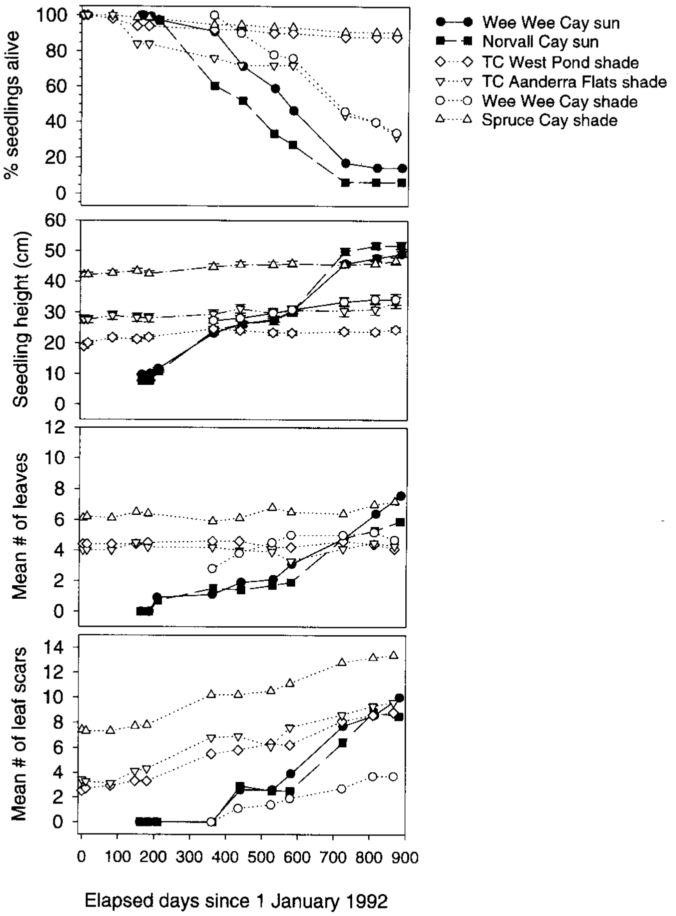

Fig. 6. Survivorship curves and dynamics of growth, leaf production, and turnover of *Rhizophora mangle* seedlings followed at six sites for >700 d. Filled symbols are sun sites (Wee Wee Cay and Norvall Cay common gardens), open symbols are shade sites (naturally occurring populations at Spruce Cay, Wee Wee Cay and Twin Cays).

Mortality of full-sun seedlings was higher over the period than that of shade seedlings (Fig. 6). The Mantel-Haenszel log-rank test for censored survivorship data was used to discern differences in survivorship dynamics (S-Plus for Windows, version 3.2, StatSci, Seattle, WA). Considering Wee Wee Cay populations only, the sun cohort showed a significantly steeper decline in survivorship than the shade cohort ($\chi^2 = 35.5$, $P < 0.0001$).

## DISCUSSION

We have investigated two main issues with respect to sun-shade flexibility in *Rhizophora mangle* leaves: (1) traits at multiple levels of biological organization that differ among light environments, with possible functional linkages among these traits; and (2) changes in the magnitude and type of sun–shade flexibility shown over ontogeny, from seedling to sapling and mature-tree phases. Photosynthetically active light level, the predominant variable changing along the small distance interval and minimal tidal gradient examined in this study, explained much of the variance in leaf anatomy, stomatal density, leaf size and shape, photosynthetic rate, and module architecture in these mangroves. "Light" itself encompasses changes in local air temperature, humidity, and vapor pressure deficits around the leaf boundary layer (Ball, Cowan, and Farquhar, 1988). It is as yet unknown to which aspects of incident radiation *R. mangle* is maximally sensitive. As *R. mangle* shows characteristics of both "early" and "late" successional species (Tomlinson, 1986), and may occupy a range of light environments over its lifetime, we hypothesized that this mangrove would exhibit moderate sun–shade flexibility, within the potential constraints of its architectural model and its need to maintain conservative water use over ontogeny (Ball, 1996) in a coastal environment that poses multiple stresses (Mooney, Winner, and Pell, 1991).

The importance of light to the survivorship and growth of mangroves has received comparatively little attention compared to other environmental factors (Smith, 1987; Ellison and Farnsworth, 1993; McKee, 1995; Turner et al., 1995). McKee (1995) noted that greenhouse-grown *R. mangle* seedlings showed comparatively small responses of biomass allocation, relative growth rate, and module production to short-term light enhancements simulating a small gap environment, relative to increases exhibited by seedlings of other neotropical mangrove species, *Avicennia germinans* (L.) Stearn and *Laguncularia racemosa* (L.) Gaertn. f. However, across a light gradient in the field ranging from shade (400 μmol photons $\cdot m^{-2} \cdot s^{-1}$) to full sun (2 300 μmol photons$\cdot m^{-2} \cdot s^{-1}$), *R. mangle* shows considerable morphological and growth flexibility, persists across a broader range of light levels than the other two species, and responds opportunistically to larger canopy gap formation (Ellison and Farnsworth, 1993), while *A. germinans* and *L. racemosa,* by contrast, are comparatively intolerant of extremes in light availability (McKee and Feller, 1994), possibly reflecting high vulnerability to photoinhibition (Cheeseman, 1994). Such apparent broad tolerance may contribute to the wider niche breadth (sensu Garbutt and Bazzaz, 1987) of *R. mangle* across neotropical tidal gradients. Manipulative field studies are required to assess the utility for light capture of these structural and allometric modifications on the part of mangroves (e.g., Ball, Cowan, and Farquhar, 1988). Such studies should: (1) experimentally separate light effects from other edaphic and biotic factors across a tidal gradient; (2) provide data on canopy architecture and growth for trees or shade saplings; and (3) incorporate belowground roots into models of whole-tree architecture and production.

In our survey, structural differences in many traits were observed in different light environments. At the leaf anatomical level, total foliar thickness was higher in leaves of sun plants; thickening of the hypodermal layer, and, to a lesser extent the cuticle, contributed to this increase (Fig. 1). Increases in leaf thickness frequently have been noted in sun leaves of other species (Hanson, 1917; Givnish, 1988). In mangroves, the appearance of such schleromorphic leaf traits has also been correlated with increases in salinity (Camilleri and Ribi, 1983) and decreases in water availability (Hutchings and Saenger, 1985), suggesting that plasticity of allocation to the hypodermal layer may function as a mechanism for foliar water storage, succulence, or osmotic regulation (Tomlinson, 1986). Feller (1996) noted that nutrient phosphorus additions reduced leaf hypodermal layer thickness and schleromorphy independent of leaf water or sodium content; thus, the precise functions of hypodermal plasticity are likely complex. Likewise, we found no consistent relationship between leaf water content and leaf light environment (E. J. Farnsworth and A. M. Ellison, unpublished data). Shade leaves were generally heavier, larger (Fig. 2), and longer (Fig. 3) than sun leaves, and showed higher SLA (Fig. 2) than sun leaves, but petiole length did not change in consistent ways across light environments (Fig. 2). For certain foliar traits, we found that variability among light environments and ontogenetic phases within a single swamp could equal or exceed that found across many swamps or degrees of latitude. For example, our measurements of leaf lengths and widths from trees alone (Fig. 3) yielded a range of values comparable to that reported by Cintrón, Lugo, and Martinez (1985) for sites ranging from Puerto Rico to South America (compare our Fig. 3 with their Fig. 2). Leaves were displayed more horizontally in shade than in sun (Table 1), but few other leaf display traits varied among light levels. Many anatomical and morphological characteristics, including SLA, photosynthetic rates, and leaf thickness, varied as leaves themselves aged (Figs. 1, 2, Table 3).

With respect to gross architectural features, *R. mangle* exhibited its greatest flexibility in standing leaf number, maintaining more leaves per branch in high-light conditions (Fig. 4). Within a given life stage, branching angle, canopy display, and bifurcation ratios did not vary consistently with light environment (Table 2). Turner et al. (1995) reported similar insensitivity of sun/shade bifurcation ratios in *Rhizophora apiculata* BL. We caution that the bifurcation ratios calculated for our mangrove population also were influenced by the fact that branching orders never exceeded 4. Many mangrove taxa, including *R. mangle* and its congeners, conform closely to Attim's architectural model, exhibiting continuous growth of a monopodial trunk with equivalent branches initiated at fixed angles (Hallé, Oldeman, and Tomlinson, 1978; Turner et al., 1995). The convergence of disparate mangrove taxa on this model suggests a constrained teleology of this growth form.

While *R. mangle* may only subtly alter its architectural baüplan in response to light, Gill and Tomlinson (1971) recognized in their studies of shoot phenology in *R. mangle* that plastochron *rates* and the *types* of structures produced are sensitive to seasonal fluctuations in resource availability. We also observed that seedling growth rates were significantly higher in full sun (Fig. 6), possibly reflecting higher photosynthetic rates under saturating PAR (Fig. 5, Table 3). Data from long-term sapling growth studies suggest at sapling growth rates and module production rates may be similarly responsive to insolation levels (A. M. Ellison and E. J. Farnsworth, unpublished data). These growth and photosynthetic differences are especially relevant to models of seedling regeneration, stand demography, stand carbon gain, leaf turnover, and ecosystem primary production (Gong and Ong, 1990; Twilley, Chen, and Hargis, 1992; Ong, 1993), and in scaling from leaf to landscape models (e.g., Reich et al., 1990; Huston, 1991; Ehleringer and Field, 1993).

Direct causal links between growth rate and photosynthetic performance have yet to be drawn definitively for long-lived woody perennials such as mangroves (Lin and Sternberg, 1992; but see Ball, 1996), and our data on physiology and growth merely suggest interesting correlations for further study. *Rhizophora mangle* at our field site showed considerable plasticity of photosynthetic maxima, light compensation point, and estimated apparent quantum yield (Table 3). From inspection of our light-assimilation curves (Fig, 5) and our estimates from nonlinear curvefitting (Table 3), it appears that shaded individuals generally exhibited higher quantum yields, smaller dark respiration rates, and lower saturating $P_{\max}$ than individuals growing in sun. Our estimates of quantum yield, in accord with those of Bjökmann, Demmig, and Andrews (1988) provide preliminary evidence for photoinhibition in this species, but also indicate that carbon assimilation and photoinhibitory dynamics shift among seasons, as leaves age and as mangroves pass from one ontogenetic stage to the next.

We also asked whether the magnitude and type of flexibility in response to light environment change as mangroves mature, comparing among seedlings, saplings, and trees. We found seedlings in general exhibited a higher number of significant morphological and physiological trait modifications attributable to light than either saplings or trees (Figs. 1–6, Tables 1–3). We might expect that prelignified seedlings could adjust growth form to local light availability, although maternal reserves in viviparous *R. mangle* propagules may buffer seedlings early in establishment (Farnsworth et al., 1995). Likewise, the largest differences between sun and shade saplings in terms of branch morphology occurred among first-order branches, the first branches initiated off the main stem as the seedling passes into the sapling growth stage (Fig. 4). One might expect higher responsiveness to light level in younger, more recently initiated (higher order) twigs at the perimeter of the canopy. In contrast, these data suggest that architectural patterns are shaped early in the existence of the seedling, and are perpetuated as *R. mangle* matures. Trees were more problematic to assess in the present study design, because meaningful sun–shade comparisons were possible only for a limited number of traits on small modules such as clusters. Leaf anatomy, winter and summer photosynthetic rates, and cluster architecture in trees showed generally small modifications among light environments, relative to seedlings and saplings.

Exposure to light changes as a long-lived perennial passes from a seedling stage in a shaded understory to a mature phase in a sunlit canopy. Leaf-level, module-level, architectural and physiological adaptations and flexibility shown by mangrove seedlings and saplings may reflect selection on traits that must serve the tree through ontogeny (Lei and Lechowicz, 1990; Ellsworth and Reich, 1996; King, 1996) and as the light environment changes over succession (Bazzaz, 1979). Growth responses to light may be generally more plastic in so-called "early successional" species (Fetcher, Oberbauer, and Strain, 1983; Ackerly, 1993). Mangroves may defy categorization as "pioneers" or "shade-tolerant" species precisely because their life history demands flexibility within the biomechanical constraints of their architectural model. For example, the ratios of crown diameter to height reported here spanned a range over ontogeny comparable to that listed for both shade-tolerant and shade-intolerant canopy "champion trees" surveyed by Givnish (1988), and "understory" to "other canopy" species measured by King (1996), while crown area : height ratios conformed allometrically to the monopodial, larger leaved archetype described by Turner et al. (1995). In the present study, aspects of plant behavior (sensu Silvertown and Gordon, 1989) that change reversibly within an ontogenetic stage (e.g., photosynthesis and leaf traits) were more flexible than traits that develop irreversibly over the growth of the whole plant (e.g., branch angle). A paucity of dynamic studies that follow presumed trade-offs in such flexibility through the growth of long-lived woody species (e.g., Clark and Clark, 1992) as yet hampers our ability to develop a broad, mechanistic theory of ontogenetic shifts in mangroves. In predicting how different mangrove species will respond to disturbance, we need to acknowledge (1) the role of light in concert with other variables across tidal gradients, and (2) that mangroves of different ages, within and among swamps, will vary in their morphology, physiology, growth and mortality in sun and shade, with implications for mixed-age stand models of carbon gain.

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