



Estimating above-ground biomass and production in mangrove communities of Biscayne National Park, Florida (U.S.A.)

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Abstract

Total above-ground production is usually estimated by a combination of allometry and litter collection. However, in coastal sites that are tidally influenced, or in juvenile or dwarf forests where the crown bases of dominant individuals may begin within a few decimeters of ground level, estimates of community leaf production that depend on litter collection may not be feasible. Thus, in this paper, we present 1) allometric equations that allow accurate estimation of total above-ground biomass of three mangrove species (*Rhizophora mangle*, *Laguncularia racemosa*, and *Avicennia germinans*) in very small to medium size classes, and 2) an alternative method of estimating total above-ground production that overcomes the limitations of litter collection. The method we employ to estimate mangrove productivity is an adaptation for woody plant communities of a procedure introduced by Dai and Weigert (1996) for grasslands. It incorporates a detailed census of all individuals within fixed sampling plots, along with periodic observations of marked leaf cohorts. The method allows the comparison of biomass allocation patterns among forests that differ widely in physiognomy and physiographic setting.

The method was applied to a South Florida fringe mangrove forest in the early stages of recovery from Hurricane Andrew (August 1992), and an adjacent dwarf forest which was not substantially damaged by the storm. Total above-ground production in the fringe forest from July 1996 through June 1997 was about 3 times higher than dwarf forest production, $26.1 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ vs. $8.1 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$, respectively. Furthermore, when compared to the dwarf forest, fringe production rates were approximately eight, six, six, and two times as high as dwarf forest rates for prop roots, branches, stems, and leaves, respectively. Calculations of leaf production were based on mean red mangrove leaf longevities that ranged from about 189 days to 281 days, depending on cohort and site. Repeated measures analysis of variance indicated that leaf life spans did not differ significantly between dwarf and fringe forests, but did differ among leaf cohorts.

Based on reported values for similar mangrove forests, the method provided reasonable estimates of above-ground biomass and production, while furnishing relevant auxiliary information on spatial and temporal variation in leaf demographic patterns. Furthermore, the partitioning of annual production between woody tissues and leaves followed the reported trend in most forest ecosystems.

Introduction

In their classification of mangrove communities, Lugo and Snedaker (1974) categorized mangrove forests into five physiographic and physiognomic types, i.e., fringe, riverine, overwash, basin, and dwarf. These forest types range broadly in stature, from the tall can-

opy and high above-ground biomass of riverine and fringe forests, to the low, open-canopied dwarf forest (Mitsch and Gosselink 1993). While it is reasonable to assume that the contrast in structure among these forests is associated with similar differences in productivity, this assumption has rarely been explored,

especially on the basis of similar methodology on adjacent sites.

Accurate assessment of production across the entire range of mangrove community types requires standard methods that may be readily applied in forests of vastly different physiognomy. For instance, in tall, closed mangrove forests within micro-tidal coastal settings, above-ground production may be estimated by a combination of allometry and litter collection methods (e.g., Day et al., 1987, 1996). However, in sites with wider tidal amplitude, or in juvenile or dwarf 'forests' in which the crown bases of dominant individuals may begin within 5 dm or so of the ground, estimates of community leaf production through litterfall collection may not be feasible. In this paper, we present a new method of estimating total above-ground production that can be used in tidal shrublands as well as in mature forests. The method incorporates (a) detailed censuses of all individuals within fixed plots, from which annual changes in stem, branch, leaf, and proproot biomass are calculated, and (b) periodic observations of marked leaf cohorts, by which leaf turnover is estimated. The method facilitates the comparison of biomass allocation patterns among sites, and the leaf demographic information is of interest with respect to the functioning of mangrove forests.

In southeastern peninsular Florida and the Florida Keys, coastal mangrove forests which reach *ca* 20 meters at maturity (fringe forests) are often found adjacent to more extensive interior basins or plains that are characterized by mangroves < 2 meters in height (dwarf forests). Total above-ground biomass in mature fringe forest frequently exceeds 150 Mg·ha⁻¹ (Ross unpublished data), but occasional severe hurricanes can eliminate nearly all live stems. In August 1992, such a storm, Hurricane Andrew, passed directly over the fringe and dwarf mangrove forests of Biscayne National Park (Smith et al., 1994). In the fringe forests, mortality was about 97%, reducing total above-ground biomass from nearly 200 Mg·ha⁻¹ to less than 1 Mg·ha⁻¹ (Ross, unpublished data). In contrast, Hurricane Andrew had little effect in the adjacent dwarf forests. As a result, both the regenerating fringe forests and the minimally impacted dwarf forests were densely vegetated shrub communities of low canopy height following the hurricane, and consequently were not amenable to standard methods of productivity measurement. We therefore developed and applied the methods described below to these two neighboring forests during a single annual period. Based on the

contrasting stature of the two forests prior to the hurricane, we expected that they would differ widely in productivity.

Study area

The study area, located in the southern Biscayne Bay watershed about 1 km north of Convoy Point (25°27'N, 80°20'W), is a thin coastal strip of about 2 km in length and 700 meters in width (Figure 1). It is semi-impounded on the west, north and south by the levees of the L-31E, Military, and Mowry Canals, respectively, and divided by old drainage ditches into five rectangular units of 25–30 hectares each. Three distinct forest types are recognizable as successive bands parallel to Biscayne Bay. The fringe forest occupies a 100–200 meter zone closest to the coast, the transition forest a 50–300 meter band further toward the interior, and the dwarf forest the remainder of the mangrove swamp east of the L-31E levee. Only the fringe and dwarf forests were examined in this study. Both contain a mixed-species assemblage of *Rhizophora mangle* L. (red mangrove), *Laguncularia racemosa* (L.) Gaertn. (white mangrove), and *Avicennia germinans* (L.) Stearn. (black mangrove), but *R. mangle* is usually dominant. The two units differ fundamentally in their hydrology. The fringe forest is inundated regularly by the semidiurnal tides, while the dwarf forest is in a basinal setting that is reached less frequently by tides but remains inundated for longer consecutive periods of time. Tidal amplitude in western Biscayne Bay is generally 0.2–0.3 meters.

Methods

Structural sampling

In April–August 1995, permanent plots were established in two of the five blocks that divide the study area. Four plots were in the dwarf forest, and eight were in the fringe forest type (Figure 1). Construction of a network of boardwalks allowed us to approach and work in the rectangular plots without disturbing the fragile mangrove sediments. Plots were 0.5 meter wide, and ranged from 3 to 10 meters in length, with smaller plots in areas of higher stem density. Each mangrove individual rooted within the plots was tagged and assigned a grid coordinate, and the following measurements were recorded: total height

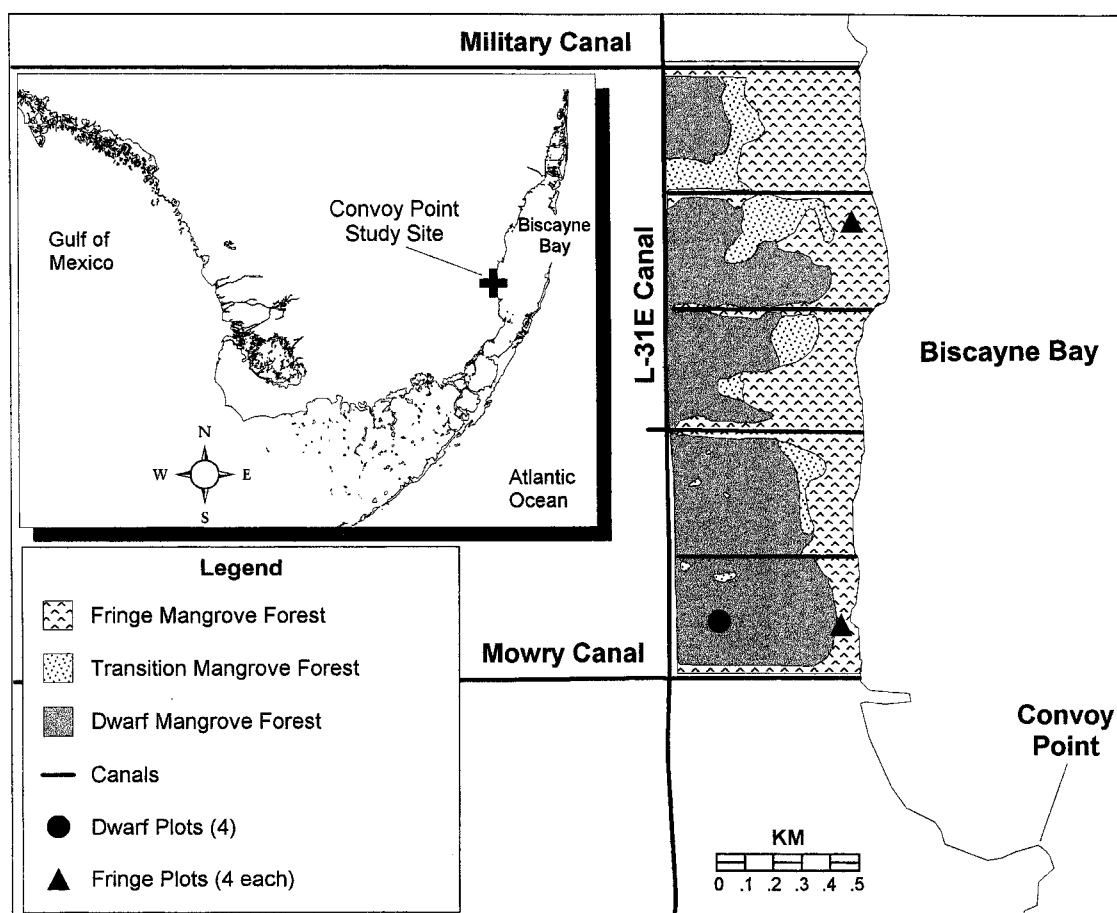


Figure 1. Plot locations and vegetation zonation within Convoy Point study area. fringe plots, $n = 8$ and dwarf plots, $n = 4$.

(TOTHT), height to base of crown (CRWNHT), crown length and width (CRWNL and CRWNW), and diameter at 30 cm (D_{30}) and 140 cm (D_{140}) (for stems taller than 40 and 150 cm, respectively). Crown depth (CRWND) was calculated by subtracting CRWNHT from TOTHT. The product $[CRWND \cdot CRWNL \cdot CRWNW]$ provided an index of crown volume (CRWNV). Measurements were repeated during the periods September–December 1996 and November–December 1997. In all, 1,635 stems were monitored.

Calculation of biomass

Biomass regressions were developed for *R. mangle*, *L. racemosa*, and *A. germinans* from collections made during the summer of 1997. Regressions were based on relationships between the structural measures listed above and biomass components (trunk, branch, propropoot, leaf, and total above-ground biomass) of

individuals harvested from adjacent areas which resembled the study plots in vegetation structure. The regression data set included 53 *R. mangle*, 44 *L. racemosa*, and 21 *A. germinans* stems. These individuals encompassed a range of sizes from 40 cm to 6.0 meters in height. The latter were as tall as the largest trees in the permanent plots. Five to fourteen individuals < 40 cm height of each species were also sampled and weighed. All possible regression models of the form

$$\ln(\text{biomass component}) = b_0 + b_a \cdot \ln(\text{independent variable } a) + \dots + b_z \cdot \ln(\text{ind. var } z)$$

were examined, where the independent variables were (D_{30}), TOTHT, CRWND, CRWNV, and $[(D_{30})^2 \cdot \text{TOTHT}]$. A single model form was chosen for each species-tissue combination, based on variance explained and the distribution of residuals. Two-

parameter models were selected over more heavily-parameterized ones when the latter did not substantially improve model performance.

For trees in the permanent plots, biomass of stems taller than 40 cm was estimated by applying the regression models to annual structural measurements. According to Baskerville (1972), if $\hat{\mu}$ = the estimate of $\ln(Y)$, and $\hat{\sigma}^2$ = the sample variance of the logarithmic equation, then the estimated value of Y in arithmetic units is:

$$\hat{Y} = e(\hat{\mu} + \hat{\sigma}^2/2)$$

Individuals 40 cm or less in height were assigned stem, branch, propoot, and leaf biomass equal to the mean of the sample of such stems of each species. Biomass components were calculated on an areal basis for each plot, and then summarized for each forest type.

Sampling of leaf demography

Estimation of leaf production relied in part on observations of leaf dynamics at *ca* four-month intervals through a two-year period. The demographic study was initiated in December 1995. In the dwarf forest, leaf production and survival were monitored on all branches of nine canopy *R. mangle* individuals (two or three in each of the four permanent plots). In the fringe forest, the fate of leaf cohorts was tracked on five branches representing different strata within the canopy of eight large *R. mangle* stems (one per permanent plot). During the first survey, a loop of thin, colored wire was tied between the distal and second-to-distal leaf pair on all shoot tips, and all leaves including the distal ones were counted on each shoot. At subsequent surveys (March, July, and December 1996; May, September, and December 1997; and April 1998), leaves of previously circumscribed cohorts were counted, and a new cohort marked in similar fashion. New branches were incorporated in the sampling design as they formed. On dwarf forest trees, the demography of leaves on all new branches was monitored. In the fringe forest, where branch production was much more prolific, one new branch per sampling period was randomly selected for monitoring. By counting and grouping all branches according to period of initiation, it was possible to scale up observations on representative branches to the tree as a whole.

Calculation of above-ground production in 1996–97

We used data from the twelve permanent plots to estimate above-ground production of mangroves for the year beginning July 1, 1996. In forest communities, above-ground production consists of the growth of woody tissues, as well as the production of leaves and reproductive parts, but the latter were not included in our estimates of production. Stem, branch, and propoot production were calculated as the sum of estimated increases in biomass between the beginning and end of the year for surviving individuals, plus component biomass of newly established individuals. Biomass components for each census date were calculated as described earlier, and a linear interpolation between successive census dates was used to estimate biomass on July 1 of both 1996 and 1997.

In combination with data from the annual structural censuses, leaf demographic observations were employed to estimate the annual biomass production of mangrove leaves. The method was based on the balance between leaf production, senescence, and standing crop: Leaf Standing Crop $Y_{R(x+1)} = \text{Leaf Standing Crop } Y_{R(x)} + \text{Leaf Prod'n } Y_{R(x+1)} - \text{Leaf Mortality } Y_{R(x+1)}$ and therefore,

$$\text{Equation 1: Leaf Prod'n } Y_{R(x+1)} = \Delta \text{ Standing Crop } Y_{R(x \rightarrow x+1)} + \text{Leaf Mortality } Y_{R(x+1)}$$

A major assumption of our method was that the production and mortality rates underlying the first and third terms in Equation 1 were similar whether expressed on a density or biomass basis. In solving Equation 1 for biomass, $\Delta \text{ Standing Crop } Y_{R(x \rightarrow x+1)}$ was calculated by applying our biomass regression equations to structural data from censuses of successive years in each plot. Leaf Mortality $Y_{R(x+1)}$ was calculated as follows:

1. Mean leaf turnover rate (in leaf generations per leaf per year) was calculated for three leaf cohorts (i.e., those tagged in June 1996, December 1996, and May 1997), based on the total number of red mangrove leaves tagged and surviving to each subsequent sampling period within each plot. Survivorship beyond the time when 95% of the tagged cohort had fallen was not considered, as these leaves frequently appeared senescent or non-functional. Leaves were assumed to have been initiated at the midpoint of the interval prior to observation. Mean cohort longevity (in days) was calculated by integrating the area under the surviv-

Table 1. Regressions used to predict total, stem, branch, leaf, and proproot biomass (grams) of individual mangrove trees from structural measurements. Equations are applicable to a range of sizes up to six meters in height. Independent variables: D= diameter (in cm) at 30 cm; H=total height (in cm); CRWNV=crown width · crown length · crown depth (each in cm).

Species	n	Equation	R ²	σ ²
<i>A. germinans</i>	21	Ln (TOTWT) = 2.134+(0.895·Ln(D ²))+ (0.184·Ln(CRWNV))	0.989	0.044
<i>L. racemosa</i>	43	Ln (TOTWT) = 1.095+(0.659·Ln(D ²))+ (0.304·Ln(CRWNV))	0.980	0.075
<i>R. mangle</i>	52	Ln (TOTWT) = 2.528+(1.129·Ln(D ²))+ (0.156·Ln(CRWNV))	0.943	0.138
<i>A. germinans</i>	21	Ln (STEMWT) = -0.339+(0.821·Ln(D ² H))	0.989	0.046
<i>L. racemosa</i>	43	Ln (STEMWT) = 0.226+(0.758·Ln(D ² H))	0.975	0.104
<i>R. mangle</i>	52	Ln (STEMWT) = 0.133+(0.780·Ln(D ² H))	0.945	0.105
<i>A. germinans</i>	20	Ln (BRANCHWT) = -7.355+(0.532·Ln(D ²))+ (0.758·Ln(CRWNV))	0.912	0.653
<i>L. racemosa</i>	42	Ln (BRANCHWT) = -4.347+(0.489·Ln(D ²))+ (0.569·Ln(CRWNV))	0.907	0.488
<i>R. mangle</i>	46	Ln (BRANCHWT) = -3.026+(0.901·Ln(D ²))+ (0.476·Ln(CRWNV))	0.911	0.371
<i>A. germinans</i>	21	Ln (LEAFWT) = 0.131+(0.677·Ln(D ²))+ (0.246·Ln(CRWNV))	0.981	0.061
<i>L. racemosa</i>	43	Ln (LEAFWT) = -2.145+(0.308·Ln(D ²))+ (0.479·Ln(CRWNV))	0.959	0.124
<i>R. mangle</i>	52	Ln (LEAFWT) = -2.030+(0.539·Ln(D ²))+ (0.435·Ln(CRWNV))	0.951	0.140
<i>R. mangle</i>	42	Ln (PROPWT) = 1.879+(1.638·Ln(D ²))	0.739	0.751

orship curve, assuming a linear decrease in leaf density between periods. Turnover rate therefore equaled 365 divided by the mean longevity (Dai and Wiegert, 1996). Annual turnover rate on a density basis, T_{dens} , was calculated by weighting the turnover rate of each cohort by its relative contribution to the total leaf population during the year beginning July 1, 1996.

2. We calculated $Biom_{Yr(x+1)}$, the annual mean standing crop of leaves, as the average of crop estimates for July 1, 1996 and July 1, 1997 in each plot, interpolating between the actual census dates.
3. Equating T_{dens} with T_{biom} (turnover rate on a biomass basis), we calculated leaf mortality as:

$$\text{Equation 2: Leaf Mortality } Yr(x+1) = T_{biom} \cdot Yr(x+1) \cdot Biom_{Yr(x+1)}$$

and solved for Leaf Prod'n $Yr(x+1)$ in Equation 1.

Results

Biomass regressions

The regressions equations used to calculate biomass components for the three mangrove species are listed in Table 1. For stem biomass, we chose a two-parameter model in which $(D_{30})^2 \cdot TOTHT$ was the

Table 2. Mean biomass (Mg/ha) of Convoy Point fringe and dwarf mangrove forests between 1995–1997.

Year	Community type			
	Dwarf forest (n = 4)		Fringe forest (n = 8)	
	mean	± S.E.	mean	± S.E.
1995	15.82	4.31	18.19	4.84
1996	19.11	4.83	38.36	9.83
1997	22.28	5.18	56.02	11.96

single independent variable. For proproot biomass, total height was the lone independent variable in the selected model. For branch, leaf, and total biomass, regression models which included crown volume and diameter as independent variables were selected. Coefficients of determination were highest for stem biomass, and exceeded 0.90 for all species-tissue combinations except *R. mangle* proproot biomass ($R^2 = 0.74$). While these models generally provided a better fit than models based on stem diameter alone, models based on the latter may provide useful biomass estimates for studies in which height or crown dimensions were not measured. Regression equations for models predicting biomass components from $(D_{30})^2$ are listed in Appendix 1.

Table 3. Structural characteristics of fringe and dwarf forest plots ($n = 8$ and $n = 4$, respectively) at Convoy Point, December 1997.

Parameter	Community type			
	Dwarf forest		Fringe forest	
	mean	\pm S.E.	mean	\pm S.E.
Basal area ($\text{m}^2 \cdot \text{ha}^{-1}$)	–	–	13.54	3.44
Density (#/ha)				
stems $> 1\text{m}$	8,800	8,800	57,800	9,000
stems $\leq 1\text{m}$	608,200	122,100	107,200	42,900
Total Biomass ($\text{Mg} \cdot \text{ha}^{-1}$)	22.28	5.18	56.02	11.96
Biomass apportionment by tissue (%)				
Stem	55.3	–	42.7	–
Branch	10.7	–	21.6	–
Leaf	16.1	–	13.6	–
Proprout	17.8	–	22.1	–
Biomass apportionment by species (%)				
<i>R. mangle</i>	96.3	–	90.5	–
<i>L. racemosa</i>	3.6	–	8.2	–
<i>A. germinans</i>	0.1	–	1.3	–
Maximum stem height (m)	0.97	0.05	4.04	0.52

Fringe and dwarf forest biomass

Mortality from Hurricane Andrew in the fringe forest was near-complete, but by the winter of 1995 most of the area had been reoccupied by a dense stand of mangrove saplings established soon after the storm, and stand biomass was $18 \text{ Mg} \cdot \text{ha}^{-1}$. Subsequent stand development was rapid. By the winter of 1997, five years after Hurricane Andrew, above-ground biomass averaged more than $56 \text{ Mg} \cdot \text{ha}^{-1}$ (Table 2). 64% was accounted for by woody tissues, 14% by leaves, and 22% by proproots (Table 3). *R. mangle* comprised about 90% of stand biomass, but localized areas were dominated by *L. racemosa* (8%). Canopy height also exhibited wide local variation, ranging from about 3 to 6 meters.

Compared to the rapidly developing fringe forest, the increase in dwarf forest biomass from 16 to $22 \text{ Mg} \cdot \text{ha}^{-1}$ between 1995 and 1997 was modest (Table 2). Compartmentalization of biomass was similar to the fringe forest, with slightly higher percentages of total above-ground biomass in leaves (16%) and stems/branches (66%), and slightly lower percentages (18%) in proproots (Table 3). As in the fringe forest, dwarf plots were dominated by *R. mangle* on a biomass basis.

Red mangrove leaf demography

Mean red mangrove leaf longevities ranged from about 189 days (dwarf forest, April 1996 cohort) to 281 days (fringe forest, September 1996 cohort) (Figure 2). Repeated measures analysis of variance indicated that leaf life spans did not differ between forest types ($F = 0.004$, $p = 0.95$), but did differ among cohorts ($F = 45.42$, $p < 0.001$). Post-hoc multiple comparison testing demonstrated that the April 1996 leaf cohort had significantly shorter longevity than the September 1996 or February 1997 cohorts, but the latter two cohorts did not differ (Scheffé test, $p \leq 0.05$). The longevities illustrated in Figure 2 equate to turnover rates (T_{dens}) of 1.3 to 1.7 generations per year.

Patterns of annual production

Total above-ground production in the fringe forest ($26.1 \text{ Mg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$) was about 3.2 times higher than dwarf forest production ($8.1 \text{ Mg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$) (Table 4). This difference was accompanied by an equally striking contrast in tissue allocation, i.e., leaves constituted about 73% of above-ground production in the dwarf community, but only 47% in fringe. This pattern was a consequence of the highly accelerated production of woody tissues in the fringe forest. Compared to

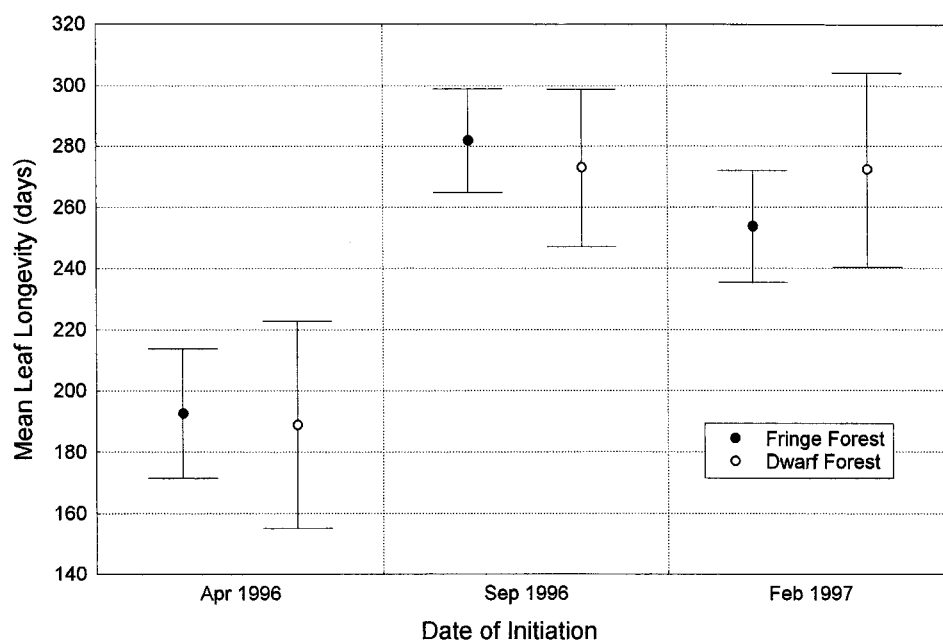


Figure 2. Mean life span (+1 S.E.) of three *R. mangle* leaf cohorts in fringe and dwarf mangrove forests at Convoy Point.

Table 4. Annual above-ground production ($\text{Mg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$) in two South Florida mangrove community types, July 1996–June 1997.

Biomass component	Community type				Fringe: Dwarf ratio
	Dwarf forest (n =4)		Fringe forest (n = 8)		
	mean	± S.E.	mean	± S.E.	
Stems	1.2	0.2	6.7	1.0	5.6
Branches	0.5	0.1	3.2	0.6	6.4
Proproots	0.5	0.1	4.0	1.2	8.0
Leaves	5.9	1.8	12.2	2.9	2.1
Total	8.1	2.1	26.1	5.5	3.2

the dwarf forest, fringe production rates were approximately eight, six, six, and two times as high as dwarf forest rates for proproots, branches, stems, and leaves, respectively (Table 4). The comparatively modest response of leaf production reflected the site-insensitivity of leaf turnover rate (Figure 2).

Discussion

The research described above explores a new method of estimating above-ground production in mangrove forests in which litter collection is difficult or impossible. Several factors limit interpretation of the results, however. First, we were unable to test our estim-

ates against results based on standard techniques from the same sites, since these methods were not feasible in the conditions of our study area. We therefore are limited to placing our results within the context of several studies that employed alternative methods in similar mangrove communities. Second, the Convoy Point fringe forest was in an early stage of post-hurricane recovery at the time of measurement, while the dwarf forest, despite its proximity, was not similarly disturbed. For this reason, estimates of biomass, production, or the allocation of biomass to different tissues are not easily comparable between the two forests we studied, since these attributes all change during the early stages of stand development (Sprugel, 1985; Waring and Schlesinger, 1985). Between-site

patterns are nevertheless discussed to illustrate the potential of the method, and to suggest further research directions.

Biomass and structure

Allometric equations for the estimation of mangrove biomass frequently use stem diameter as the sole independent variable (Fromard et al., 1998; Putz and Chan, 1986; Amarasinghe and Balasubramaniam, 1992). However, canopy width provides the best predictions of above-ground biomass in *Avicennia marina* (Woodroffe, 1985), and many published equations for terrestrial shrubs are based on crown width or cover (e.g., Ohmann et al., 1980; Smith and Brand, 1983). In our data set, inclusion of a term for crown volume improved diameter-based predictions of branch, leaf, and total biomass for *A. germinans*, *L. racemosa*, and *R. mangle*. We attribute this to the wide range of crown shapes included in our sample, which ranged from dwarf trees 45 cm tall to fast-growing individuals nearly 7 meters in height.

At more than 60 individuals per m² (Table 3), the stem density in the Convoy Point dwarf forest is exceptionally high. Although 99% of these stems are less than 1 meter in height, this community is characterized by a mixture of age classes, including many reproductive individuals. Propagule production and seedling establishment is observed each year. Seedlings exhibit a clumped distribution, with high concentrations at the base of larger adults. Seedling mortality is high in the first year, but drops off sharply thereafter. One factor that may contribute to the relatively high longterm survival of seedlings in these unproductive forests, and thus the high stem density, is the low and open mangrove canopy, which creates a high light environment in the forest understory.

We are aware of two studies in which the biomass of mangrove communities similar in height (< 1.5 m) to our dwarf forest were estimated. Lugo and Snedaker (1974) harvested leaves, stems, and proproots in three 9-m² plots in another location in the Biscayne Bay watershed, and found a total above-ground biomass of 7.9 Mg·ha⁻¹. Woodroffe (1985) found even lower above-ground biomass (6.8 Mg·ha⁻¹) in an *Avicennia*-dominated dwarf forest in New Zealand. Our dwarf forest mean of 22.3 Mg·ha⁻¹ in 1997 included plot estimates ranging from 9.7 to 31.8 Mg·ha⁻¹. Plots with higher biomass were generally located closer to the fringe forest, while low-biomass plots were farthest from the coast. The gradient of decreasing biomass

with distance from the coast within the dwarf mangrove zone parallels the interzonal contrast between fringe and dwarf forest, and may be a widespread pattern in the Biscayne Bay watershed, if not more generally.

Among mangrove studies reviewed by Saenger and Snedaker (1993), no research site above 10° north or south latitude exceeded 200 Mg·ha⁻¹ in total above-ground biomass. While mangrove forests of large stature are increasingly rare in Florida, biomass in mature fringe or riverine forest in southwest Florida averaged 170–180 Mg·ha⁻¹, and exceeded 200 Mg·ha⁻¹ in individual plots (Lugo and Snedaker 1975). Based on the rapid rate of biomass accumulation following Hurricane Andrew (56 Mg·ha⁻¹ in five years), it seems likely that, given no major disturbance, a forest approaching 200 Mg·ha⁻¹ may develop within a few decades on productive sites in South Florida. Certainly, the current 2.5:1 ratio in biomass between the Convoy Point fringe and dwarf forests greatly underestimates their ratio at maturity.

Production

Our assessment of mangrove production at the two Convoy Point sites included separate estimates for above-ground woody tissues (including proproots) and leaves, but did not incorporate reproductive parts or below-ground tissues. We used standard dimension analysis methods to estimate wood production (e.g., Whittaker and Woodwell, 1968), but introduced a new, demographically-based procedure for estimating leaf production.

Standard methods for estimating leaf production in mangrove or other forest ecosystems equate annual leaf fall with annual leaf production, usually integrating collections over several years (e.g., Day et al., 1987; Megonigal et al., 1997). Litter traps need to be emptied relatively frequently, and secondary dispersal by water, wind, or animals (for instance, sesarmid crabs; Robertson, 1986) may be a problem. Moreover, effective litter sampling methods are especially difficult to devise in tidal shrublands, where tide waters sometimes rise well into the crowns of dominant stems, and thus above the level of the traps.

We attempted to circumvent these problems by adapting a non-destructive method applied by Dai and Wiegert (1996) in *Spartina alterniflora* marsh. In their study, leaf demography of all stems within nine small (0.25–1 m²) quadrats was monitored at short intervals over a 21-month period. Annual leaf

production was calculated as the product of mean stem density, mean leaf number per stem, mean leaf turnover, and mean leaf mass. In contrast, we calculated leaf turnover rates from a small sample of mangrove individuals, then multiplied this rate by the mean standing crop of leaves in our larger (1.5–5 m²) plots, assuming that a density-based turnover rate (leaves·leaf⁻¹·year⁻¹) was equal to a biomass-based turnover rate (grams·grams⁻¹·year⁻¹). This assumption should be valid if all leaves grow to full size before senescing, and the size distribution of leaves does not change substantially within the year. Field observations lead us to believe that these assumptions are reasonable on our sites. Another assumption of our method is that the leaf longevity patterns exhibited by the sampled individuals are representative of the community as a whole. While the demographic patterns of *L. racemosa* and *A. germinans* probably differ somewhat from the *R. mangle* stems we surveyed, these species represent only 4% and 10% of the total biomass in fringe and dwarf forest, respectively, and therefore should not exert much influence on estimates of total community production.

Our estimates of above-ground biomass production were near the high end of the range of values reported from similar mangrove forests. Convoy Point fringe production of 26.1 Mg·ha⁻¹·yr⁻¹ exceeded the 16.0 Mg·ha⁻¹·yr⁻¹ and 24.6 Mg·ha⁻¹·yr⁻¹ found by Day et al. (1987) in adjacent fringe and riverine forests in Campeche province, Mexico. In an *A. germinans*-dominated basin forest near the above sites, annual above-ground production over a seven-year period was lowest in mid-basin (3.2–4.8 Mg·ha⁻¹·yr⁻¹) and highest near the fringe (6.6–7.6 Mg·ha⁻¹·yr⁻¹) (Day et al. 1996); measured production in the Convoy Point dwarf forest (8.0 Mg·ha⁻¹·yr⁻¹) was slightly above this range. Teas (1979) calculated production rates of 32.1 and 3.8 Mg·ha⁻¹·yr⁻¹ in adjacent fringe and dwarf forest sites in South Florida, using an expansion factor of 3 times to estimate NPP from litterfall measurements. It is not possible to determine how much of the variation among these studies is attributable to differences in methodology, and how much to (1) inter-annual variation associated with climatic or hydrologic conditions, (2) fundamental differences in site potential, and (3) differences in the developmental stage of the mangrove community. With regard to the last source of variation, most models of successional change in forest production following disturbance include an early reorganization period during which stand production increases steadily to a

maximum level (Peet, 1981; Sprugel, 1985). Though this recovery period sometimes lasts less than a decade (Marks, 1974), at five years old the Convoy Point fringe forest may not yet have passed entirely through it.

Partitioning of above-ground production among woody tissues and leaves

The partitioning of annual production in our sites followed the trend of most forest ecosystems (Cannell, 1985), i.e., as productivity increased, the proportion allocated to stems and branches likewise increased. While the difference in allocation between the two Convoy Point stands was quite dramatic, it was consistent with results from other mangrove forests. For instance, in the stands studied by Day and collaborators (Day et al., 1987, 1996), woody tissues accounted for 58% and 57% of (leaf + wood) production in riverine and fringe forest, respectively, but accounted for only 27%–35% in the less productive basin forest. Our results are similar in magnitude as well as in direction (53% of above-ground production in woody tissues in the fringe forest, 27% in the dwarf forest).

One advantage of the demographic approach over litter collection methods is that variation in leaf production among sites may be attributed to either (a) difference in leaf turnover rate, or (b) difference in leaf standing crop. In our sites, the twofold difference in leaf production between fringe and dwarf forest was clearly a result of variation in standing crop, since turnover rates did not differ between sites (Figure 2). This may not be the case for all site comparisons, as mean leaf longevities reported for *R. mangle* in other Florida sites (Gill and Tomlinson, 1971) and in Belize (Ellison and Farnsworth, 1996) range from six to twelve months. Our demographic sampling protocols also provided supplemental observations of branch production and extension that add insight regarding fringe and dwarf forest development. Between March 1996 and April 1998, the eight trees whose leaf demography was monitored in the fringe forest initiated an average of 96.3 primary, secondary, or tertiary branches, which reached a mean length of 25.7 cm. Comparable figures for the nine trees monitored in the dwarf forest were 1.4 branches, with mean length of 8.2 cm. Extension of existing branches was also depressed in the dwarf forest *viz* the fringe forest. Identical leaf turnover rates resulted in a more diffuse arrangement of leaves in the fringe forest, while those

on dwarf forest trees were crowded together near the branch tips.

Conclusion

More and more of the world's mangrove forests are affected by human activities in the surrounding landscape, and all may be influenced by global changes in climate or sea level. To assess the health of these forests, or to evaluate the environmental impacts of specific management actions, it is often necessary to develop monitoring systems that address fundamental ecosystem characteristics such as diversity, structure, or productivity. Ideally, sampling methods should be applicable in forests in all stages of development, and across the entire range of site variability. Because standard methods of estimating production may not provide dependable results in very young or small-statured mangrove forests, the demographically-based method introduced above may extend our understanding to sites not presently being sampled.

Besides its applicability to certain difficult-to-sample sites, this method offers several potential advantages over standard techniques. For instance: 1) The demographic information is of interest in its own right, providing a more nuanced view of canopy development; 2) Sites may be visited less frequently than the monthly or bimonthly intervals usually associated with litter collections. The method's disadvantages include the following: 1) Sampling may be time-consuming and difficult at each visit, especially in tall forests where towers or scaffolding are necessary, 2) Implementation may be problematic in forests dominated by *L. racemosa* or *A. germinans*, whose branching patterns are not as regular or predictable as those of *R. mangle*, and 3) As described, the method does not account for the production of reproductive parts, or for turnover in woody tissues, though demographic observations of those tissues may be incorporated to do so. Nonetheless, as applied to two South Florida mangrove forests, the method appeared to provide reasonable estimates of above-ground biomass and production, as well as their allocation to leaf and woody tissues. Further development requires applying the technique in situations where standard methods can be used for comparison. If it proves reliable after additional testing, the method may prove especially useful in assessing productivity during the early stages of mangrove reforestation or mitigation projects, or

after catastrophic events of natural or anthropogenic origin.

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Appendix 1

Intercept and slope coefficients (b_0 and b_1 , respectively) of regressions used to predict total, stem, branch, and leaf biomass (in grams dry weight) of individual mangrove trees from stem diameter (in mm) 30 cm above the ground (D_{30}). Equations are applicable to a range of sizes up to six meters in height. Equations are of the form $\text{Ln}(\text{biomass component}) = b_0 + b_1 \cdot \text{Ln}(D_{30})$.

Species	Biomass component	n	b_0	b_1	R^2	σ^2
<i>A. germinans</i>	Total weight	21	4.310	1.124	0.984	0.066
<i>L. racemosa</i>		43	4.411	1.021	0.962	0.145
<i>R. mangle</i>		52	3.960	1.481	0.925	0.182
<i>A. germinans</i>	Stem weight	21	3.804	1.132	0.987	0.056
<i>L. racemosa</i>		43	3.920	1.069	0.975	0.104
<i>R. mangle</i>		52	3.483	1.295	0.904	0.182
<i>A. germinans</i>	Branch weight	20	1.668	1.447	0.862	1.026
<i>L. racemosa</i>		42	1.869	1.148	0.863	0.718
<i>R. mangle</i>		46	1.424	1.922	0.804	0.820
<i>A. germinans</i>	Leaf weight	21	3.040	0.982	0.969	0.101
<i>L. racemosa</i>		43	3.068	0.877	0.901	0.296
<i>R. mangle</i>		52	1.965	1.523	0.830	0.482

