Standing crop and aboveground biomass partitioning of a dwarf mangrove forest in Taylor River Slough, Florida

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Abstract

The structure and standing crop biomass of a dwarf mangrove forest, located in the salinity transition zone of Taylor River Slough in the Everglades National Park, were studied. Although the four mangrove species reported for Florida occurred at the study site, dwarf *Rhizophora mangle* trees dominated the forest. The structural characteristics of the mangrove forest were relatively simple: tree height varied from 0.9 to 1.2 meters, and tree density ranged from 7062 to 23 778 stems ha^{-1}. An allometric relationship was developed to estimate leaf, branch, prop root, and total aboveground biomass of dwarf *Rhizophora mangle* trees. Total aboveground biomass and their components were best estimated as a power function of the crown area times number of prop roots as an independent variable ($Y = B \times X^{-0.5083}$). The allometric equation for each tree component was highly significant ($p < 0.0001$), with all r^2 values greater than 0.90. The allometric relationship was used to estimate total aboveground biomass that ranged from 7.9 to 23.2 ton ha^{-1}. *Rhizophora mangle* contributed 85% of total standing crop biomass. *Conocarpus erectus*, *Laguncularia racemosa*, and *Avicennia germinans* contributed the remaining biomass. Average aboveground biomass allocation was 69% for prop roots, 25% for stem and branches, and 6% for leaves. This aboveground biomass partitioning pattern, which gives a major role to prop roots that have the potential to produce an extensive root system, may be an important biological strategy in response to low phosphorus availability and relatively reduced soils that characterize mangrove forests in South Florida.

Introduction

Hydrology, nutrient input, soil salinity, and soil type are the most important factors that affect the structure and productivity of mangrove forests (Brown and Lugo 1982). Since the effects of these factors vary over geographical regions, mangrove forests exhibit wide regional and local variation in structural characteristics. Based on differences among the above environmental factors, Lugo and Snedaker (1974) developed a mangrove classification that included six basic types of mangrove forests: riverine, fringe, overwash, basin, hammock and dwarf. This classification identifies common patterns of mangrove re-

sponses to daily, seasonal, and long-term patterns in environmental conditions occurring in coastal tropical regions. Accordingly, dwarf and hammock forests located in the Southern Everglades are recognized as special sub-types that respond to localized hydrogeologic and edaphic conditions (Cintrón and Schaeffer-Novelly 1984).

In ecological studies, reliable estimates of biomass and growth rates are essential for estimating total net primary production (Clough and Scott 1989). A common non-destructive method for estimating biomass of trees or shrubs is to fit equations that relate tree biomass to some dimensional characteristics of the plant. For instance, stem diameter at breast height

(dbh), tree height, and a combination of both variables have been commonly used (Causton 1985; Day et al. 1987). For shrubs, other dimensional variables have been used to predict biomass, including the greatest diameter of the canopy (Uresk et al. 1977), crown diameter axes (Rittehnhouse and Sneva 1977), and height times circumference (Azocar et al. 1981). Allometric relationships between aboveground biomass and dbh have been reported for *Rhizophora mangle*, *Avicennia germinans*, *Laguncularia racemosa* (Golley et al. 1962; Day et al. 1987; Fromard et al. 1998), and other mangrove species in Thailand, Malaysia, and Australia (Ong et al. 1982; Putz and Chan 1986; Clough and Scott 1989; Tam et al. 1995; Clough et al. 1997). For dwarf *R. mangle*, the dominant species in our study site, there is no literature on the optimal dimensional variables that can be used to estimate its biomass. In this paper, we focus on the structure and standing crop biomass of a dwarf mangrove forest and develop an allometric equation to estimate aboveground biomass of a red dwarf mangrove community located in the salinity transition zone of Taylor Slough in the Everglades National Park, South Florida.

Study site

The Everglades salinity transition zone is located in the southern part of Everglades National Park at 25° 10′ N and 80° 45′ W. It borders Florida Bay, a large, shallow, sub-tropical embayment, bounded on the south and east by the Florida Keys (Figure 1). The region is characterized as sub-tropical savanna with distinctive rainy (May–October) and dry (November–April) seasons (Hela 1952). During the rainy season, winds are dominated by a southerly sea breeze system that promotes the formation of daily convection thunderstorms (Chen and Gerber 1990). Tropical storms and hurricanes also contribute significant amounts of rainfall during the rainy season. Low rainfall and mild temperatures, associated with the passage of winter cold fronts, characterize the dry season (Chen and Gerber 1990). In NE Florida Bay, tides are semi-diurnal with an average range of 30 cm. However, the mean tidal range in the Taylor Slough area is approximately 5 cm due to restricted water circulation (Wang et al. 1994).

The study site is located at Taylor Slough, which drains into an inland basin where several shallow ponds and an extensive dwarf mangrove forest domi-

nate the landscape before reaching Florida Bay (Figure 1). Spatially, Taylor Slough can be divided into Upper, Middle, and Lower zones. Freshwater marsh species, such as sawgrass (*Cladium jamaicense*) and spike rush (*Eleocharis cellulosa*), dominate the upper zone. The middle zone is a marsh dominated by willow (*Salix caroliniana*), sawgrass and spike rush. In the lower zone the freshwater vegetation is replaced by mangrove forests, salt barrens, and tropical hardwood hammocks. The soil in this site consists of recently developed calcareous marl overlaying peat deposits (Pool et al. 1977).

Methods

Forest structure

Trees with a diameter greater than 2 cm, measured at 60 cm from the ground (D60), were sampled using the point centered quarter method (Cottam and Curtis 1956; Pool et al. 1977). Four 75 m long transects perpendicular to the channel edge, and with points 5 m apart, were randomly chosen. At each transect, floristic composition, diameter (D60), total height, crown diameter and number of prop roots were measured. Data from each transect were used to estimate standing crop biomass using the allometric equation obtained with the methodology described below.

Aboveground biomass

To estimate biomass of the dwarf red mangroves, ten trees ranging from 0.7 to 1.6 m in total height were harvested. From each tree, height, diameter (D60), number of prop roots, and crown diameter were recorded, and then all leaves were stripped. Fresh weights of all tree components were measured in the field, and a subsample was taken to the laboratory. Subsamples were oven-dried at 70 °C to constant weight and then re-weighed. A dry to wet ratio of each component was obtained, and dry weights of all tree components were calculated. Because most shrubs, including dwarf *Rhizophora mangle* trees, have several stems at the ground level and no recognizable main stem from which dbh can be measured, biomass can not be calculated using dbh as an independent variable. Thus, other variables have been used including crown diameter axes (Rittehnhouse and Sneva 1977), crown volume (Crow 1978), and height times circumference (Azocar et al. 1981; Et-
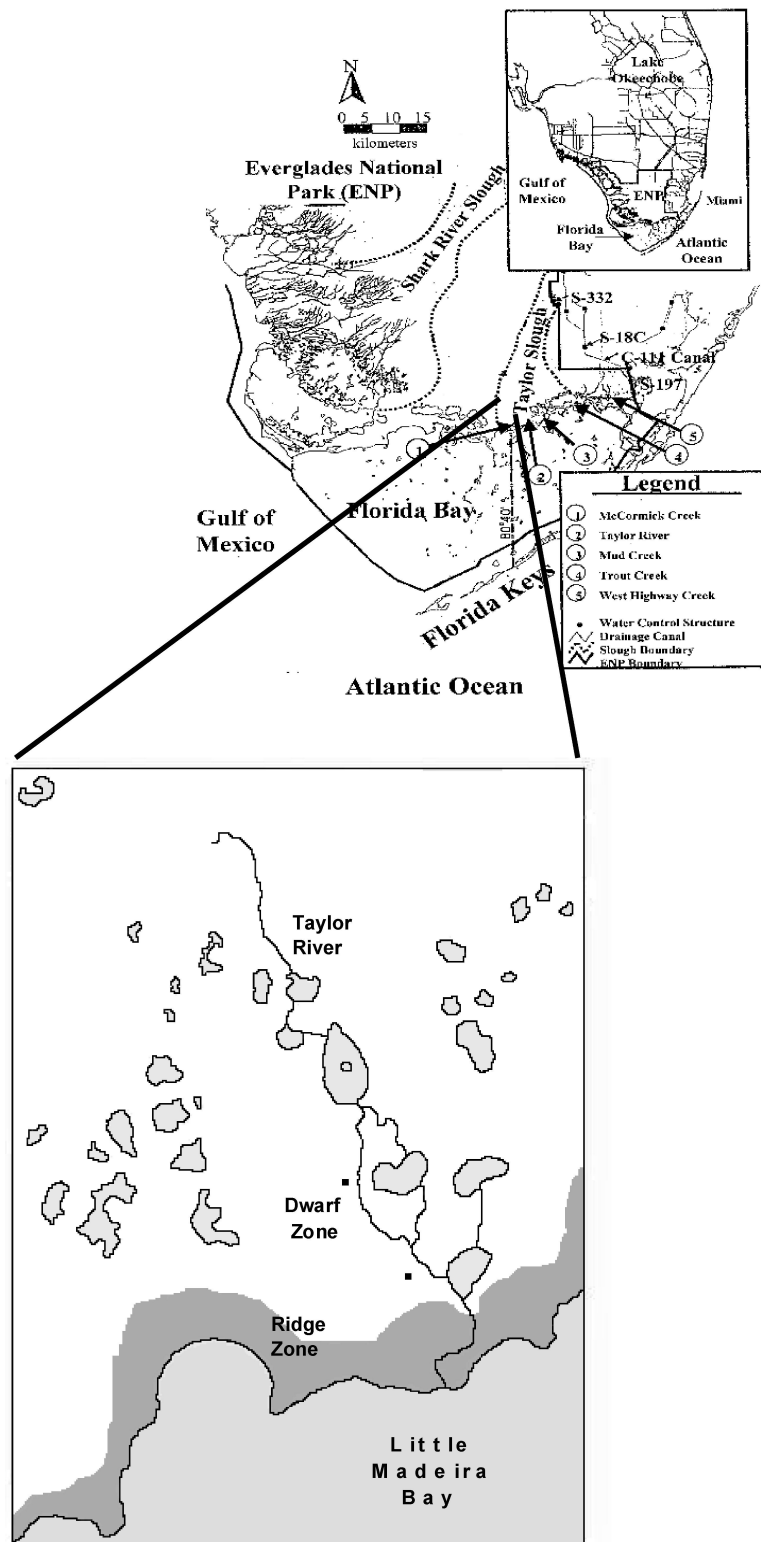
Figure 1. Everglades Salinity Transition Zone showing Taylor Slough and the basin area dominated by dwarf red *R. mangle*.

tiene 1989). We developed an allometric equation to estimate dwarf *Rhizophora mangle* biomass using several dimensional characteristics of the plant such as height, crown area, number of prop roots, and a combination of crown area × number of prop roots. Data were natural log transformed and a multiple linear analysis was performed using JMP 4.0 (SAS Institute 2000). A significance level of p = 0.05 was used to interpret results of all statistical tests.

Results

Forest structure

Tree density ranged from 7062 to 23 778 stems ha^{-1}, basal area ranged from 2.35 to 6.44 m^2 ha^{-1}, and tree height varied from 0.9 to 1.2 meters. *Rhizophora mangle* was the dominant species and accounted for 99% of the dominance and 97% of the density. Although *L. racemosa* and *A. germinans* individuals occurred in two of the transects, they were few in number and were dwarfed as well.

Above-ground biomass

The allometric relationship that best fit our data was based on two different types of multivariate analysis: stepwise and backward regression. Both models contained the same subset of variables: Ln (height), Ln (crown diameter), Ln (number of prop roots), and Ln (crown area × number of prop roots). This analysis was useful to determine the relative importance of the variables in explaining the data variance. The newly created variable Ln (crown area × number of prop roots) was the first and only variable to enter both models, and it explained the majority of the total biomass variability (R^2 = 0.96). Ln (height), Ln (crown diameter), and Ln (number of prop roots) explained very little of the mangrove biomass variability, and did not remain in the model. A linear relationship was obtained by plotting dry weight against the natural logarithm of the variable crown area × number of prop roots. The least square line of best fit is described as:

$$LnBiomass = 1.2522 + 0.5083 \times Ln \text{ (crown area} \times \text{number of prop roots)}$$

While the natural log-log equation provides a convenient method for estimating the values of the intercept and slope, it is more useful to display the allometric relationship as the power function of the independent variable. Thus, the allometric equation that best explained the biomass variability of dwarf *Rhizophora mangle* trees was:

$$Y = B \times X^{-0.5083} \quad R^2 = 0.96 \quad (p < 0.0001)$$

where: Y = total above-ground biomass; B = 3.4980 (natural antilog of intercept in Equation 1); X = crown area × number of prop roots.

The regression constants (B and X), the correlation coefficient (R^2), and p values for each component (leaves, stem and branches, prop roots, and total biomass) are summarized in Table 1. Even though the Ln (crown diameter) variable did not enter the model when the multiple-linear regression analysis was run, a simple linear model was obtained explaining 89% of the total aboveground variability. The allometric equation was:

$$Y = B \times X^{-0.8166} \quad R^2 = 0.89 \quad (p < 0.0001)$$

where: Y = total above-ground biomass; B = 0.84126; X = crown area.

This allometric model can also be used to estimate the aboveground biomass of dwarf *R. mangle*. However, biomass calculated by this equation was underestimated by 22% compared to that of the former equation. Similarly, we estimated the partitioning of aboveground biomass using the allometric equations developed for each component (Table 1). According-

Table 1. Linear regression equations used to estimate aboveground biomass.

Plant component	Intercept (A)	Slope (B)	R^2	Significance of F value
Leaf	−2.0045	0.5568	0.97	p < 0.0000
Branch	−0.6769	0.5751	0.96	p < 0.0001
Prop root	1.1809	0.4806	0.91	p < 0.0000
Total	1.2522	0.5083	0.96	p < 0.0000

The equations are in the form log e Y = A + B long e X, where Y = dry biomass (g), and X = log e (crown area × number of prop roots).

ly, dwarf *R. mangle* allocated biomass as follows: prop roots (69%), stem-branches (25%), and leaves (6%).

Discussion

Few studies have estimated biomass of mangrove species and most of the available estimates are for the genus *Rhizophora* (Brown and Lugo 1982; Day et al. 1987). Ross et al. (2001) developed an allometric equation for mixed dwarf and fringe red mangroves from a site at Biscayne Bay, Florida, using DBH × Crown Volume as an independent variable to estimate biomass for trees located at fringe and dwarf sites. Average aboveground biomass, estimated by Ross et al. (2001), was 18.2 t ha^{-1}. Using our allometric equation, aboveground biomass estimation ranged from 7.9 to 21.2 t ha^{-1} which is similar to the biomass of dwarf red mangroves located at Biscayne Bay. Thus, we are confident of the biomass estimations obtained using our allometric relationship; however, care should be taken in applying the allometric equation developed in this study to other mangrove stands.

Our aboveground biomass estimation (7.9 to 23.2 t ha^{-1}) is lower than that of Riverine, Fringe, or Basin mangrove forests located in the Caribbean and Atlantic regions (Table 2). However, our biomass estimation was slightly higher than that of a similar red mangrove dwarf forest (7.9 t ha^{-1}) located in Turkey Point, Florida (Lugo and Snedaker 1974) and relatively higher than that of a dwarf forest dominated by *Avicennia marina* (6.8 t ha^{-1}) located in Tuff Crater, New Zealand (Woodroffe 1985). The low aboveground biomass, observed at Tuff Crater, New Zealand, was directly related to ecological factors such as low nutrient availability and high-reduced soil conditions (Woodroffe 1985). Additionally, low aboveground biomass has been linked to long hydroperiods (Pool et al. 1977), high soil salinity (Ball 1988; Lin et al. 1992), sulfide accumulation (McKee 1993), reduced soils (Pezeshki et al. 1997) and nutrient limitation (Boto and Wellington 1983). At our study site, low aboveground biomass (Table 2) might be related to low nutrient resources particularly nitrogen and phosphorus. Accordingly, total soil nitrogen ranged from 1.9 to 2.9 mg cm^{-3}, total soil phosphorus ranged from 0.07 to 0.09 mg cm^{-3}, and interstitial soil salinity ranged from 10 to 15 g kg^{-1}. In contrast, at Shark River, Florida, where mangrove forest de-

velopment in South Florida is highest, soil salinity, total soil nitrogen and phosphorus values averaged 20 g kg^{-1}, 2.2 mg cm^{-3}, and 0.24 mg cm^{-3}, respectively (Chen and Twilley 1999). Those results suggest that soil salinity and soil nitrogen were not limiting forest development at our study site. However, low P availability might be a limiting factor as has been shown for other red dwarf mangrove communities in Belize and Florida where tree growth and development are the poorest among Caribbean mangrove forests (Feller 1995; Koch 1997; Chen and Twilley 1999; Feller et al. 1999). Additionally, Koch (1997) working in two red dwarf mangrove forests similar to our study site, showed that soil redox potentials were highly reduced (−100 to −200 mV). Thus, it is possible that both low phosphorus availability and highly reduced soils are important factors limiting mangrove tree growth and, therefore, aboveground biomass accumulation.

The partitioning of dry matter between different components of the tree is affected by factors such as age, environmental conditions, forest structure, and competitive interactions (Landsberg 1986; Koslowski et al. 1991). *Rhizophora apiculata* and *R. mangle* individuals growing in optimal conditions of light and nutrients allocate more dry matter to stem and branches at expense of the prop roots (Clough 1992; Lugo and Snedaker 1974). Working with multi-stemmed *Rhizophora stylosa* trees, located in northwestern Australia, Clough et al. (1997) showed that the contribution to stem-branches increased from 25% to 50% when mangrove trees increased their dbh from 5 to 25 cm. In contrast, prop roots contribution decreased from 40% to 30% when trees increased from 5 to 25 cm in dbh. At our study site, dwarf *R. mangle* showed a similar pattern in which stem-branch dry matter contribution increased and prop root dry matter contribution decreased (Figure 2). However, the average prop root contribution was higher in dwarf *R. mangle* (69.2%) than in multi-stemmed *R. stylosa* (35%) (Clough et al. 1997). In contrast, average stem-branch contribution was higher in *R. stylosa* (53%) than in dwarf *R. mangle* (25.2%). Clough et al. (1997) argued that the dry matter partitioning pattern in *R. stylosa* was due to extreme dry conditions that characterized their study area and that more dry matter was invested in developing an extensive root system to cope with high soil gradient salinities around the roots. At our study site, soil salinity is not considered a constraint since it ranged from 10 to 25 g kg^{-1}, falling within the range in which *R. mangle* grows optimally (Day et al. 1987, 1996; Twilley et al. 1996). In contrast,

Table 2. Aboveground biomass, and biomass partition among mangrove forests in North and South America.

| Mangrove location	Forest type	Above-ground biomass (ton ha^{-1})	Above-ground biomass partitioning			Source
			% Leaves	% Prop roots	% Stems and branches	
Florida						
Ten Thousand Islands	Riverine	135.5	4.7	8.3	87.0	Lugo and Snedaker (1974)
Ten Thousand Islands	Fringe	102.5	5.8	18.5	75.8	Lugo and Snedaker (1974)
Ten Thousand Islands	Overwash	124.0	5.7	37.6	56.6	Lugo and Snedaker (1974)
Turkey Point	Dwarf	7.9	9.1	40.6	50.3	Lugo and Snedaker (1974)
Biscayne Bay	Fringe	57.8	13.6	22.1	64.3	Ross et al. (2001)
Byscaine Bay	Dwarf	8.8	16.4	17.7	65.9	Ross et al. (2001)
Taylor Slough	Dwarf	12.5	5.6	69.2	25.2	This study
Caribbean						
Puerto Rico	Fringe	63.0				Golley et al. (1962)
Mexico						
Terminos Lagoon						
Boca Chica	Riverine	135.0	–	29.1	70.9	Day et al. (1987)
Estero Pargo	Fringe	120.0	–	22.4	77.6	Day et al. (1996)
Estero Pargo	Basin	49.4	–	–	–	Day et al. (1996)
Central America						
Panama	Riverine	280.0				Golley et al. (1975)
South America						
French Guiana	Riverine	188.6	2.8	–	97.2	Fromard et al. (1998)
French Guiana	Riverine	122.2	2.8	–	97.2	Fromard et al. (1998)
French Guiana	Fringe	31.5	9.1	–	91.8	Fromard et al. (1998)
French Guiana	Fringe	71.8	6.0	–	94.0	Fromard et al. (1998)
French Guiana	Fringe	35.1	10.2	–	89.8	Fromard et al. (1998)
French Guiana	Basin	247.5	2.9	–	97.2	Fromard et al. (1998)
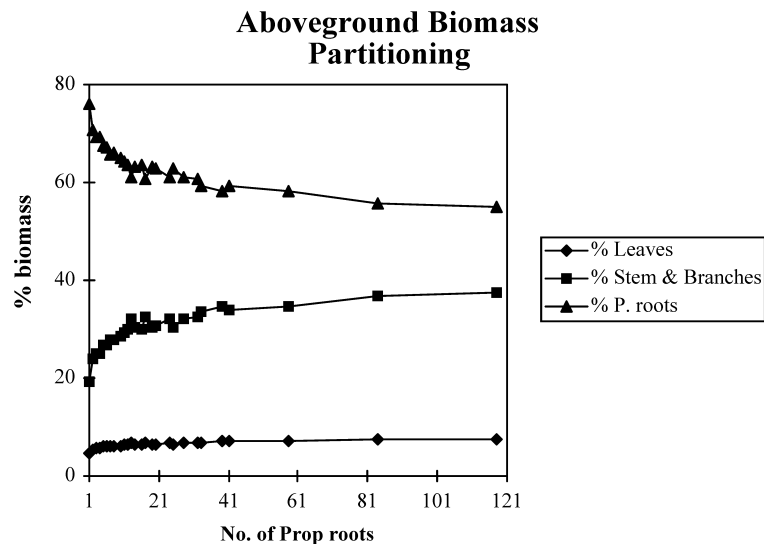
Figure 2. Aboveground biomass partitioning at Taylor Slough. X-axis shows the number of prop roots in each tree that was used as a proxy for increase in tree biomass.

phosphorus availability and highly reduced soils play a major role in determining tree growth and development (Twilley et al. 1996; Koch 1997; Feller 1995; Feller et al. 1999). Our results suggest that both factors may be important in explaining the partitioning pattern of dwarf *R. mangle* in South Florida.

Acknowledgements

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