

Development of allometric relations for three mangrove species in South Florida for use in the Greater Everglades Ecosystem restoration

Thomas J. Smith III^{1,*} and Kevin R.T. Whelan^{2,3}

¹U.S. Geological Survey, Florida Integrated Science Center, 600 Fourth Street South, St. Petersburg, 33701 Florida, USA; ²U.S. Geological Survey, Florida Integrated Science Center, c/o Department of Biological Sciences, Florida International University, OE Bldg - Rm 167, Miami, 33199 Florida, USA; ³South Florida/Caribbean Inventory and Monitoring Network Office, U.S. National Park Service, 18001 Old Cutler Road, Suite 419, Palmetto Bay, 33157 Florida, USA; *Author for correspondence (e-mail: Tom_J_Smith@usgs.gov; phone: +727-803-8747; fax: +727-803-2030)

Received 2 June 2005; accepted in revised form 21 December 2005

Key words: Biogeographic comparison, Biomass, Diameter, Height, Power law, Restoration, Scaling relation

Abstract

Mathematical relations that use easily measured variables to predict difficult-to-measure variables are important to resource managers. In this paper we develop allometric relations to predict total aboveground biomass and individual components of biomass (e.g., leaves, stems, branches) for three species of mangroves for Everglades National Park, Florida, USA. The Greater Everglades Ecosystem is currently the subject of a 7.8-billion-dollar restoration program sponsored by federal, state, and local agencies. Biomass and production of mangroves are being used as a measure of restoration success. A technique for rapid determination of biomass over large areas is required. We felled 32 mangrove trees and separated each plant into leaves, stems, branches, and for *Rhizophora mangle* L., prop roots. Wet weights were measured in the field and subsamples returned to the laboratory for determination of wet-to-dry weight conversion factors. The diameter at breast height (DBH) and stem height were also measured. Allometric equations were developed for each species for total biomass and components of biomass. We compared our equations with those from the same, or similar, species from elsewhere in the world. Our equations explained $\geq 93\%$ of the variance in total dry weight using DBH. DBH is a better predictor of dry weight than is stem height and DBH is much easier to measure. Furthermore, our results indicate that there are biogeographic differences in allometric relations between regions. For a given DBH, stems of all three species have less mass in Florida than stems from elsewhere in the world.

Abbreviations: DBH – diameter at breast height

Introduction

The Greater Everglades Ecosystem extends for 350 km from Lake Tohopekaliga in the north to

Florida Bay and the Florida Keys in the south and is over 150 km from east to west in places. The vast freshwater wetlands of the region have been extensively ditched, diked, and drained for

agricultural development (Bottcher and Izuno 1994), urban water supply, and flood protection (Light and Dineen 1994). The greatly altered drainage patterns have led to a decrease in freshwater inflow to the southern Everglades estuaries of more than 50% (Smith et al. 1989). Questions exist concerning the impacts of increasing freshwater inflows to coastal wetlands.

At present, the Greater Everglades is the site of a massive ecosystem restoration program, the Comprehensive Everglades Restoration Project (CERP) (Davis and Ogden 1994; Porter and Porter 2002). Numerous water-control structures will be removed, canals filled, and dikes leveled, all to restore the quantity and quality of water in the system.

Mangrove forests dominate the coastal portion of the Everglades within Everglades National Park, an International Biosphere Preserve (Smith et al. 1994). What will be the effect on primary production or species composition in mangrove forests as freshwater flow is altered? As CERP progresses resource managers need simple but accurate tools to measure restoration success. We discuss the development of a simple tool for the rapid measurement of biomass and change in biomass over time using allometric, or scaling, relations.

Scaling relations are fundamental in ecological studies from the level of the individual organism to the examination of patch structure across landscapes (Horn 1971; Niklas 1994). In forest ecology these relations have been used to examine how an individual tree's crown architecture changes during growth from seedling to sapling to adult stature (Aiba and Kohyama 1997), how life history traits and tree structure vary among species (Whittaker and Woodwell 1968; Coomes and Grubb 1998) and to explain density-dependant and gap-dynamic processes in whole forest stands (Alvarez-Buylla 1994). Allometric relations "characterize harmonious growth with changing proportions" usually with a logarithmic association (Lieth and Whittaker 1975). They are developed by establishing relations between some easily measured individual plant parameter(s) and some variable that is much harder to measure. For trees, the diameter at breast height (DBH) of the trunk is commonly used, allowing for non-destructive assessment of biomass and growth rates. Once developed, the equation can be used to calculate

an estimate of the biomass for both living and dead plants. With a calculated biomass figure it is possible to determine a change in biomass from one time to another based on change in DBH. When summed for all individuals and for each species within a known area, biomass and productivity can be expressed on an areal basis. Scaling relations have been used to estimate forest biomass and productivity in temperate regions (Rochow 1974; Whittaker and Marks 1975) and tropical regions Day et al. 1987; Clough and Scott 1989).

Several researchers have developed relations to predict aboveground biomass using DBH for mangroves from a variety of areas (Woodroffe 1985; Putz and Chan 1986; Clough and Scott 1989; Silva et al. 1991; Fromard et al. 1998). However, no allometric equations have been developed for mangroves in Florida an area at the northern limit of their distribution which is 25° N latitude. Standing biomass as well as litterfall in mangroves decreases as latitude increases, as demonstrated by Saenger and Snedaker (1993).

The purpose of this work was to develop allometric relations for above ground biomass and DBH for the three mangrove species found in Everglades National Park: *Avicennia germinans* (L.) Sterns (black mangrove), *Laguncularia racemosa* (L.) Gaertn. (white mangrove) and *Rhizophora mangle* L. (red mangrove). We also tested for relations between DBH and different components of total biomass (leaves, stems, and branches) for each species. Finally, we compared our allometric equations with those developed for the same, or similar, species from other regions of the globe.

Methods

Nomenclature

The nomenclature for mangrove names follows Tomlinson (1986).

Site descriptions

Individuals of the three mangrove species were collected from three locations in Everglades

National Park (Figure 1): the Black Forest (25°08'54" N, 80°55'00" W); Mud Bay (25°16'08" N, 81°05'02" W); and Highland Beach (25°30'0", 81°12'0" W). Historically, the Black Forest was dominated by large *Avicennia* that were devastated by the Labor Day hurricane of 1935 (Craighead 1971). Currently, the site is a mixed stand with all three species present in various size classes. The Mud Bay location is a well-developed stand of red and black mangroves with many stems in larger DBH classes. Hurricane Andrew crossed directly over the Highland Beach site in August 1992 (Smith et al. 1994). Although this site had been disturbed, recovery was underway and numerous small-stemmed individuals of all three species were readily available for sampling.

Sample collection and processing

We collected 32 specimens of the three mangrove species: 8 black, 10 white, and 14 red. We choose individuals with straight trunks that showed no obvious signs of damage (hurricane, lightning, wind, or insect damage). We did not choose stunted, dwarfed, or multi-stemmed specimens because they have extremely different allometric relations (Clough et al. 1997). Such individuals were rare in our study area. After an individual was selected its DBH was measured at 1.4 m above the sediment surface or above the highest prop root for *Rhizophora* (a commonly accepted procedure, see Clough and Scott 1989). Each specimen was cut at ground level and total stem height

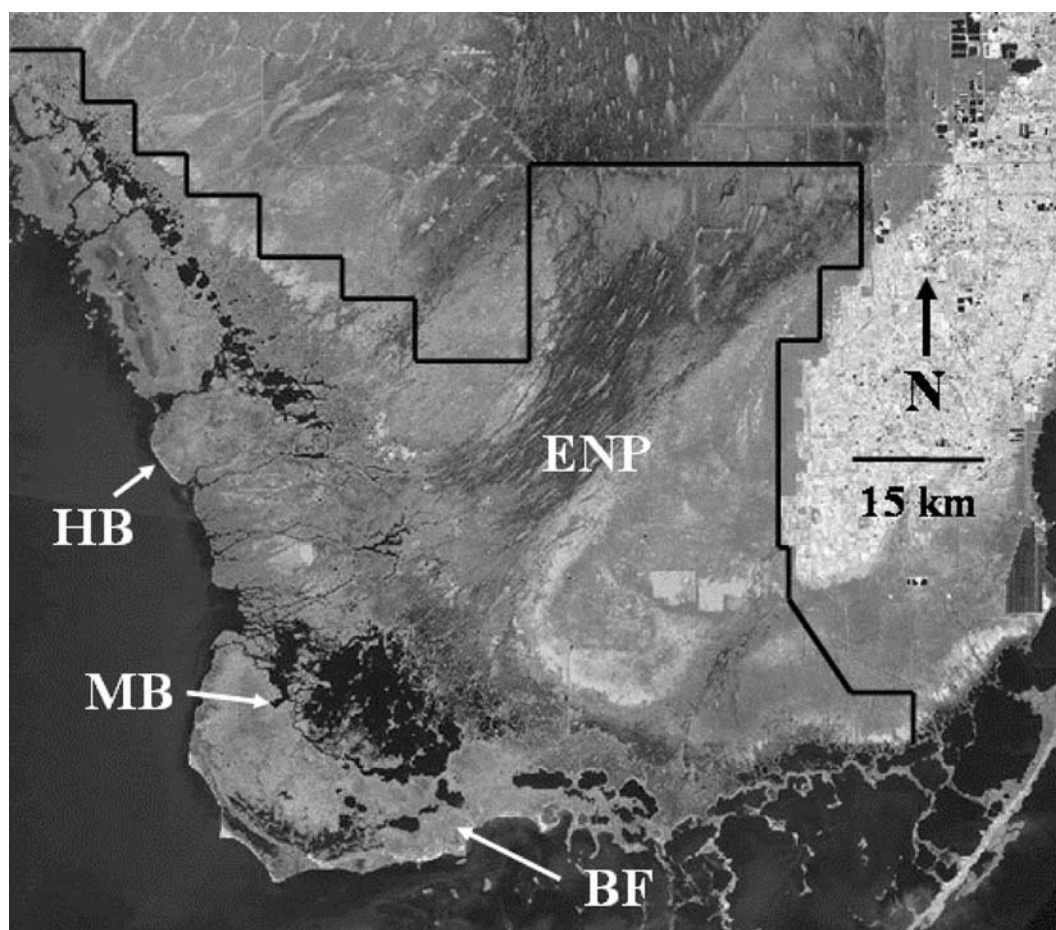


Figure 1. The southern peninsula of Florida showing the approximate boundaries of Everglades National Park (ENP). We collected samples from the Black Forest (BF), Mud Bay (MB), and Highland Beach (HB).

was measured. All above-ground biomass was harvested and separated into four components: stem, branches, leaves, and prop roots (*Rhizophora* only). We measured these components in the field using a spring scale of appropriate size to get wet-weight biomass. We collected sub-samples of each component from each tree. These were returned to the laboratory and dried to a constant mass at 70 °C using a standard drying oven and re-weighed. Wet-weight to dry-weight conversion factors were calculated and averaged by component and by species. With this information we calculated an estimate of dry weight.

Calculations

We used the equation: $\log_{10}y = a \log_{10}(DBH) + b$ to relate dry biomass to DBH (where y = above-ground dry biomass in kg and DBH is in cm). Similar equations have been used by other researchers (Putz and Chan 1986; Day et al. 1987; Clough and Scott 1989; Fromard et al. 1998). We also examined the relations of stem height to biomass using the same equation (Whittaker and Marks 1975; Clough 1992). For each species separate regressions were calculated for each component of biomass (stem, branch, and leaf for all species and also prop-roots for *Rhizophora*) using the Statistical Analysis System software package. Total biomass was determined by summing the individual components for each species and then another regression was performed.

Biogeographic comparisons

We compared our allometric equations for *Avicennia* and *Laguncularia* with those generated by Fromard et al. (1998) at 4–5° N latitude and by Day et al. (1987) at 18° N. We included the equations of Silva et al. (1991) from 23° S for comparisons with *R. mangle*. We also compared *R. mangle* with *Rhizophora* species (*R. apiculata*, *R. mucronata*, *R. stylosa*) from the Indo-West Pacific region (Putz and Chan 1986; Clough and Scott 1989). Our comparisons spanned only the range of DBHs reported in other studies. We did not extrapolate predicted values from reported equations past the data ranges over which they had been calculated.

Using the equations to assess the Everglades restoration

As CERP proceeds one of the expected impacts is altered salinity regimes in the lower Shark River estuary. Growth rate and biomass accumulation in mangroves is at least partially related to sediment pore-water salinity (Sobrado 1999; Tuffers et al. 2001). We used the allometric equations to derive biomass estimates for several long-term plots along the Harney River (Smith 2004). The plots were established in 1998. Stems were identified and individually tagged with aluminum tree tags. DBH was measured as described above. The plots have been re-sampled four times. We calculated the total biomass of each stem from the species specific regression equation. Growth was calculated as the change in total biomass between sampling intervals. Individual growth estimates were summed for each plot by species and by time interval. Sediment pore-water salinity was also measured in the plots at a depth of 30 cm which is in the middle of the root zone. We calculated the mean salinity for each sampling interval for each plot. We then regressed the change in biomass, for each species, plot, and sampling interval against mean salinity.

Results and discussion

Biomass vs. stem height and DBH

Both stem height and DBH were excellent predictors of total above-ground biomass for all three species (Figures 2, 3) with total variance explained (R^2) greater than 0.92 in all cases (Table 1). DBH yielded R^2 s that were slightly higher than those for stem height. However, we consider the difference to be insignificant. The best fits were higher for *Laguncularia* than for either *Avicennia* or *Rhizophora*. Given these results, and the fact that DBH is measured very accurately and with great ease in the field, whereas stem height is very difficult to measure non-destructively, we consider only DBH for the remainder of the study.

Stem, branch, leaf, and prop root biomass vs. DBH

Highly significant relationships were found for all components of above-ground biomass and

DBH for all three species. In general, regressions for stem biomass had higher variance explained ($R^2 \geq 0.95$) than did regressions for branch and leaf biomass (Table 1 and Figures 4–6). The latter two components of biomass were much more variable. No differences were found among species with respect to total stem biomass and DBH (Figure 4). However, *Rhizophora* seems to

allocate more biomass to branches than either *Avicennia* or *Laguncularia* over the entire range of DBHs measured (Figure 5). *Rhizophora* also seems to allocate more biomass to leaf tissue than *Avicennia* and *Laguncularia*, but only at larger DBHs (Figure 6). For *Rhizophora*, prop root biomass was significantly related to DBH (Figure 7).

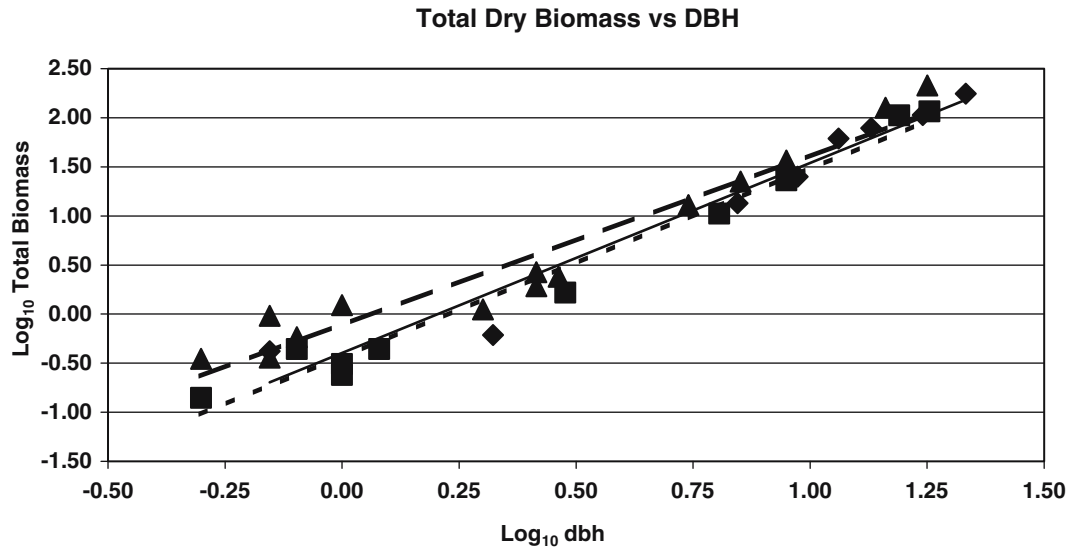


Figure 2. Total dry biomass as a function of DBH for the three mangrove species. *Avicennia* = diamonds with solid line, *Laguncularia* = squares with dotted line, and *Rhizophora* = triangles with dashed line.

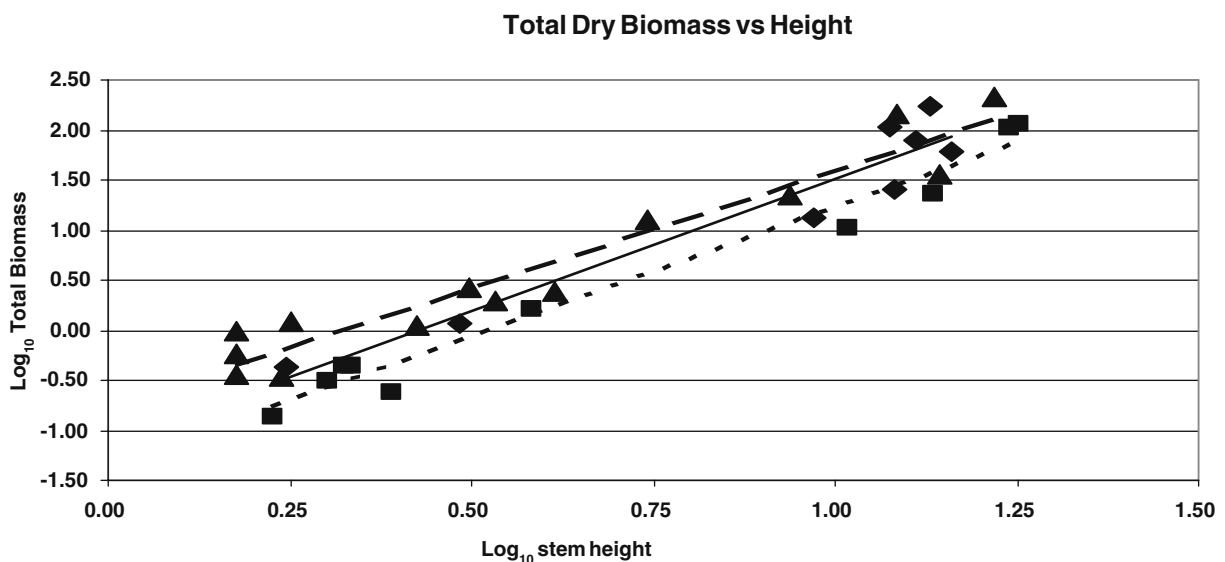


Figure 3. Total dry biomass as a function of stem height for the three mangrove species. Symbols as in Figure 2.

Table 1. Results from the regression analyses are given.

Regression Parameters	a	b	R ²
Total Dry Biomass vs. height			
<i>Avicennia</i>	2.641	-1.124	0.921
<i>Laguncularia</i>	2.585	-1.355	0.973
<i>Rhizophora</i>	2.357	-0.769	0.931
Total Dry Biomass vs. DBH			
<i>Avicennia</i>	1.934	-0.395	0.951
<i>Laguncularia</i>	1.930	-0.441	0.977
<i>Rhizophora</i>	1.731	-0.112	0.937
Stem Dry Biomass vs. DBH			
<i>Avicennia</i>	2.062	-0.590	0.982
<i>Laguncularia</i>	2.087	-0.692	0.981
<i>Rhizophora</i>	1.884	-0.510	0.958
Branch Dry Biomass vs. DBH			
<i>Avicennia</i>	1.607	-1.090	0.773
<i>Laguncularia</i>	1.837	-1.282	0.951
<i>Rhizophora</i>	1.784	-0.853	0.958
Leaf Dry Biomass vs. DBH			
<i>Avicennia</i>	0.985	-0.855	0.714
<i>Laguncularia</i>	1.160	-1.043	0.889
<i>Rhizophora</i>	1.337	-0.843	0.927
Prop Root Dry Biomass			
<i>Rhizophora</i>	0.160	-1.041	0.821

Parameters: a = slope of the regression line, b = intercept of the regression line, R² = coefficient of determination. All regression equations are significant at the p ≤ .05 level. DBH size ranges, in cm, were: *Avicennia* (0.7–21.5), *Laguncularia* (0.5–18.0), and *Rhizophora* (0.5–20.0).

Biogeographic comparisons

Our equations give the lowest estimate of biomass for all three species when compared to results from other studies (Table 2, see our Figures 8–10 for references). A mangrove with a given DBH will have a greater predicted biomass near the equator than one with the same DBH that is growing in a location to the north or south of the equator. The differences are least for *Laguncularia* and greatest for *Rhizophora*. For example, *Laguncularia* with a DBH 10 cm is predicted to have 60 kg dry mass in French Guiana (Fromard et al. 1998), 50 kg dry mass in the Yucatan of Mexico (Day et al. 1987), and 45 kg dry mass in the Florida Everglades (the present study, see Figure 8). Unfortunately the studies by Fromard et al. (1998) and Day et al. (1987) spanned a small range in DBH (1–10 cm). Therefore we could not compare to the largest *Laguncularia* trees we sampled (18 cm). For *Avicennia*, specimens 10 cm DBH are predicted to be equal in biomass for French Guiana and Florida (≈35 kg), and both of these areas will be less than predicted for Mexico (67.5 kg, see Figure 9). As DBH increases for *Avicennia*, the predicted biomass for French Guiana and Florida also diverge (Figure 9). At a DBH of 20 cm, *Avicennia* in

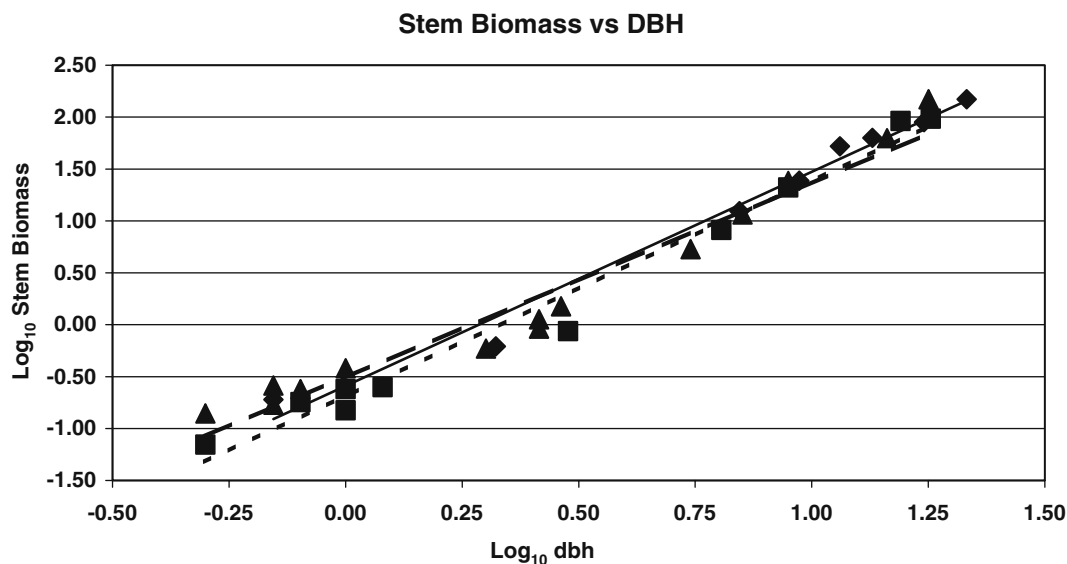


Figure 4. Stem dry biomass as a function of DBH for three mangrove species. Symbols as in Figure 2.

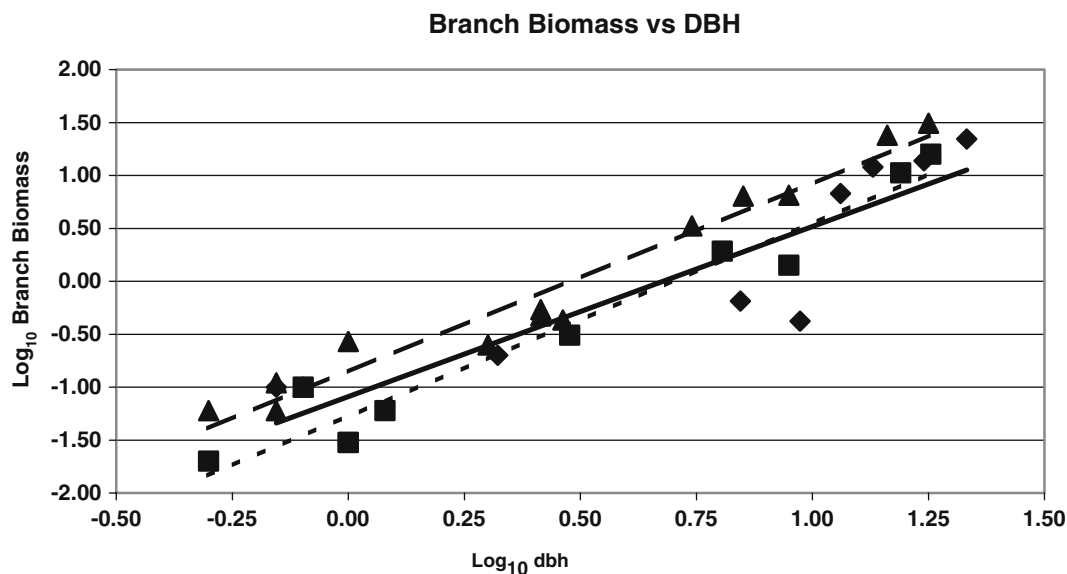


Figure 5. Branch dry biomass as a function of DBH for three Florida mangrove species. Symbols as in Figure 2.

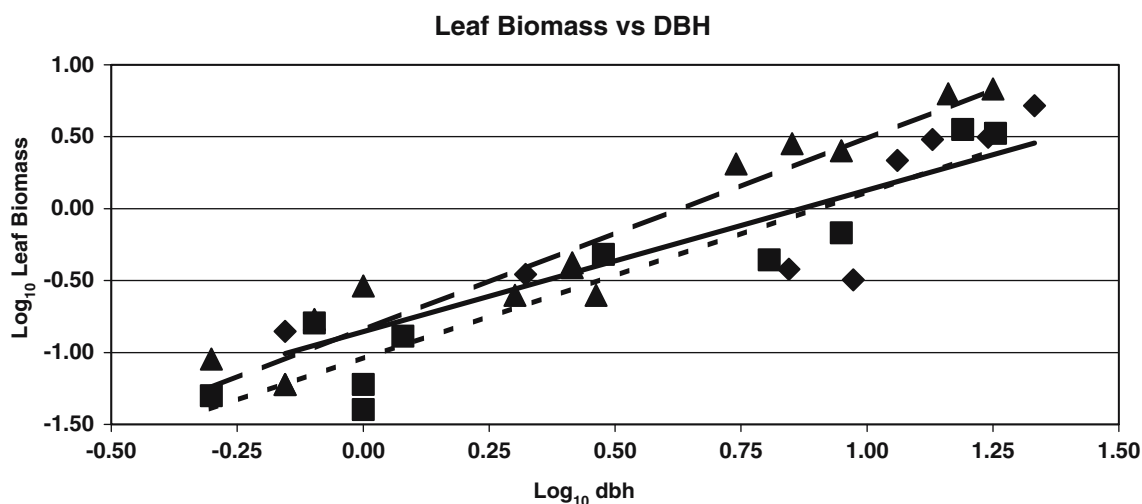


Figure 6. Leaf dry biomass as a function of DBH. Symbols as in Figure 2.

French Guiana are predicted to weigh some 246 kg, whereas in Florida the same size stem is predicted to weigh a mere 136 kg (Figure 9). The differences are most striking however for *Rhizophora* (Figure 10). At smaller size classes (< 10 cm DBH) differences are indicated with stems in Australia, Malaysia, French Guiana and Puerto Rico predicted to have more biomass than stems in Florida, Mexico or Brazil (Figure 10). Larger stems (> 15 cm DBH) were not measured by many

researchers so comparisons are limited to French Guiana, Florida, Australia and Malaysia. A *Rhizophora* in Florida with a 20 cm DBH stem is predicted to have approximately ≈ 140 kg of above-ground dry biomass (this study). *Rhizophora* from northern Australia, French Guiana and Malaysia are predicted to have from 300–350 kg of dry biomass (Figure 10).

The general outcome of the model comparisons is that allometric relations differ by species and region

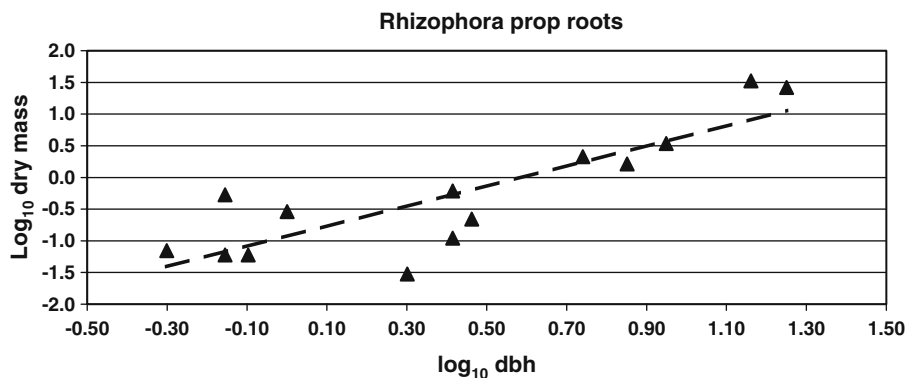


Figure 7. *Rhizophora* prop root biomass as a function of DBH.

Table 2. Regression equations developed by other studies.

Species	DBH Range cm	Equation	<i>a</i>	<i>b</i>	Reference
Atlantic/Caribbean					
<i>A. germinans</i>	1–10	$\log_e y = a \log_e \text{DBH} + b$	2.507	-1.561	Day et al. (1987)
<i>L. racemosa</i>	1–10	$\log_e y = a \log_e \text{DBH} + b$	2.192	-1.592	Day et al. (1987)
<i>R. mangle</i>	1–10	$\log_e y = a \log_e \text{DBH} + b$	2.302	-1.580	Day et al. (1987)
<i>A. germinans</i>	1–32	$y = b (\text{DBH})^a$	2.4	0.140	Fromard et al. (1998)
<i>L. racemosa</i>	1–10	$y = b (\text{DBH})^a$	2.5	0.102	Fromard et al. (1998)
<i>R. mangle</i>	1–42	$y = b (\text{DBH})^a$	2.6	0.128	Fromard et al. (1998)
<i>R. mangle</i>	3–11	$y = b e^{a(\text{DBH})}$	0.3	1.41	Silva et al. (1991)
Indo-West Pacific					
<i>R. apiculata</i>	5–31	$\log_{10} y = a \log_{10} \text{DBH} + b$	2.516	-0.767	Putz and Chan (1986)
<i>Rhizophora</i> spp.	3–25	$\log_{10} y = a \log_{10} \text{DBH} + b$	2.685	-0.979	Clough and Scott (1989)

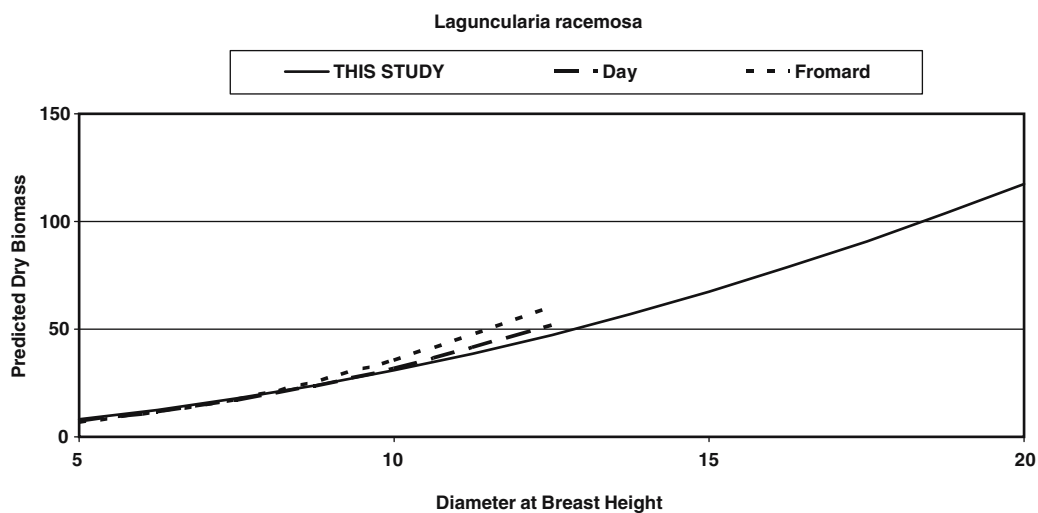


Figure 8. Predicted total biomass for *Laguncularia racemosa* based on the allometric equations from Day et al. (1987) as shown by dashed line, from Fromard et al. (1998) as shown by dotted line, and by this study as shown by solid line. Predicted values have been calculated and plotted only for the range in DBHs reported by each study.

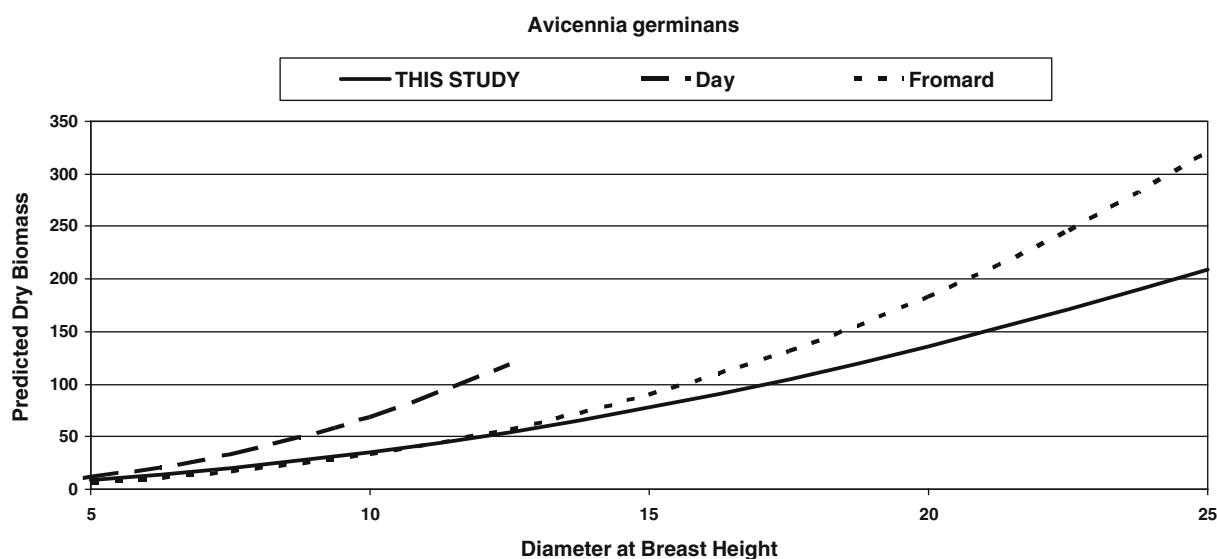


Figure 9. Predicted total biomass for *Avicennia germinans* based on the allometric equations from Day et al. (1987) as shown by dashes line, from Fromard et al. (1998) as shown by dotted line, and by this study as shown by solid line. Predicted values have been calculated and plotted only for the range in DBHs reported by each study.

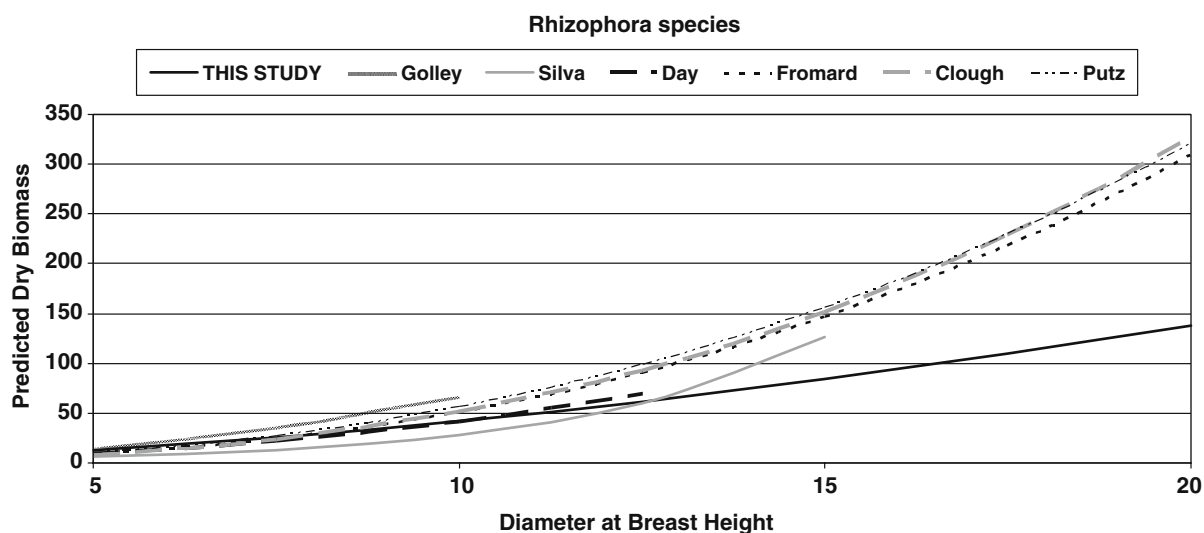


Figure 10. Predicted total biomass for *Rhizophora* spp. based on the allometric equations from this study and other studies as shown in the legend.

and do not necessarily follow latitudinal or general area trends. The biomass values generated with allometric equations should be considered with caution when used to extrapolate outside of the size range sampled or from areas with inherently different environmental parameters (for example, salinity, nutrients, hydrological exchange, stem density, net primary productivity, and herbivory).

Using the equations to assess the Everglades restoration

Mean sediment salinity predicted change in biomass relatively well for *Laguncularia* but not for *Rhizophora* or *Avicennia* (Figure 11). This is not totally unexpected as *Laguncularia* is the least tolerant species. Both *Avicennia* and *Rhizophora*

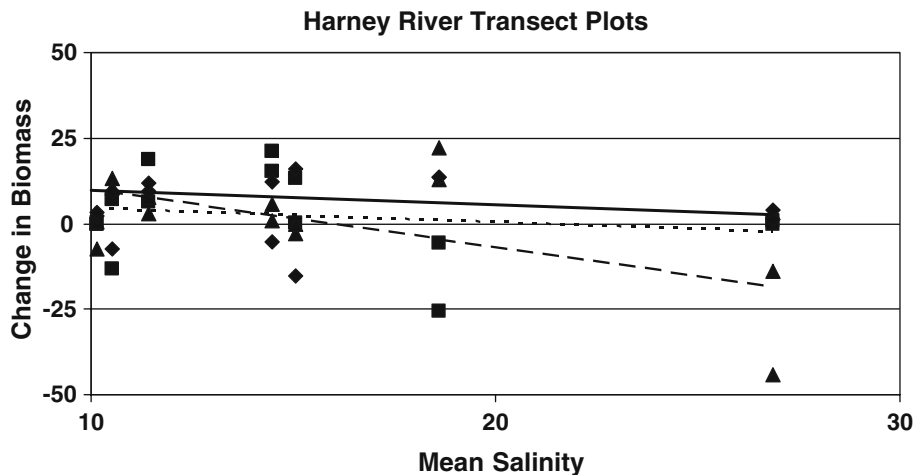


Figure 11. Change in biomass as a function of mean sediment porewater salinity for plots along the Harney River in Everglades National Park. The regression equations for *Avicennia* (squares) and *Rhizophora* (diamonds) are not significant. The regression for *Laguncularia* is significant. The regression equation is: Change in biomass = $-1.691(\text{mean salinity}) + 26.905$, $r^2 = 0.38$, $p < 0.01$.

have broad salinity tolerances with *Avicennia* capable of surviving in hypersaline conditions (Pool et al. 1977). Plot biomass decreased with increasing sediment salinity for *Laguncularia*. Based on predictions of the hydrological models used in CERP (Fennema et al. 1994, Langevin et al. 2005), we expect salinities to decrease as freshwater inflows increase. Thus, we should be able to monitor an increase in biomass of *Laguncularia* in these plots as CERP proceeds.

Acknowledgements

Many individuals assisted with sampling, including S. Beeler, S. Cleaves, J. Merickel, D. Riggs, L. Romero, W. Wiebe and numerous Earth Watch volunteers. Funding was provided by the Critical Ecosystems Studies Initiative, administered by Everglades National Park, under Interagency Agreement #5280-5-9020. Additional support was provided by the U.S. Geological Survey's Priority Ecosystems Studies Program for the South Florida Ecosystem and from the Global Climate Change Program. C. McIvor, K. Yates, and two anonymous reviewers provided helpful comments on an earlier version of the manuscript. Use of trade and/or product names does not imply endorsement by the U.S. Geological Survey.

References

- Aiba S.-I. and Kohyama T. 1997. Crown architecture and life-history traits of 14 tree species in a warm-temperate rain forest: significance of spatial heterogeneity. *J. Ecol.* 85: 611–624.
- Alvarez-Buylla E.R. 1994. Density dependence and patch dynamics in tropical rain forests: matrix models and applications to a tree species. *Am. Nat.* 143: 155–191.
- Bottcher A.B. and Izuno F.T. (eds) 1994. Everglades Agricultural Area (EAA): Water, Soil, Crop and Environmental Management. University Press of Florida, Gainesville, FL, USA.
- Clough B.F. 1992. Primary productivity and growth of mangrove forests. In: Robertson A.I. and Alongi D.M. (eds), *Tropical Mangrove Ecosystems*. Coastal and Estuarine Studies #41. American Geophysical Union, Washington DC, USA, pp. 225–250.
- Clough B.F. and Scott K. 1989. Allometric relationships for estimating above ground biomass in six mangrove species. *Forest Ecol. Manage.* 27: 117–127.
- Clough B.F., Dixon P. and Dalhaus O. 1997. Allometric relationships for estimating biomass in multi-stemmed mangrove trees. *Aust. J. Bot.* 45: 1023–1031.
- Coomes D.A. and Grubb P.J. 1998. A comparison of 12 tree species of Amazonian caatinga using growth rates in gaps and understorey, and allometric relationships. *Funct. Ecol.* 12: 426–435.
- Craighead F.C.Sr. 1971. *The Trees of South Florida, Vol 1. The Natural Environments and their Succession*. University of Miami Press, Coral Gables, FL, USA.
- Davis S.M. and Ogden J.C. (eds) 1994. *Everglades: The Ecosystem and its Restoration*. St. Lucie Press, Delray Beach, FL, USA.

- Day J.W., Conner W.H., Ley-Lou F., Day R.H. and Navarro A.M. 1987. The productivity and composition of mangrove forests, Laguna de Terminos, Mexico. *Aquat. Bot.* 27: 267–284.
- Fennema R.J., Neidrauer C.J., Johnson R.A., MacVicar T.K. and Perkins W.A. 1994. A computer model to simulate natural Everglades hydrology. In: Davis S.M. and Ogden J.C. (eds), *Everglades: The Ecosystem and its Restoration*. St. Lucie Press, Delray Beach, Florida, USA, pp. 249–290.
- Fromard F., Puig P., Mougin E., Marty G., Betoulle J.L. and Cadamuro L. 1998. Structure, above-ground biomass and dynamics of mangrove ecosystems: new data from French Guiana. *Oecologia* 442: 1–15.
- Horn H.S. 1971. *The Adaptive Geometry of Trees*. Princeton University Press, Princeton, NJ, USA.
- Langevin C., Swain E. and Wolfert M. 2005. Simulation of integrated surface-water/ground-water flow and salinity for a coastal wetland and adjacent estuary. *J. Hydrol.* 314: 212–234.
- Lieth H. and Whittaker R.H. (eds) 1975. *Primary Productivity of the Biosphere*. Springer-Verlag, New York, NY USA.
- Light S. and Dineen W. 1994. Water control in the Everglades: An historical perspective. In: Davis S.M. and Ogden J.C. (eds), *Everglades: The Ecosystem and Its Restoration*. St. Lucie Press, Delray Beach, FL, USA, pp. 47–84.
- Niklas K.J. 1994. *Plant Allometry*. University of Chicago Press, Chicago, IL, USA.
- Pool D.J., Snedaker S.C. and Lugo A.E. 1977. Structure of mangrove forests in Florida, Puerto Rico, Mexico and Central America. *Biotropica* 9: 195–210.
- Porte J. and Porter K. 2002. *The Everglades, Florida Bay and Coral Reefs of the Florida Keys*. CRC Press, Boca Raton, FL, USA.
- Putz F.E. and Chan H.T. 1986. Tree growth, dynamics, and productivity in a mature mangrove forest in Malaysia. *Forest Ecol. Manage.* 17: 211–230.
- Rochow J.J. 1974. Estimates of above-ground biomass and primary productivity in a Missouri forest. *J. Ecol.* 62: 567–577.
- Saenger P. and Snedaker S.C. 1993. Pantropical trends in mangrove above-ground biomass and annual litterfall. *Oecologia* 96: 293–299.
- Silva C.A.R., Lacerda L.D., Silva L.F.F. and Rezende C.E. 1991. Forest structure and biomass distribution in a red mangrove stand in Sepetiba Bay, Rio de Janeiro. *Rev. Brasil Bot.* 14: 21–25.
- Smith T.J.III. 2004. Development of a Long-Term Sampling Network to Monitor Restoration Success in the Southwest Coastal Everglades: Vegetation, Hydrology and Sediments. U.S. Geological Survey. Fact Sheet FS-2004-3015, St. Petersburg, FL, USA.
- Smith T.J.III, Hudson J.H., Robblee M.B., Powell G.V.N. and Isdale P.J. 1989. Freshwater flow from the Everglades to Florida Bay: A historical reconstruction based on fluorescent banding in the coral *Solenastrea bournoni*. *Bull. Mar. Sci.* 44: 274–282.
- Smith T.J.III, Robblee M.B., Wanless H.R. and Doyle T.W. 1994. Mangroves, hurricanes and lightning strikes. *Bioscience* 44: 256–262.
- Sobrado M.A. 1999. Leaf photosynthesis of the mangrove *Avicennia germinans* as affected by NaCl. *Photosynthetica* 36: 547–555.
- Tomlinson P.B. 1986. *The Botany of Mangroves*. Cambridge University Press, Cambridge, MA, USA.
- Tuffers A., Naidoo G. and von Willert D.J. 2001. Low salinities adversely affect photosynthetic performance of the mangrove, *Avicennia marina*. *Wetlands Ecol. Manage.* 9: 225–232.
- Whittaker R.H. and Marks P.L. 1975. Methods of assessing terrestrial productivity. In: Lieth H. and Whittaker R.H. (eds), *Primary Productivity of the Biosphere*. Springer-Verlag, New York, NY, USA, pp.106–109.
- Whittaker R.H. and Woodwell G.M. 1968. Dimension and production relations of trees and shrubs in the Brookhaven Forest, New York. *J. Ecol.* 56: 1–25.
- Woodroffe C.D. 1985. Studies of a mangrove basin, tuff crater, New Zealand: I Mangrove biomass and production of detritus. *Estuarine, Coastal, Shelf Sci.* 20: 265–280.