Seasonal and spatial variation in leaf area index, litter production and light levels in *Myrica cerifera* shrub thickets across a barrier island chronosequence.

A thesis submitted in partial fulfillment of the requirements for the degree
of Master of Science at Virginia Commonwealth University

by

Steven Brantley

B.S. Virginia Commonwealth University 2003
M.S. Virginia Commonwealth University 2005

Director: Donald R. Young
Professor
Department of Biology

Virginia Commonwealth University
Richmond, Virginia
July 2005

Acknowledgements

I would like to thank my advisor, Dr. Donald Young, for his guidance and support throughout the course of the project. I will always be grateful to him for the opportunity to work on the barrier islands of Virginia. I am thankful to the other members of my committee, Dr. Leonard Smock, Dr. D'arcy Mays and Dr. Greg Garman, for their guidance and advice on how to improve this project. I thank the staff of the Virginia Coast Reserve LTER site for working with us to provide safe and dependable transportation to the island. I owe a great deal to Jaime Fuest, Julie Naumann, Charles Clarkson and Jackie Vick for field help and other advice. I would also like to thank Ed Crawford for his willingness to share his extensive knowledge of wetland plants as well as general ecology. Finally, I'd like to thank my wife Julia for all of her patience and support over the years.

Table of Contents

List of Tables

List of Figures

Abstract

SEASONAL AND SPATIAL VARIATION IN LEAF AREA INDEX, LITTER PRODUCTION, AND LIGHT LEVELS IN *MYRICA CERIFERA* SHRUB THICKETS ACROSS A BARRIER ISLAND CHRONSEQUENCE.

Steven T. Brantley, Master of Science

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science at Virginia Commonwealth University

Virginia Commonwealth University, 2005

Director: Dr. Donald R. Young, Professor, Department of Biology

Leaf area index (LAI), litter production and understory light levels of *Myrica cerifera* shrub thickets were assessed on Hog Island, Virginia to quantify spatial and seasonal variations in leaf area and light attenuation among four thickets representing a successional chronosequence and compare methods of estimating LAI in shrub-dominated systems. Seasonal LAI estimates were made seven times throughout the year with a portable integrating radiometer (Li-Cor LAI-2000) and three times by measurement of photosynthetically active radiation (PAR) and use of the Beer-Lambert law. Leaf area index was also estimated through leaf litter collection and use of allometric relationships between stem diameter and leaf area. The oldest of the four thickets had the lowest LAI and litter production throughout the year. Peak LAI measurements with the portable integrating radiometer ranged from 2.0 ± 0.2 to 4.0 ± 0.3

for the oldest and youngest thickets, respectively which appear to be substantial underestimates of the actual values. According to annual litterfall, LAI ranged from 4.1 ± 0.5 for the oldest thicket to 10.2 ± 0.4 for a 20 year old thicket. Leaf area index varied from 6.4 ± 0.2 for the oldest thicket to 11.4 ± 2.1 for the 40 year old thicket according to the allometric relationships, which may overestimate LAI in stands with many large stems. The high light attenuation by the shrub canopy and heavy litterfall may contribute to the low diversity within thicket canopies by inhibiting germination and growth of other species. The study demonstrates that these low diversity shrub thickets have a higher LAI and litter production, and thus higher potential for primary productivity, than many temperate forested systems and that stand age may be the major determinant of productivity.

Introduction

Barrier islands represent a highly dynamic landscape and provide unique opportunities to study the effects of rapid environmental changes across multiple spatial and temporal scales (Hayden et al., 1991). Barrier island plant communities show a strong tendency for zonation based on physiological constraints imposed by steep environmental gradients (Oosting and Billings, 1942; Ehrenfeld, 1990; Levy, 1990; Hayden et al., 1991). Environmental factors, such as availability of fresh water, high solar load, low nutrient soils, salinity, wind, and burial by sand, determine species composition and the amount of vegetative cover (Oosting and Billings, 1942; Ehrenfeld, 1990; Levy, 1990; Hayden et al., 1991). The study of key community characteristics across the island landscape can provide valuable information on the factors that drive ecosystem function.

Spatial variation in environmental stresses on barrier islands is particularly high relative to landscape position (Ehrenfeld, 1990; Levy, 1990). The availability of fresh water depends on site topography and is primarily a function of the relative positions of the terrestrial surface and the freshwater lens (Ehrenfeld, 1990; Hayden et al., 1991; Young et al., 1994). Other stresses, such as salinity stress from saltwater flooding and exposure to sea spray, decrease with increasing distance from the beach (Oosting and Billings, 1942; Boyce, 1954; Young et al., 1994). However, reduced exposure to sea spray may also reduce inputs of micronutrients, such as potassium, magnesium, and calcium, in inland sites possibly increasing nutrient stress (Art et al,. 1974).

Temporal variation in community processes and the factors that drive species composition is also high due to the dynamic nature of barrier islands. Long-term changes include sea-level rise, island migration, and allogenic succession due to climate change (Hayden et al., 1991). Long-term changes are accompanied by episodic disturbances, particularly coastal storms, that can rapidly cause system-wide changes and alter ecosystem trajectory (Hayden et al., 1991). Short-term variations in long-shore currents also change accretion and erosion patterns and result in large variations in soil ages as beaches expand (Hayden et al., 1991; Shao et al., 1998).

Accreting shorelines provide one of the few opportunities to study primary succession. Succession on newly deposited sand begins with colonization by dune forming grasses and development of a primary dune (Ehrenfeld, 1990; Levy, 1990). Changes in plant species composition often increase community structure ameliorating environmental stresses such as high light levels and wind. As litter accumulates, soil organic matter, soil water holding capacity and soil nutrient levels increase, reducing water and nutrient stress on older soils (Ehrenfeld, 1990; Levy, 1990). Succession may proceed toward development of a maritime forest or the trajectory may be mitigated by disturbances such as tropical or extratropical storms, fire, or introduction of an invasive species (Hayden et al., 1991; Stalter and Odum, 1993; Stallins and Parker, 2003).

Formation of primary dunes on accreting shorelines often occurs repeatedly, resulting in a series of parallel dune ridges and interdunal swales across an island creating a successional chronosequence (Hayden et al. 1991). On the barrier islands of Virginia, such as Hog Island (Fig. 1), colonizing grasses trap sand in swales increasing elevation and reducing frequency of flooding (Levy, 1990). The swales may then be colonized by the actinomycete *Frankia* , a nodulating mycobacterium capable of fixing atmospheric nitrogen (Young et al., 1992). Drier sites, inhabited by *Frankia,* can then be colonized by the evergreen shrub *Myrica cerifera* L. (Myricaceae) which rapidly grows into dense thickets (Levy, 1990; Young et al., 1992).

Commonly known as wax myrtle or southern bayberry, *M. cerifera* is not tolerant of the high levels of salt occurring closer to the shoreline (Tolliver et al., 1997; Young et al., 1994). However, these shrubs are well adapted to the low nutrient levels of recently deposited sand and are the dominant woody species on many of Virginia's barrier islands (Young, 1992). The symbiotic association with *Frankia* assures an adequate source of nitrogen and the evergreen leaf habit helps to conserve other nutrients (Monk, 1966; Morris et al., 1974; Young, 1992). As the north end of Hog Island has grown, a well-defined chronosequence of dense shrub thickets has also formed from west to east across the island (Young et al., 1995). The four thickets on Hog Island vary in age and structure with the younger sites exhibiting higher stem densities and closed canopies and the oldest thicket declining due to an increase in plant senescence, vine growth and gap formation (Young et al., 1995; Crawford and Young, 1998a).

The ecological impact of *M. cerifera* in coastal environments has been well documented. *Myrica cerifera* plays an important role in coastal succession by improving soil nutrient content and acting as a nurse plant to less light-tolerant species such as *Prunus serotina* (Morris et al., 1974; Permar and Fischer, 1983; Levy, 1990). Permar and Fischer (1983) showed that *M. cerifera* in the understory of *Pinus ellotii* plantations can fix substantial amounts of nitrogen throughout the year improving nitrogen accumulation rates in the soil. *Myrica cerifera* fruits are also a valuable food resource for wildlife, especially wintering birds (Borgmann et al., 2004; Kwit et al., 2004a; Kwit et al., 2004b).

While much is known about general growth and life-history characteristics of *M. cerifera*, many of the factors that determine photosynthesis, transpiration and net primary production (NPP) of shrub thickets have yet to be quantified across complex spatial and temporal scales. However, there is growing interest in the increased abundance of shrubs in historically herbaceous ecosystems and the effect this shift will have on NPP (Jobbagy and Sala, 2000; McCarron and Knapp, 2003; Heisler et al., 2004). Measurement of NPP in communities dominated by woody species, including shrub-dominated systems, is often difficult due to the size and structural complexity of such communities (Whitaker, 1961; Young, in press). Many recent efforts to estimate NPP have focused on the use of remote sensing and computer modeling to simulate production based on light use efficiency (Gower et al., 1999). These models have many advantages but reliability depends on accurate estimation of vegetation characteristics such as leaf area index (Runyon and Waring, 1994; Gower et al., 1999).

Leaf area index (LAI) is defined here as the ratio of leaf surface area of one side of the leaf to projected ground area. Leaf area index is an important structural variable in any plant community and can be used as an indicator for a variety of ecosystem processes such as photosynthesis, transpiration, and nutrient cycling (Bonan, 1993; Runyon et al., 1994; Barbour et al., 1999). Leaf area index directly influences both the amount of solar radiation that can be intercepted and the plant-atmosphere exchange of CO_2, thus directly affecting NPP (Bonan, 1993; Runyon et al., 1994; Norby et al., 2003). In coastal systems, higher leaf area is also important in capturing nutrients from sea spray and improving soil nutrient levels (Art et al., 1974; Joy and Young, 2002).

Leaf area index is also an important determinant of community structure through competitive inhibition. In deeply shaded forests, high LAI can reduce incident light levels by 98% or more and light availability may become the primary limiting resource for understory plants (Chazdon, 1988; Neufeld and Young, 2003). On Hog Island, development of shrub thickets with low light levels and heavy litterfall limits germination and seedling growth of resident grasses as well as other herbaceous and woody species (Tolliver et al., 1995; Crawford and Young, 1998a). Development of a diverse understory under low light conditions is also limited by the seed bank within the thickets which is devoid of shade-tolerant plants because it still reflects a pioneer successional community (Crawford and Young, 1998b).

Leaf area index can be estimated either directly using total leaf mass within a plot and specific leaf area or estimated indirectly by comparing light above and below the canopy (Marshall and Waring, 1986; Welles, 1990; Gower et al., 1999; Turner et al., 2000). Direct estimates use annual litterfall, destructive sampling of representative plots, or allometric relationships between stem size and leaf area (Marshall and Waring, 1986; Gower et al., 1999; Turner et al., 2000). Estimation of LAI using annual litterfall is the most time consuming method, especially in evergreens, and may require several years of data due to interannual variability (Marshall and Waring, 1986; Gower et al., 1999). Specific leaf area can also vary substantially within layers of the canopy due to variation in sun exposure (Gower et al., 1999). Other forms of direct estimation may require large amounts of destructive sampling and are cumbersome for all but short-statured communities (Gower et al., 1999).

Allometric relationships are often developed for woody communities to take advantage of the strong relationship between stem size and leaf area (Marshall and Waring, 1986). Rather than harvesting entire plots or stands, allometric models require harvest of a subsample of stems that represent the range of stem sizes found in a stand (Gower et al., 1999). The primary disadvantage of allometric modeling based on stem diameter is that LAI for stands with many large stems often tends to be overestimated (Marshall and Waring, 1986; Turner et al., 2000). Alternatives to stem diameter, including stem cross-sectional area and sapwood area, have been suggested to reduce overestimates of LAI (Marshall and Waring, 1986; Turner et al., 2000). Allometric modeling of LAI in shrubs may also be complicated by variations in trunk morphology that may make consistent diameter measurements difficult.

Indirect estimation of LAI is accomplished either by measuring canopy gap fraction or light attenuation (Marshall and Waring, 1986; Welles, 1990; Gower et al., 1999). Measurement of gap fraction using a portable integrating radiometer, such as the Li-Cor LAI-2000, is often the quickest method to gather many LAI estimates with a minimum of effort. However, there are several disadvantages to using such instruments. Calculation of LAI from gap fraction is based on two assumptions rarely met in natural systems: random distribution of foliage in the canopy and spherically arranged leaf angles (Welles, 1990; Gower et al., 1999). Additional error may be introduced from rapidly changing sky conditions or from light interception by stems, although error from light interception by stems depends largely on seasonality and the presence or absence of dead stems (Gower et al., 1999). Additionally, for best results sensors should not be exposed to direct sunlight so these instruments are best used when solar angle is low or the sky is overcast (Welles, 1990).

The second indirect method commonly used to estimate LAI utilizes the Beer-Lambert law, a light extinction coefficient and two measurements of photosynthetically active radiation or PAR (one measurement above the canopy and one measurement below the canopy) (Marshall and Waring, 1986; Welles, 1990; Gower et al., 1999). The Beer-Lambert law is also based on the assumptions of randomly and spherically arranged leaves (Marshall and Waring, 1986; Welles, 1990; Gower et al., 1999). To improve consistency, measurements of solar radiation for estimating LAI should be taken on cloudless days to reduce variation in levels of reflected and diffuse light (Gower et al., 1999). Light measurements should also be taken within two hours of solar noon because light extinction coefficients vary with solar angle (Pierce and Running, 1988; Norby et al., 2003). Both light attenuation and gap fraction methods require above-canopy readings for each estimate of LAI which may be difficult without large enough gaps in the canopy.

Leaf area index is a key structural parameter in terrestrial ecosystems and reliable estimation is important as an indication of ecosystem function and for ground truthing of remote sensing equipment. Comparison of LAI across dynamic landscapes can also provide valuable information about trends in habitat development and the effects of environmental gradients but estimates of LAI must be accurate, repeatable, and efficient for long-term monitoring to be supported. Characteristics directly related to LAI, such as litter production and understory light levels are also important indicators of nutrient cycling, competition and other factors driving succession. The objective of the current study was to quantify variation in leaf area index, litter production and light levels in four *Myrica cerifera* shrub thickets across a successional chronosequence. Leaf area index was estimated using a commercially available plant canopy analyzer, annual litterfall, light attenuation, and allometric modeling and compared among thickets. Seasonal variation in LAI and litterfall rates were used to determine differences in the timing of leaf development and leaf loss among the thickets. Light levels within thickets were quantified to determine the role of understory light levels in the lack of diversity within thickets. This study demonstrates the complex and interacting effects of succession and steep environmental gradients on the primary production potential of a shrub-dominated community.

Methods and Materials

Study site

Field work was conducted from April 2004 to April 2005 on the northern end of Hog Island (37° 27' N, 75° 40' W), VA, a barrier island located approximately 10 km east of the Eastern Shore of Virginia, USA (Fig. 1). Hog Island is ~1200 ha, 10 km long and 2.5 km across at its widest point. The island is part of the Virginia Coast Reserve, managed by the Nature Conservancy, and is a Long-Term Ecological Research (LTER) site. The northern end of the island has been accreting ~5 m yr^{-1} on the ocean side for ~140 years resulting in a chronosequence of progressively younger soils as one moves east from the bayside marsh to the ocean (Hayden et al., 1991; Shao et al., 1998) (Fig. 1). As the beach has accreted, a parallel series of dunes and swales has developed running north to south with a distinct zonation pattern and sharp transitions between vegetation types. While dunes are dominated by the grasses *Ammophila breviligulata*, *Spartina patens*, and *Panicum amarum*, swales are dominated by dense thickets of the evergreen shrub *Myrica cerifera* (Young et al., 1995).

The four extant thickets on the North end of the island represent a range of ages and successional stages. The oldest site, the *Bay Side thicket*, has previously shown poor recruitment and high mortality (Young et al., 1995). The second, or *Mid-Island thicket* is located in the most stable part of the island and forms a nearly impenetrable thicket (Young et al., 1995). The third site, or *Young thicket* is located ~300 m from the shoreline, just behind a large and relatively young (~30 yr. old) dune. The easternmost site, or *Colonizing thicket*, lies just 200 m from the shoreline and contains discontinuous but dense patches of relatively young (<10 years) shrubs.

Seasonal litter and leaf area index measurements

To quantify spatial variation in litter production and leaf area index, ten sites within each thicket were selected using a stratified baseline technique. A baseline was established parallel to each thicket and transects were established every 25 m along the baseline. Two sites were selected along each transect using random numbers to determine the distance along the transect at which traps would be placed. All sites were established at least 3 m into the thicket to avoid edge effects. A plastic litter trap, ~0.30 m^2 in area and 0.15 m deep, was placed at each site in early April 2004. Litter was collected seven times throughout the year from May 2004 to April 2005. Litter was dried at 75 °C for four days, separated into leaf, woody and reproductive components, and weighed to the nearest 0.1 g.

To determine specific leaf area (SLA), 80 leaves were selected from eight stems 2.0 cm in diameter or larger. The area of each leaf was determined by tracing the leaf onto paper of a known mass per unit area and weighing leaf tracings to the nearest 0.001 g. Leaves were dried for four days at 75 °C and weighed to the nearest 0.001 g. Specific leaf area for each leaf was calculated by dividing leaf area by leaf mass and average SLA was determined. Annual leaf litter production was then used, along with specific leaf area, to estimate peak LAI for each thicket.

During each litter collection, leaf area index (LAI) was estimated with a portable integrating radiometer (Li-Cor LAI 2000). The LAI-2000 estimates LAI based on measurements of canopy gap fraction using five photodiodes arranged in concentric circles with each diode measuring light at a different angle (Welles, 1990). One above-canopy and three below-canopy readings were taken at ~1 m above each litter trap to get an accurate spatial average for the site and more thoroughly relate litter production to LAI.

Seasonal litter data and LAI estimates from the LAI-2000 were analyzed using two-way ANOVA to test for interactions between location and season. Post-hoc comparisons (Tukey-HSD) were used to test for significant differences among thickets and among seasons. ANOVA was performed in SPSS 11.5 for windows. Post-hoc comparisons (Tukey-HSD) were performed as described in Zar (1999).

Seasonal measurement of understory light

To quantify the understory light environment in the thickets, Li-Cor quantum sensors and LI-1400 data loggers were subjectively placed in each thicket for two-week intervals during the summer solstice, winter solstice and spring equinox. Incident PAR was measured every 5 min. and the minimum, maximum and integrated hourly values were recorded. Integrated light levels (mol m^{-2} day^{-1}) were compared to above-canopy light readings from the Hog Island and Oyster meteorological stations (Krovetz et al., 2004). The percentage of above-canopy light was determined for each site from the total daily integrated light readings for each day of the sampling period. LAI was also calculated as described in Marshall and Waring (1986) and Pierce and Running (1988) using the Beer-Lambert Law:

$$LAI = -\ln(Q_b/Q_a)\ k^{-1}$$

where Q_a is above canopy light, Q_b is the below canopy light and k is an extinction coefficient. An extinction coefficient of 0.60 was selected based on Maass et al. (1995). As with gap fractions, calculation of LAI based on the Beer-Lambert Law assumes that leaves are randomly distributed in the canopy and that leaf angles are spherically and randomly arranged (Marshall and Waring, 1986; Pierce and Running, 1988). Only values within one hour of solar noon on days with full sun were used in the calculations for LAI.

Allometric method for estimation of leaf area index

To estimate leaf area index using the relationship between stem size and leaf area, three 50 m^2 plots were delineated in each thicket (25 m^2 in the Colonizing thicket) and the diameter of all live stems within each plot was measured at 0.7 m height from the soil surface. Seven to ten stems were selected from each thicket to represent the range of sizes measured in the plots. All leaves were removed from each stem and dried for five days at 75 °C. Dried leaves were then weighed to the nearest 0.1 g. Leaf mass and stem diameter data were log transformed to correct for the effects of heteroscedasticity (Gower et al., 1999; Zar, 1999). Transformed data were analyzed using simple linear regression and a predictive model was created for each thicket to estimate leaf mass based on stem diameter:

$$L_m = 10^{m(\log Ds) + c}$$

where L_m is the mass of leaves expected from a stem of a given size, c is a constant, m is the regression coefficient, and Ds is the stem diameter. The regression coefficients and elevations of the four models were then compared as described in Zar (1999) to test whether individual models were significantly different from one another and possibly determine whether all data should be combined into a single model.

Using the individual models, total leaf area for each plot was calculated using the allometrically derived leaf mass values for all stems within a given plot and the specific leaf area. Leaf area index was estimated by dividing the total leaf area by the area of the plot. A one-way ANOVA was performed on the allometrically derived values of LAI to detect significant differences among thickets. Post-hoc comparisons (Tukey-HSD) were performed among thickets. Variation in stem density among the thickets was also analyzed using ANOVA and Tukey-HSD. All statistics were performed in SPSS 11.5 for windows unless otherwise noted.

Results

Spatial and seasonal variation in leaf area index and litter production

Based on estimates from the LAI-2000, LAI varied substantially throughout the year. Minimum LAI for all four thickets occurred during April and early May and maximum LAI values at all sites occurred from late June through September (Fig. 2). There was also a significant interaction between site and season ($F = 3.064$, $P < 0.001$). Leaf area index for the Bay Side thicket was significantly lower than LAI for Mid-Island and Young thickets throughout the year. However, LAI for the Bay Side thicket and Colonizing thicket did not differ significantly during May ($P > 0.05$) but was significantly ($P \leq 0.05$) higher for the Colonizing thicket from June to April.

Rates of leaf litter production also demonstrated significant seasonal and spatial variation. Litter production increased significantly ($P < 0.05$) for all thickets from early May to late June (Fig. 3). Lowest leaf litter production for all thickets was observed from late June to mid-August. Litter production increased significantly ($P < 0.05$) for all four thickets beginning in late September (Fig. 3). There was a significant ($F = 8.221$, $P < 0.001$) interaction between site and season. The Mid-Island thicket had the highest leaf litter production of the four thickets during the late spring pulse but litter production in this thicket did not increase as substantially in the fall indicating higher levels of leaf retention throughout the winter when the other thickets lost a large proportion of leaves.

Annual leaf litter production of *M. cerifera* per unit area varied significantly ($F = 54.87$, $P < 0.001$) among the thickets. Annual leaf litter production rates were 270.4 ± 32.0 g m^2 yr^{-1} for the declining Bay Side thicket, 512.7 ± 18.9 g m^2 yr^{-1} for the Mid-Island thicket, 678.4 ± 27.1 g m^2 yr^{-1} for the Young thicket, and 663.4 ± 22.3 g m^2 yr^{-1} in the Colonizing thicket. The Bay Side thicket produced significantly less leaf litter ($P < 0.001$) than the Mid-Island thicket while the Mid-Island thicket produced significantly less leaf litter ($P < 0.001$) than the other two thickets. The Colonizing and Young thickets did not differ significantly ($P = 0.976$) from one another in annual leaf litter production.

Spatial and seasonal variation of understory light

The understory light levels within *Myrica cerifera* thickets demonstrated spatial and temporal variation concurrent with the patterns observed in LAI and litter production (Fig. 4). For the current study, photosynthetically active radiation (PAR) measurements represent the range of values measured over several days at a single site rather than a spatial average for the thicket and, therefore, were not statistically tested. During late June and early July integrated PAR in the Bay Side thicket, which had the most open canopy of the four sites, varied from 1.62 mol m^{-2} day^{-1} to 3.68 mol m^{-2} day^{-1} while above-canopy PAR varied from 19.5 to 43.7 mol m^{-2} day^{-1} depending on cloud cover. In contrast, understory PAR in the Colonizing thicket varied from 0.18 mol m^{-2} day^{-1} to 0.33 mol m^{-2} day^{-1}. Maximum understory PAR in the Mid-Island and Young thickets was 0.51 mol m^{-2} day^{-1} and 2.77 mol m^{-2} day^{-1} respectively. Despite the seasonal decrease in LAI during the winter, light levels under the canopy decreased during the winter solstice due to lower levels of incident PAR (Fig. 4). In spring, integrated PAR within the Mid-Island thicket and Colonizing thicket increased to 5.07 and 6.11 mol m^{-2} day^{-1}, respectively due to the minimal seasonal LAI coupled with the increased solar angle and resultant increase in incident PAR (Fig. 4).

Short-term temporal patterns of light within thickets also varied among sites in summer (Fig. 5). Maximum PAR measurements within the Bay Side thicket were as high as 1413 umol m^{-2} s^{-1} and reached levels exceeding 100 umol m^{-2} s^{-1} multiple times throughout the day, indicating that substantial direct solar radiation was reaching the thicket understory. Light levels in the Young thicket also exceeded 100 umol m^{-2} s^{-1} during the middle of the day although maximum light levels were lower than those in the Bay Side thicket. Light levels within the Mid-Island thicket were consistently lower than levels in the Bay Side or Young thicket and rarely exceeded 100 umol m^{-2} s^{-1}. The Colonizing thicket had the most deeply shaded environment with maximum PAR below 30 umol m^{-2} s^{-1} the entire day with one exception when PAR reached ~200 umol m^{-2} s^{-1}.

Stem density and size class frequency

Stem density in *Myrica cerifera* thickets varied significantly ($F = 8.771$, $P = 0.007$) according to thicket age. Younger thickets had higher stem densities and/or a less diverse age structure than older thickets (Fig. 6). Stem density in the Colonizing thicket was the highest of the four thickets with 3.51 ± 0.21 stems m^{-2}. Nearly 40% of stems in the Colonizing thicket were < 20 mm in diameter and this site contained no large stems (>100 mm). The Young thicket had a significantly lower ($P = 0.049$) stem density than the colonizing site (1.90 ± 0.61 stems m^{-2}) with few large stems and many small, dead stems indicating self-thinning. The low frequency of small stems also showed that there was a lack of recruitment. There were 1.96 ● 0.28 stems m^{-2} in the Mid-Island thicket and this thicket contained the largest stems of any site. The Bay Side thicket had the lowest stem densities (0.98 ± 0.03 stems m^{-2}) although it did not differ significantly from the Mid-Island or Young thicket ($P = 0.278$ and 0.324, respectively). The Bay Side and Mid-Island thickets each had a very diverse age structure with a relatively high frequency of large stems (> 100 mm). Both had a relatively high frequency of stems <20 mm indicating high levels of recruitment.

Leaf area index

Leaf area index according to the portable integrating radiometer ranged from 1.9 ± 0.1 for the Bay Side thicket to 3.9 ± 0.1 for the Young thicket during late June (Table 1). Leaf area index estimates using light attenuation and the Beer-Lambert law demonstrated similar seasonal and spatial patterns of variation but were generally much higher than estimates made with the portable integrating radiometer (Table 2). Light attenuation showed that the Colonizing thicket had the highest LAI of the four thickets in late June and early January, while in April, the Colonizing Site had a slightly lower LAI than the Mid-Island thicket. The Bay Side thicket had a lower LAI than either Mid-Island or Colonizing thickets in late June and early January. Leaf area index estimates in the Young thicket were very similar for both indirect methods during June. A more complete analysis of seasonal variation in the Bay Side and Young thickets could not be accomplished using light attenuation due to damage to some of the sensors incurred during the course of the study.

Results from allometric models varied significantly ($F = 4.126$, $P = 0.048$) among thickets (Table 3). Four models, one for each thicket, were derived from the stem diameter-leaf area relationships (Table 3 and Fig. 7). There were no significant differences ($P > 0.05$) in either the regression coefficients or elevations among the four models. The data were combined into a single model but the results using the single model are not reported because they do not reflect realistic LAI values for some of the plots and may be unreliable because of possible differences in allocation to leaves among the four thickets. The lack of significant differences may be caused by the small sample sizes for each thicket rather than an actual lack of variation in the allometric relationships.

Leaf area index according to the individual allometric models ranged from 6.4 ± 0.4 for the Bay Side thicket to 11.4 ± 2.1 for the Mid-Island thicket although some of the values in plots with a relatively high occurrence of large stems may be overestimates

(Marshall and Waring, 1986 and Turner et al. 2000). Leaf area index based on annual leaf litter production and a specific leaf area of 0.015 m^2 g^{-1} dry mass ranged from 4.1 ± 0.5 in the Bay Side thicket to 10.2 ± 0.4 in the Young thicket (Table 1). Estimates derived form allometric models agreed very closely with values obtained using annual litterfall for the two younger thickets but allometric estimates for the two older thickets appear somewhat high (Table 1).

DISCUSSION

Spatial patterns of variation in the structure and productivity of coastal plant communities, including those on barrier islands, have primarily been explained by the effects of steep environmental gradients on plant morphology and physiology (Oosting and Billings, 1942; Boyce, 1954; Levy, 1990; Ehrenfeld, 1990; Young et al., 1994). *Myrica cerifera* shrub thickets represent an important successional stage in the development of plant communities in coastal environments (Levy, 1990). On accreting shorelines, the formation of a chronosequence facilitates the study of successional dynamics and the interaction between age and the environment (Hayden et al., 1991; Stallins and Parker, 2003). In the current study, LAI, litter production and the understory light environment within *Myrica cerifera* shrub thickets all varied across the barrier island landscape. Although landscape position and associated environmental variation were important, biotic processes related to succession were also influential.

Four different methods of LAI estimation showed similar spatial variation in shrub thickets across Hog Island. Seasonal patterns of LAI using indirect methods also generally agreed with one another and these data were supported by seasonal patterns of litter production. However, the accuracy of each method in estimating the LAI of these communities needs to be addressed because of the growing interest in shrub encroachment in historically herbaceous ecosystems and the effects it will have on NPP (Jobbagy and Sala, 2000; McCarron and Knapp, 2003; Heisler et al., 2004). Although many studies have published similar data for forested systems (Marshall and Waring, 1986; Pierce and Running, 1988; Runyon et al., 1994; Gower et al., 1999; Norby et al., 2003), little work has been published to date specifically addressing the accurate estimation of LAI in shrub canopies. If LAI values on the ground are to be used to model NPP or calibrate remote sensing equipment in shrub-dominated communities, then accurate estimates are essential (Bonan, 1993; Runyon et al., 1994; Gower et al., 1999).

The portable integrating radiometer underestimated LAI substantially throughout the year. Norby et al. (2003) and Deblonde et al. (1994) had similar results in forested systems when they studied LAI in stands of *Liquidambar styraciflua* and *Pinus resinosa,* respectively. The algorithms that calculate LAI based on gap fraction are highly sensitive to deviations from the assumptions of leaf orientation previously discussed (Gower et al, 1999; Norby et al., 2003). The arrangement of leaves on branches of *Myrica cerifera* may create a highly clumped canopy and leaf angles, particularly in young thickets, appear biased towards an orthotrophic growth pattern. Despite the potential errors, measurements using the LAI-2000 did provide a means of comparing spatial and seasonal dynamics of the four thickets. Determination of a clumping factor, as described by

Gower and Norman (1991), based on canopy structure may be possible to correct LAI measurements.

Annual litter production may be the simplest and most reliable method of estimating peak LAI but minimal leaf loss and subsequent replacement during the growing season must be assumed. Seasonal differences in litter production are also a good indicator of differences in leaf expansion and senescence among sites. The primary disadvantage of using litter production to estimate LAI is the time required compared to indirect methods. Whereas most leaf litter in deciduous forests can be gathered within a few months, the evergreen leaf habit of *M. cerifera* dictates that litter must be collected for an entire year. In other evergreen systems, several years of data are often required to determine leaf turnover rate (Marshall and Waring, 1986). Additionally, interannual variability in leaf production due to climate may require several years of monitoring to obtain an accurate temporal average of LAI (Marshall and Waring, 1986; Norby et al., 2003).

Leaf area index estimates using light attenuation and the Beer-Lambert law agreed more closely with the litterfall and allometric models than with the portable integrating radiometer. The Beer-Lambert law uses diffuse and reflected light in addition to direct beam radiation, and therefore, it may be more appropriate in highly clumped canopies (Pierce and Running, 1988; Maass et al., 1999). For the current study, logistic and instrument limitations dictated that light could be quantified at only one site within each thicket for a given time period. Temporal averaging of instantaneous values should provide an accurate characterization of temporal light patterns with just one sensor

(Neufeld and Young, 2003) but the design limited the ability to apply statistics to estimate LAI for the entire thicket. The results did demonstrate that the reproducibility of LAI estimates at the same location using the Beer-Lambert law was good relative to other methods when light measurements were taken during mid-day on clear days.

Measurement at a single site may explain why LAI and light levels in the Young thicket do not agree more closely with the results of annual litterfall and allometric modeling. Integrated PAR at the site selected in the Young thicket was much higher than expected and should generally be disregarded with respect to variation across the chronosequence. The site was selected relatively early in the growing season and the lower LAI at this site may reflect residual damage from Hurricane Isabel. Had ten different sites been measured in the thickets, as was done with the litter production and the portable integrating radiometer, light attenuation would likely reflect a spatial mean similar to the other methods.

The allometric models appeared to be very accurate for sites dominated by smaller stems but may have overestimated LAI in older sites dominated by large stems (> 10 cm diameter at a height of 0.7 m). There were two potential sources of error in the models, both related to stem size. Each of the plots used to estimate LAI in the Bay Side and Mid-Island thicket had a number of large stems. However, due to the time and labor required, I was unable to sample an adequate number of large stems during the initial field season. Larger stems need to be added to the models to cover the entire range of stem sizes in the study plots. Additionally, similar studies have reported an inherent tendency for allometric methods based on stem diameter to overestimate the contribution of large stems to stand LAI (Marshall and Waring, 1986 and Turner et al., 2000). For the current study, however, a linear equation between stem diameter and leaf area had a very strong relationship and a recalculated linear equation should be reliable once large stems are included.

Myrica cerifera shrub thickets are much shorter than most forested communities (~5 m or less) and lack the stratification associated with most forests. However, the results of the current study generally agree with the results of similar studies in forested systems. Specifically, the portable integrating radiometer underestimated LAI while the allometric models tended to overestimate LAI when large stems were present (Marshall and Waring, 1986; Pierce and Running, 1988; Runyon et al., 1994; Gower et al., 1999; Norby et al., 2003). Further refinement of the allometric models to include larger stems may improve the accuracy of this method and provide the most accurate means of measuring LAI.

Although there was considerable variation in the results using the four methods, the data do provide some clear patterns of spatial and seasonal variation. Spatial variation in LAI and annual litter production has typically been explained by differences in site water availability due to the high transpirational demand associated with large amounts of foliage (Poole and Miller, 1981; Martinez-Yrizar et al., 1999; Norby et al., 2003). On barrier islands, variations in water, nutrient and salinity stress relative to landscape position and soil age often determine the extent of vegetative cover (Oosting and Billings, 1942; Levy, 1990). However, for the four *Myrica cerifera* thickets on Hog Island, stand age may also be an important factor in determining LAI. In the two youngest sites on Hog Island, peak leaf area index for the study period was ~10 according to both litterfall and the allometric methods, a value often cited as the lower boundary for tropical rain forest and higher than most other forested communities (Marshall and Waring, 1986; Pierce and Running, 1988; Barbour et al., 1999; Larcher, 2003; Norby et al., 2003). The Mid-Island thicket had an LAI approaching 8 according to annual litterfall, higher than many temperate deciduous forests (Larcher, 2003; Norby et al., 2003; Barbour et al., 1999). Leaf area index and litter production declined with increasing age but even the declining Bay Side thicket had an LAI ~4 according to litterfall data, comparable to many temperate forests and higher than most shrub dominated systems (Larcher, 2003; Norby et al., 2003; Barbour et al., 1999; Martinz-Yrizar et al., 1999; Lichter, 1998; Maass et al. 1995).

The Bay Side thicket consistently had the lowest leaf area index, litter production, and stem density of the four thickets. The Bay Side thicket occupies the oldest soils on the island and is likely unaffected by salinity from sea-spray or flooding except during severe storms. Young et al. (1995) showed that both tissue and soil sodium levels were lowest at this site. Levels of nitrogen, calcium and potassium were also highest in the Bay Side soils and soil phosphorus did not vary from the other sites (Young et al., 1995). Still, the Bay Side thicket showed an increase in shrub mortality, a decline in shrub growth and recruitment, and an increase in the formation of gaps which allowed vines to establish and compete with shrubs for resources (Young et al., 1995).

The decline of the Bay Side thicket may follow the pattern described in Hilbert and Larigauderie (1990) who examined stand senescence in chaparral and similar ecosystems. The oldest shrubs in the Bay Side thicket approach 40 years but mortality increases markedly after 30 years (Young et al., 1995; Crawford and Young, 1998a). The decline of individual shrubs, coupled with a lack of recruitment (as detailed in Young et al., 1995), causes a reduction in stem density, basal area and LAI and an increase in light levels under the thicket canopy.

The lack of recruitment in the Bay Side thicket in the study by Young et al. (1995) was likely caused by the low light environment and heavy litter fall that accompanies the higher LAI when the thicket is expanding. However, the distribution of stem sizes in the current study includes a large number of stems < 20 mm diameter indicating a substantial increase in recruitment during recent years. Crawford and Young (1998b) showed that seed banks represented a pioneer community rather than the next successional sere and *Myrica cerifera* was the dominant woody component of seed banks within intact thicket canopies and a major component in gaps (Crawford and Young, 1998b). As shrub mortality has increased, the decline in LAI and resulting increase in light levels has allowed recent establishment of new *M. cerifera* seedlings. However, the recent increase in recruitment is not enough to maintain the high LAI values seen in younger thickets.

Seasonal variation in LAI and litterfall in *Myrica cerifera* thickets was also high. Three of the four sites experienced two periods of increased leaf litter production during the year: a brief spring pulse coinciding with the beginning of new leaf growth and a longer period of increased litter production in the autumn. Litterfall rates for all sites were lowest during July and August. The Mid-Island thicket did not experience a substantial leaf litter pulse during the autumn relative to the other thickets. In spring, the Mid-Island thicket had the highest level of litterfall even though the two younger sites produced more annual leaf litter. Shrubs at this site were able to retain more leaves and maintain a higher LAI throughout the winter possibly indicating a greater ability to gain carbon during brief warm periods in the winter.

Similar to peak LAI and annual litter production, leaf development and leaf senescence has been related to site water balance. Wright (1991) demonstrated that irrigation increased annual leaf production in some instances but also changed patterns of leaf flush in tropical shrubs. Similarly, Norby et al. (2003) showed that forest stands of *Liquidambar styraciflua* exhibit shorter leaf duration in years with low rainfall in August and September. Environmental cues related to site water balance that could affect leaf phenology include soil moisture content, understory humidity, and understory temperature (Wright, 1991).

Although the availability of fresh water is often the primary environmental driver of barrier island vegetation dynamics, the likelihood that water stress had a major effect on spatial variation in leaf duration in the current study on Hog Island seems remote. Precipitation during the 2004 growing season was much higher than average (~700 mm compared to ~450 mm) (Krovetz et al., 2004). During July and August, all sites experienced flooding from heavy precipitation and water levels in the thickets remained relatively high throughout the fall and winter (personal observation). Rather than water balance, the differences in leaf duration among the thickets could be due to other environmental stresses such as salt or nutrient stress. Young et al. (1995) showed that both soil and tissue sodium concentrations were highest in thickets closest to the shoreline and declined across the island. Plants under stress from resource limitations have a generalized mechanism of response that changes hormonal balance to favor production of abscissic acid (Chapin, 1991). This response may explain a greater loss of leaves in highly stressed shrubs.

Like the two youngest thickets, the Bay Side thicket also demonstrated a substantial increase in litter production in fall. Again, the greater seasonal loss of leaves may be a generalized response to stress (Chapin, 1991). Although the greater distance from the shoreline should make the Bay Side thicket the least susceptible to the environmental stresses typically associated with coastal environments, the proximity of this thicket to Hog Island Bay should also be considered an important environmental factor. There is no primary dune to protect the Bay Side thicket from stresses such as wind or saltwater intrusion during extremely high tides. The occurrence of these stresses in the Bay Side thicket may explain why the Mid-Island thicket actually had the largest stems of any site even though that thicket is younger than the Bay Side thicket. The difference in leaf duration at this site may also be the result of increasing competition following the model described by Bertness (1999). The increased abundance of vines such as *Parthenocissus quinquefolia* and *Vitis aestivalis* and rapid establishment of herbaceous plants in the understory may be affecting the phenology of the Bay Side thicket as competition for light and soil resources increases.

Parthenocissus quinquefolia, *Toxicodendron radicans*, and *Vitis aestivalis* are among the few species in the seed bank able to germinate and establish within thickets as light levels begin to increase due to shrub mortality (Crawford and Young, 1998b). The light environment across the chronosequence generally followed the same pattern as LAI and litter production as canopy light interception decreased with stand age. Although most of the shrubs in the colonizing site were < 3 m tall, the high stem density and high LAI from extensive edges created the most deeply shaded environment of the four sites following the pattern described in Neufeld and Young (2003). The low light was likely a key factor inhibiting germination of most of the species present in the seed bank (Crawford and Young, 1998b). The Bay Side thicket, however, has declined such that light within intact canopies exceeds the germination and growth requirements of most mid-to-late successional species (Larcher, 2003). The lack of diversity in the seed bank appears to be the primary mechanism limiting diversity and potential succession at this site rather than competitive inhibition although episodic disturbances, such as Hurricane Isabel, may also limit the complexity of the community development.

Leaf area index, light attenuation and litter production in the *Myrica cerifera* shrub thickets on Hog Island were higher than many mature forests and approached levels often associated with tropical rain forest or freshwater marshes indicating that the potential for primary productivity in shrub-dominated communities is extremely high even in the harsh barrier island environment. The comparison of characteristics such as leaf area index and light levels across multiple spatial and temporal scales can help distinguish between the effects of disturbance, environmental stress and stand age on productivity. The accurate estimation of leaf area index is important to quantify this variation. Indirect methods of estimating LAI tend to plateau around 6 because of gap fraction saturation and may be of limited use unless they are calibrated by direct methods (Gower et al., 1999). Litter production should also be monitored for several years to determine the effects of interannual variability in climate, especially precipitation.

Distinguishing between the effects of disturbance, environmental gradients and changes in shrub morphology due to age can be difficult but is ultimately necessary because of the complexity inherent in even relatively simple systems. The results of the current study demonstrate that, while the effects of environmental gradients are important in determining species composition, once a species is established factors driving succession may have a greater impact on stand structure than slight variations in the environment. To some degree, environmental stresses can be ameliorated by slight changes in leaf phenology rather than by reducing growth and sacrificing competitive ability as demonstrated by the four thickets in the current study. While complex, the spatially and temporally dynamic nature of barrier islands does allow researchers to determine the primary drivers of ecosystem structure and function.

Literature Cited

Art, H.W., F.H. Bormann, G.K. Voigt, and G.M. Woodwell. 1974. Barrier island forest ecosystems: role of meteorological nutrient inputs. *Science* 184: 60-62.

Barbour, M.G., J.H. Burk, W.D. Pitts, F.S. Gilliam, and M.W. Schwartz. 1999. Terrestrial plant ecology. Addison Wesley Longman, CA.

Bertness, M.D. 1999. The ecology of Atlantic shorelines. Sinauer Associates, Inc., Massachusetts.

Bonan, G.B. 1993. Importance of leaf area index and forest type when estimating photosynthesis in boreal forests. *Remote Sensing of Environment* 43: 303-314.

Borgmann, K.L., S.F. Pearson, D. J. Levey, and C.H. Greenberg. 2004. Wintering yellow-rumped warblers (*Dendroica coronata*) track manipulated abundance of *Myrica cerifera* fruits. *The Auk* 121: 74-87.

Boyce, S.G. 1954. The salt spray community. *Ecological Monographs* 24: 29-67.

Chapin, F.S. 1991. 1991. Integrated response of plants to stress. *Bioscience* 41: 29-36.

Chazdon, R. 1988. Sunflecks and their importance to forest understory plants. Advances in ecological research 18. Academic Press, London.

Crawford, E.R. and D.R. Young. 1998a. Comparison of gaps and intact shrub thickets on an Atlantic coast barrier island. *American Midland Naturalist* 140: 68-77.

Crawford, E.R. and D.R. Young. 1998b. Spatial/temporal variations in shrub thicket soil seed banks on an Atlantic coast barrier island. *American Journal of Botany* 85: 1739-1744.

Deblonde, G., M. Penner and A. Royer. 1994. Measuring leaf area index with the Li-Cor LAI-2000 in pine stands. *Ecology* 75: 1507-1511.

Ehrenfeld, J.G. 1990. Dynamics and processes of barrier island vegetation. *Aquatic Sciences* 2: 437-480.

Gower, S.T. and J.M. Norman. 1991. Rapid estimation of leaf area index in conifer and broad-leaf plantations. *Ecology* 72: 1896-1900.

Gower, S.T., C. J. Kucharik and J.M. Norman. 1999. Direct and indirect estimation of leaf area index, f_{par}, and net primary production of terrestrial ecosystems. *Remote Sensing of Environment* 70: 29-51.

Hayden, B.P., Dueser, R.D., Callahan, J.T., and H.H. Shugart. 1991. Long-term research at the Virginia coast reserve. *Bioscience* 41: 310-318.

Heisler, J.L., J.M. Briggs, A.K. Knapp, J.M. Blair and A. Seery. 2004. Direct and indirect effects of fire on shrub density and aboveground productivity in a mesic grassland. *Ecology* 85: 2245-2257.

Hilbert, D.W. and A Larigauderie. 1990. The concept of stand senescence in chaparral and other Mediterranean type ecosystems. *Acta Ecologica* 11: 181-190.

Jobbagy, E.G. and O.E. Sala. 2000. Controls of grass and shrub aboveground production in the Patagonian Steppe. *Ecological Applications* 10: 541-549.

Joy D.A. and D.R. Young. 2002. Promotion of mid-successional seedling recruitment and establishment by *Juniperus virginiana* in a coastal environment. *Plant Ecology* 160: 125-135.

Krovetz, D.K., J.H. Porter, J.R. Spitler and P.H. Smith. 2004. Meteorological measurements of the Virginia Coast Reserve LTER. Data of the Virginia Coast Reserve Long-term Ecological Research Project VCR97018.

Kwit, C., D. J. Levey, C.H. Greenberg, S.F. Pearson, J.P. McCarty, and S. Sargent. 2004. Cold temperature increases winter fruit removal rate of a bird-dispersed shrub. *Oecologia* 139: 30-34.

Kwit, C., D. J. Levey, C.H. Greenberg, S.F. Pearson, J.P. McCarty, S. Sargent, and R. Mumme. 2004. Fruit abundance and local distribution of wintering hermit thrushes (*Catharus guttatus*) and yellow-rumped warblers (*Dendroica coronata*) in South Carolina. *The Auk* 121: 46-57.

Larcher, W. 2003. Physiological plant ecology. Springer-Verlag, Berlin.

Levy, G.F. 1990. Vegetation dynamics on the Virginia Barrier Islands. *Virginia Journal of Science* 41: 300-306.

Lichter, J. 1998. Primary succession and forest development on coastal Lake Michigan sand dunes. Ecological Monographs 68: 487-510.

Maass, J.M., J.M. Vose, W.T. Swank, and A.M. Martinez-Yrizar. 1995. Seasonal changes of leaf area index (LAI) in a tropical deciduous forest in west Mexico. *Forest Ecology and Management* 74: 171-180.

Marshall, J.D. and R.H. Waring. 1986. Comparison of methods of estimating leaf-area index in old growth douglas-fir. *Ecology* 67: 975-979.

Martinez-Yrizar, A., S. Nunez, H. Miranda, and A. Burquez. 1999. Temporal and spatial variation of litter production in Sonoran Desert communities. *Plant Ecology* 145: 37-48.

McCarron, J.K. and A.K. Knapp. 2003. C_3 shrub expansion in a C_4 grassland: positive post-fire responses in resources and shoot growth. *American Journal of Botany* 90: 1496-1501.

Monk, C.D. 1966. An ecological significance of evergreeness. *Ecology* 47: 504-505.

Morris, M., Eveleigh, D.E., Riggs, S.C.; and W.N. Tiffney, Jr. 1974. Nitrogen fixation in the bayberry (*Myrica pennsylvanica*) and its role in coastal succession. *American Journal of Botany* 61: 867-870.

Oosting, H.J. and W.D. Billings. 1942. Factors effecting vegetational zonation on coastal dunes. *Ecology* 23: 131-142.

Neufeld, H.S. and D.R. Young. 2003. Ecophysiology of the herbaceous layer in temperate deciduous forests. In F.S. Gilliam and M.R. Roberts. The herbaceous layer in forests of eastern North America. Oxford University Press, NY.

Norby, R.J., J.D. Sholtis, C.A. Gunderson, and S.S. Jawdy. 2003. Leaf dynamics of a deciduous forest canopy: no response to elevated CO2. Oecologia 136: 574-584.

Permar, T.A. and R.F. Fischer. 1983. Nitrogen fixation and accretion by wax myrtle (*Myrica cerifera*) in slash pine (*Pinus ellotii*) plantations. *Forest Ecology and Management* 5: 39-46.

Pierce, L.L. and S.W. Running. 1988. Rapid estimation of coniferous forest leaf area index using a portable integrating radiometer. *Ecology* 69: 1762-1767.

Poole, D.K. and P.C. Miller. 1981. The distribution of plant water stress and vegetation characteristics in southern California chaparral. *American Midland Naturalist* 105: 32-43.

Runyon, J., R.H. Waring, S.N. Goward, and J.M. Welles. 1994. Environmental limits on net primary productivity and light use efficiency across the Oregon transect. *Ecological Applications* 4: 226-237.

Shao, G., D.R. Young, J.H. Porter, and B.P. Hayden. 1998. An integration of remote sensing and GIS to examine the responses of shrub thicket distributions to shoreline changes on Virginia barrier islands. *Journal of Coastal Research* 14: 299-307.

Stallins J.A. and A.J. Parker. 2003. The influence of complex systems interactions on barrier island dune vegetation patterns and process. *Annals of the Association of American Geographers* 93: 13-29.

Stalter, R. and W.E. Odum. 1993. Maritime Communities. In W.H. Martin, S.G. Boyce, and A.C. Echternacht. Biodiversity of the southeastern United States. John Wiley, NY.

Tolliver, K.S., D.M. Colley, and D.R. Young. 1995. Inhibitory effects of *Myrica cerifera* on *Pinus Taeda*. *American Midland Naturalist* 133: 256-263.

Tolliver, K.S., D.W. Martin and D.R. Young. 1997. Freshwater and saltwater flooding response for woody species common to barrier island swales. *Wetlands* 17: 10-18.

Turner, D.P., S.A. Acker, J.E. Means, S.L. Garman. 2000. Assessing alternative allometric algorithms for estimating leaf area of Douglas-fir trees and stands. *Forest Ecology and Management* 126: 61-76.

Welles, J.M. 1990. Some indirect methods of estimating canopy structure. *Remote Sensing Reviews* 5: 31-43.

Whittaker, R.H. 1961. Estimation of net primary productivity of forest and shrub communities. *Ecology* 42: 177-180.

Wright, S.J. 1991. Seasonal drought and the phenology of understory shrubs in a tropical moist forest. *Ecology* 72: 1643-1657.

Young, D.R. 1992. Photosynthetic characteristics and potential moisture stress for the actinorhizal shrub, *Myrica cerifera* (Myricaceae), on a Virginia barrier island. *American Journal of Botany* 79: 2-7.

Young, D.R., E. Sande, and G.A. Peters. 1992. Spatial relationships of *Frankia* and *Myrica cerifera* on a Virginia, USA Barrier Island. *Symbiosis* 12: 209-220.

Young, D.R., D.L. Erickson and S.W. Semones. 1994. Salinity and the small-scale distribution of three barrier island shrubs. *Canadian Journal of Botany* 72: 1365-1372.

Young, D.R., G. Shao, and J.H. Porter. 1995. Spatial and temporal growth dynamics of barrier island shrub thickets. *American Journal of Botany* 82: 628-645.

Zar, J.H. 1999. Biostatistical Analysis: fourth edition. Prentice Hall, NJ.

Some data used in this publication was provided by the Virginia Coast Reserve LTER project, which was supported by National Science Foundation grants BSR-8702333-06, DEB-9211772, DEB-9411974 and DEB-0080381.

Table 1. Comparison of leaf area index estimates in four *Myrica cerifera* thickets on Hog Island during the summer of 2004 using four common methods of measurement. Estimates of LAI using light attenuation represent a range of values measured over several days at a single site in late June rather than a spatial average. The mean ± one standard error is provided for other methods.

Thicket	**LAI-2000 (late June)**	**Light attenuation (k= 0.6)**	**Annual litterfall**	**Allometric modeling**
Bay Side	1.9 ± 0.1	4.5 – 5.1	4.1 ± 0.5	6.4 ± 0.2
Mid-Island	3.5 ± 0.2	7.2 – 7.7	7.7 ± 0.3	11.4 ± 2.1
Young	3.9 ± 0.1	4.0 – 4.4	10.2 ± 0.4	10.2 ± 1.3
Colonizing	3.6 ± 0.2	8.6 – 8.8	10.0 ± 0.3	9.8 ± 1.8

Table 2. Comparison of seasonal leaf area index measurements using light attenuation and a portable integrating radiometer for four *Myrica cerifera* thickets on Hog Island. Measurements of LAI using light attenuation represent a range of values measured over several days at a single site rather than a spatial average. The mean ± one standard error is provided for the portable integrating radiometer (n =10). An * denotes missing data.

	June		January		April	
Thicket	**Portable integrating radiometer**	**Light attenuation (k =0.6)**	**Portable integrating radiometer**	**Light attenuation (k =0.6)**	**Portable integrating radiometer**	**Light attenuation (k =0.6)**
Bay Side	1.9 ± 0.2	4.5 - 5.1	1.5 ± 0.2	3.8 - 4.8	1.2 ± 0.1	*
Mid-Island	3.5 ± 0.2	7.2 - 7.7	2.9 ± 0.2	5.5 - 6.3	2.4 ± 0.1	3.2 - 3.8
Young	3.9 ± 0.1	4.0 - 4.4	3.4 ± 0.2	*	2.3 ± 0.1	*
Colonizing	3.6 ± 0.2	8.6 - 8.8	2.8 ± 0.1	7.9 - 8.0	1.9 ± 0.1	2.4 - 2.9

Table 3. Individual allometric relationships used to predict dry leaf mass based on stem diameters (Ds) for four *Myrica cerifera* thickets on Hog Island. For each thicket predicted leaf mass = $10^{m(\log Ds)+c}$. Mean leaf area index ± one standard error is then calculated from specific leaf area and the predicted dry leaf mass of three plots in each thicket.

Site	**Regression Coefficient (m)**	**Constant (c)**	**r^2**	**Mean Leaf Area Index ± 1 S.E.**
Bay Side	1.635	-0.230	0.966	6.4 ± 0.2
Mid-Island	1.689	-0.417	0.904	11.4 ± 2.1
Young	2.097	-1.131	0.968	10.2 ± 0.7
Colonizing	2.411	-1.525	0.958	9.8 ± 1.8

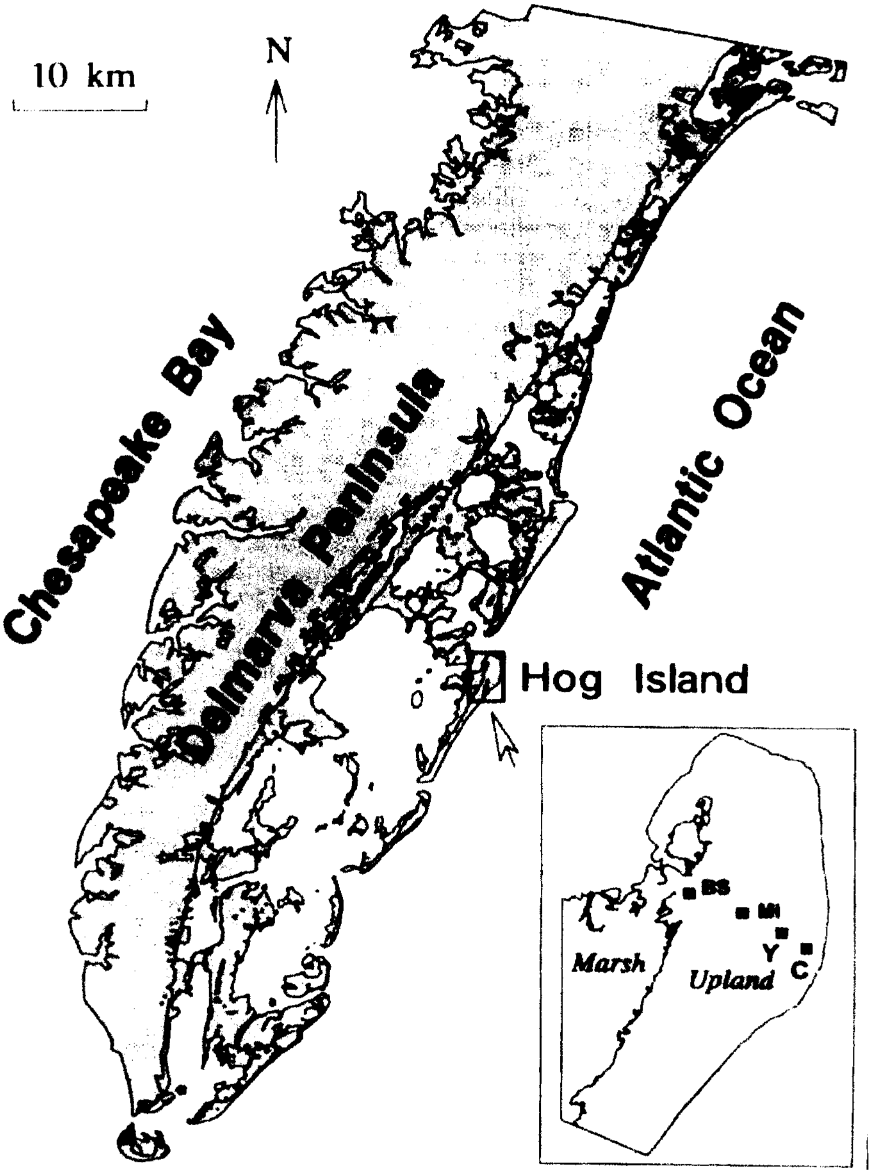

Figure 1. The southern portion of the DelMarVa peninsula and the barrier islands of the Virginia Coast Reserve including Hog Island. Inset shows the positions of the four *Myrica cerifera* thickets on the north end of the island. BS = Bay Side, MI = Mid-island, Y = Young, C = Colonizing.

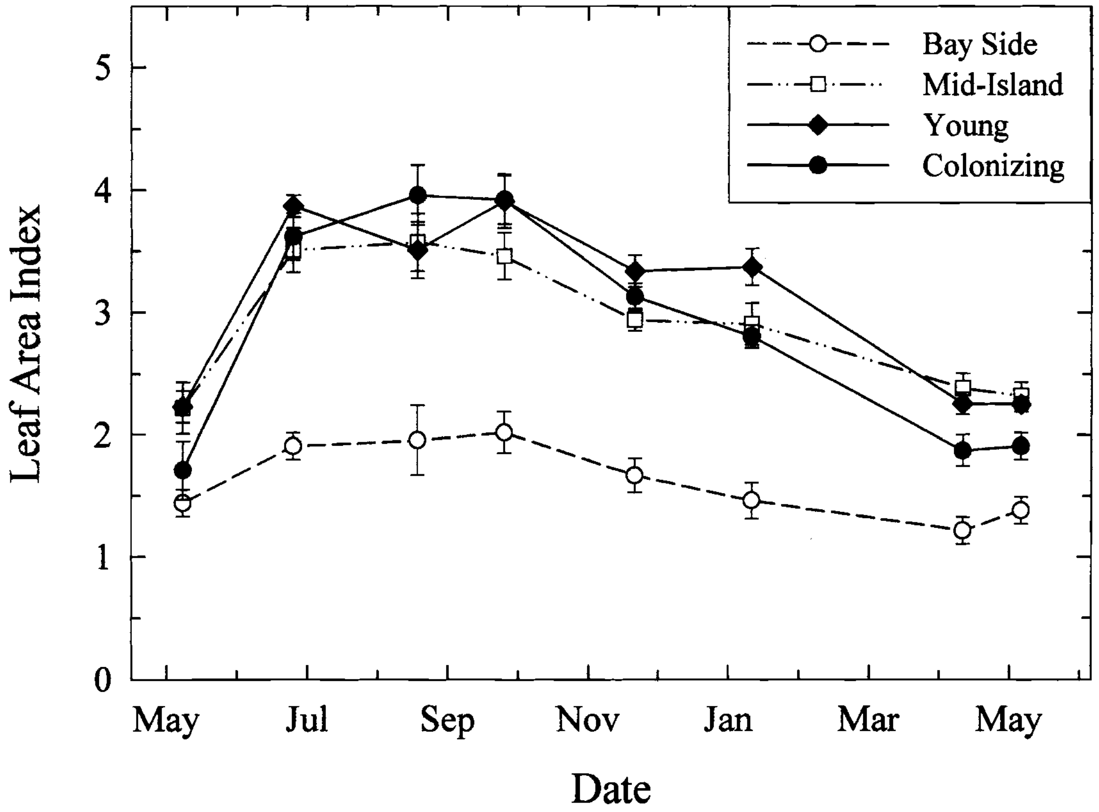

Figure 2. Seasonal variation in leaf area index of four *Myrica cerifera* thickets on Hog Island. Each value is based on measurement at ten sites using a portable integrating radiometer. Error bars represent ± one standard error.

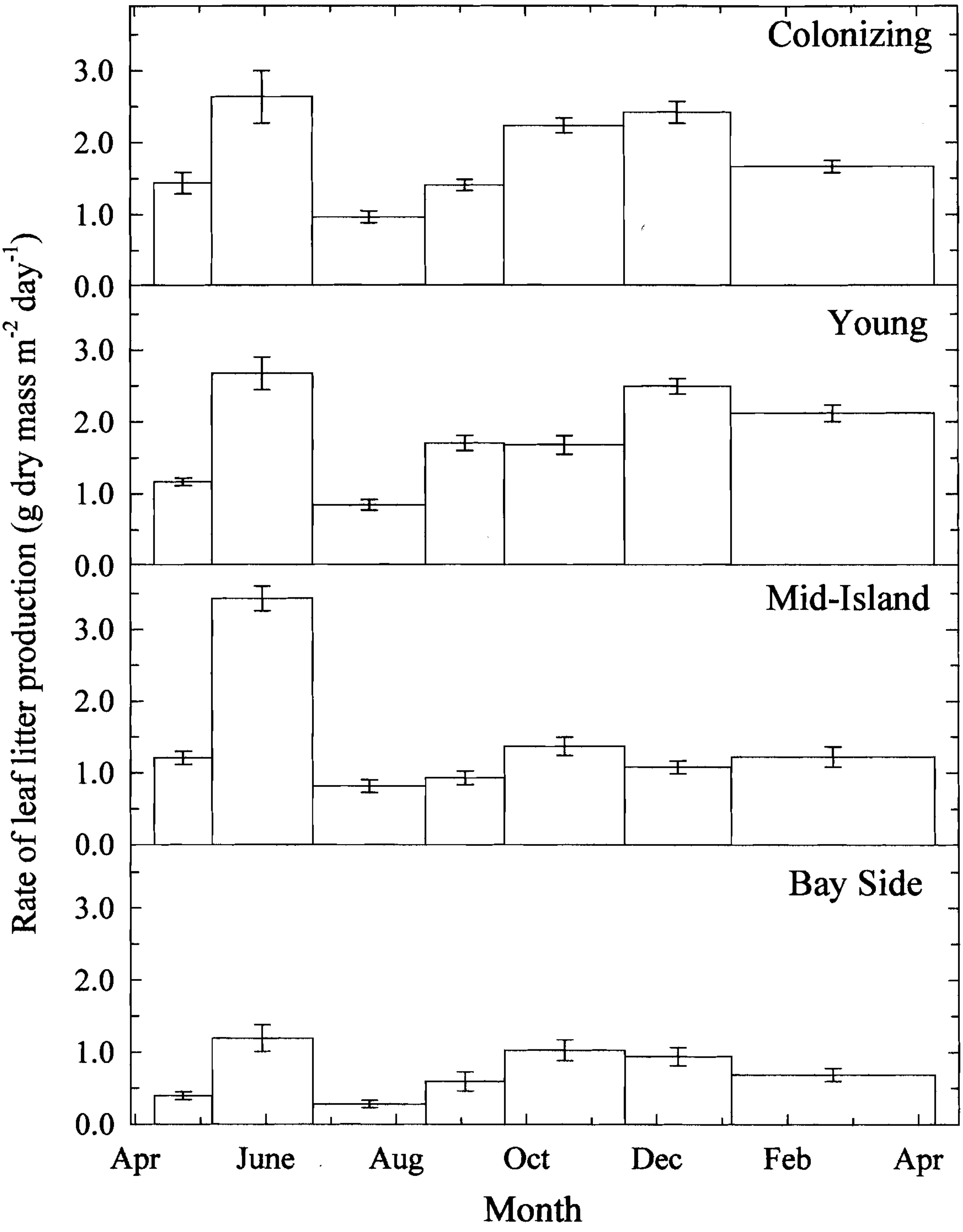

Figure 3. Seasonal production of leaf litter for four *Myrica cerifera* thickets on Hog Island. Error bars represent ± one standard error.

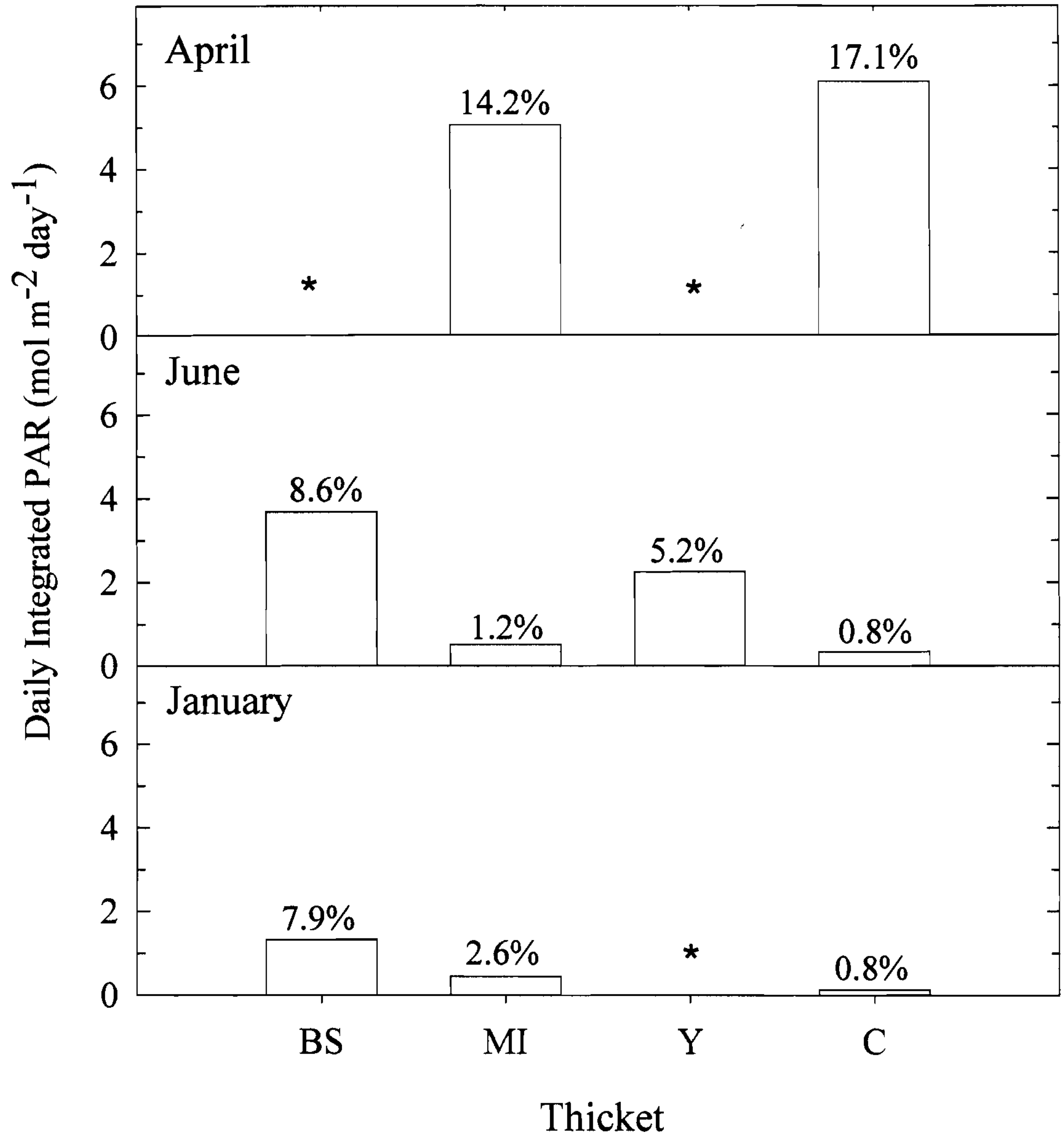

Figure 4. Seasonal variation in photosynthetically active radiation (PAR) below four *Myrica cerifera* thickets on Hog Island (BS = Bay Side, MI = Mid-Island, Y = Young, C = Colonizing). The percentage of above canopy radiation is noted above each bar. An * denotes missing data.

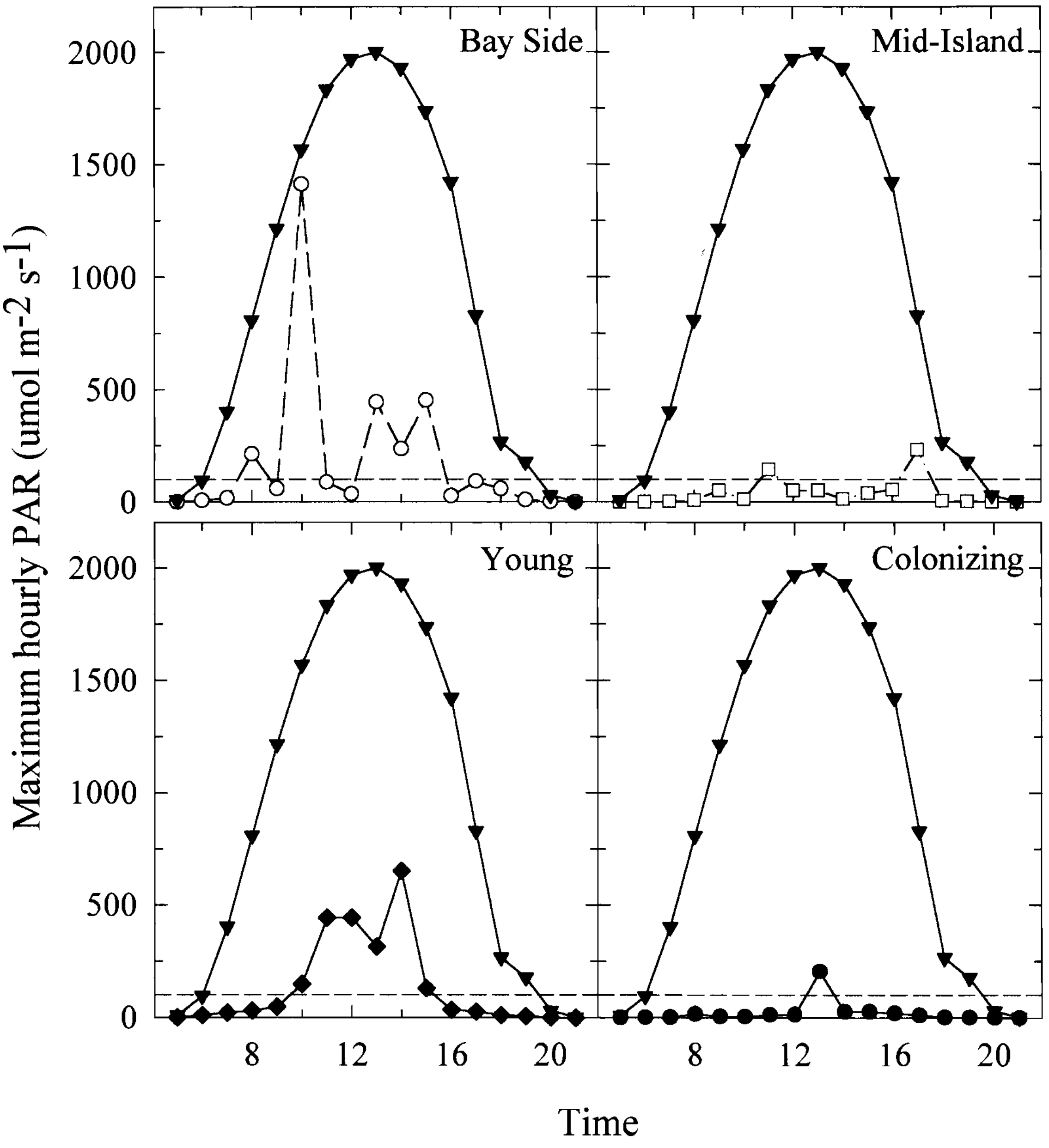

Figure 5. Spatial variation in maximum photosynthetically active radiation (PAR) in the understory of four *Myrica cerifera* thickets on Hog Island. Maximum incident PAR is shown for comparison. Reference lines demonstrate the relative magnitude of 100 umol m^{-2} s^{-1} to understory light.

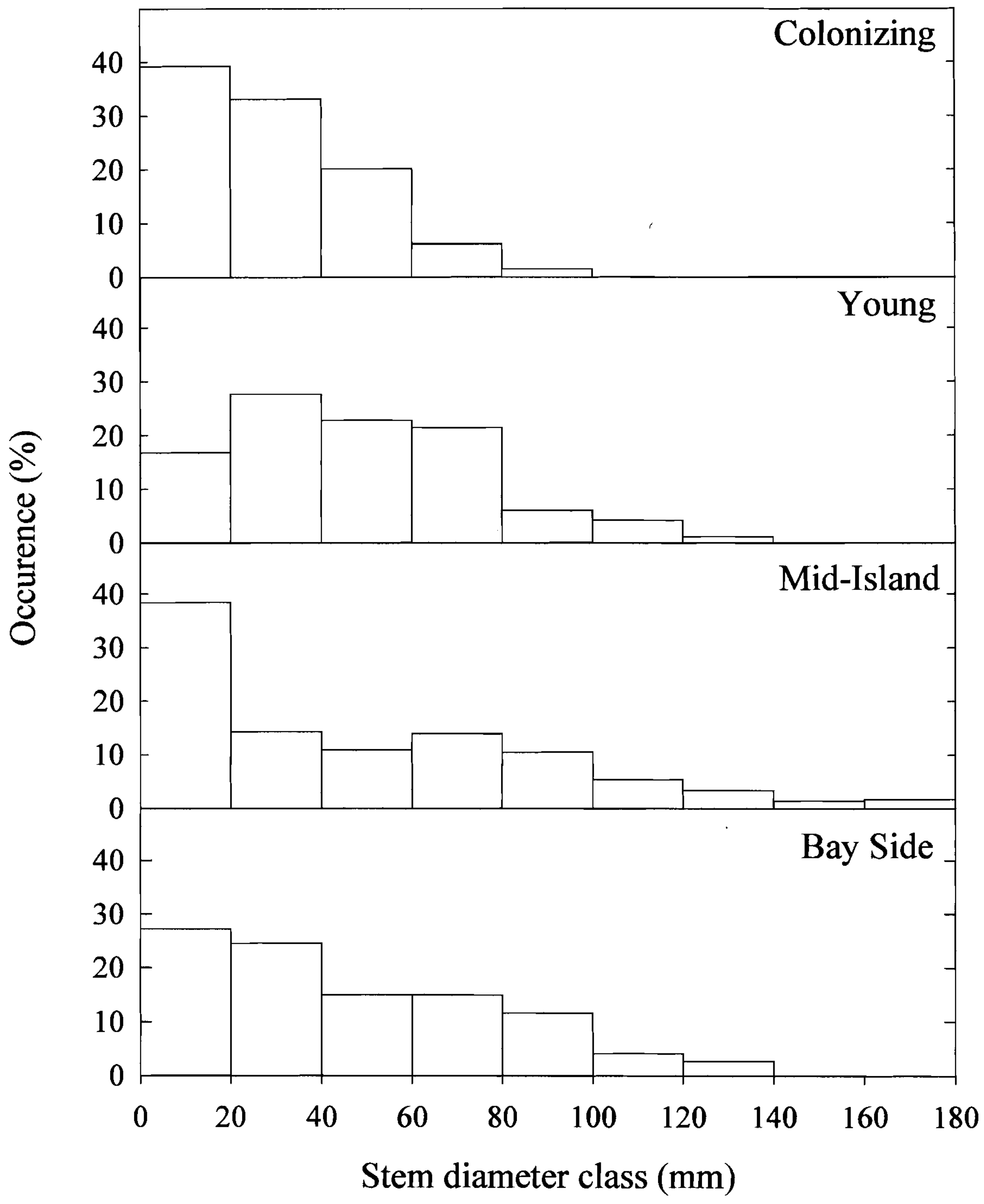

Figure 6. Frequency distribution of stem diameters in four *Myrica cerifera* thickets on Hog Island.

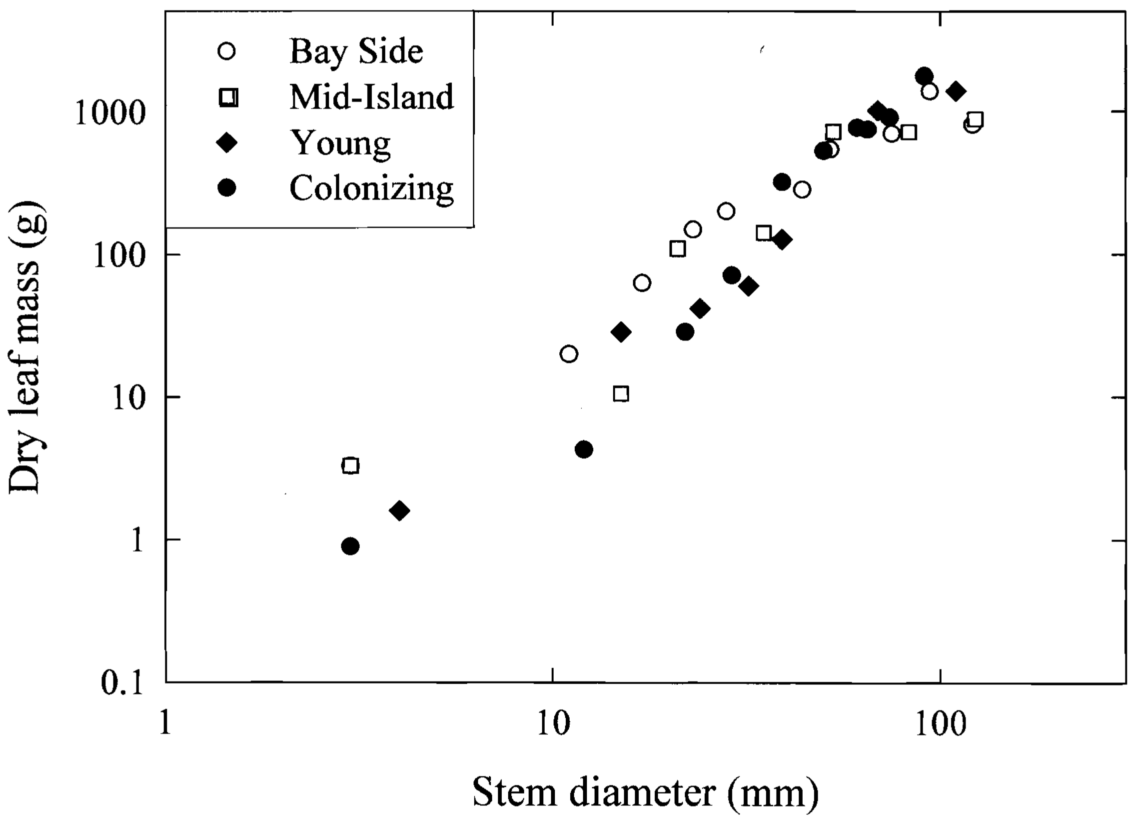

Figure 7. Leaf mass vs. stem diameter for 34 *Myrica cerifera* stems from four shrub thickets on Hog Island.

Vita

Steven Terry Brantley was born on November 9, 1975 in Portsmouth, Virginia. He graduated from Lakeland High School in Suffolk, Virginia in June 1993 where he was a member of the National Honor Society. After high school, Steven served four years in the United States Army and continued to serve part-time in the Maryland Army National Guard for five years while attending college. He attended Anne Arundel Community College before transferring to Virginia Commonwealth University in 2001. He received a Bachelor of Science in Biology, with honors, in August, 2003 and received a Master of Science in Biology in August, 2005 from Virginia Commonwealth University where he studied coastal plant ecology. Steven will continue his research in coastal plant ecology in the Ph.D. program for Integrative Life Sciences at VCU.