Biotic Interactions Influencing Shrub Establishment on an Atlantic Coast Barrier Island

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ABSTRACT

BIOTIC INTERACTIONS INFLUENCING SHRUB ESTABLISHMENT ON AN ATLANTIC COAST BARRIER ISLAND.

Elucidating mechanisms influencing the establishment of woody species is essential for understanding community dynamics and successional processes on barrier islands. The relative intensity of facilitation and inhibition of grasses on seedling establishment of two woody species common to Atlantic Coast barrier islands, _Myrica cerifera_ and _Baccharis halimifolia_, were examined in a grassy swale on Hog Island in 1995 and 1996. Biomass, mortality, and physiological responses were quantified in a factorial experiment that included above-ground clipping and root exclosure treatments. In addition, effects of grass density on biomass and mortality were examined in 1996 for three density levels: low, medium and high. Insect herbivore damage was categorized by degree of above-ground damage.

The 1995 and 1996 field seasons were distinctly different in amount of precipitation, with greater than 200% increase in precipitation in 1996 relative to 1995. Grasses had a net inhibitory effect on *Myrica* in both years, regardless of precipitation regime. In the dry year, herbivory was higher in the presence of grasses, suggesting facilitation of insect herbivores by grasses, though no mortality occurred. Further, during periods of water stress, net photosynthesis for *Myrica* was greater in treatments without above or below-ground competition. Additionally, *Myrica* growth integrated over the season was greatest in treatments without above or below-ground competition. However, no herbivory occurred in 1996, and mortality was highest with grasses present, suggesting negative effects from flooding over the growing season.

In contrast, *Baccharis* growth was greatest and mortality lowest in the presence of grasses in the dry year. Soil surface temperature significantly decreased with grasses, and may have facilitated *Baccharis* growth. Additionally, herbivory increased when the grass canopy was removed. However, in the wet year there was a net inhibitory effect on _Baccharis_, though causal mechanisms are unclear.

Thus, based on two field seasons, biotic mechanisms of facilitation and inhibition by grasses, as well as herbivory, may influence woody seedling establishment, with temporal and species specific differences varying with intensity of water stress and the precipitation regime over the growing season.

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INTRODUCTION

Currently, there is no single, unifying theoretical framework for plant community succession. The relative importance of underlying mechanisms of succession as well as interrelationships among these mechanisms are not well understood (Connell and Slatyer 1977; Walker and Chapin 1986; Pickett et al. 1987). Coastal succession research has reflected the conflict between early theoretical models of succession proscribed by Clements and Gleason, as well as more modern theories that view community change as a process of individual replacement, resulting from interrelationships among environmental factors, life history traits, and biotic interactions (Connell and Slatyer 1977; Tilman 1985; Walker and Chapin 1986; Huston and Smith 1987; Pickett et al. 1987; Ehrenfeld 1990; Chapin et al. 1994).

The application of modern successional theories to coastal systems has been questioned (Ehrenfeld 1990). Despite considerable controversy over the application of specific mechanisms and pathways within a given sere (Ehrenfeld 1990; Stalter and Odum 1993), most models of coastal succession suggest a progression from a grass seral stage, to shrub thickets, and finally to maritime forest, depending on environmental and physiographic conditions (Ehrenfeld 1990; Stalter and Odum 1993). The underlying mechanisms in this general sere have yet to be quantified.

Mechanisms influencing colonization and establishment are particularly important in early succession (Connell and Slatyer 1977; Walker and Chapin 1987), such as in the severe environments characteristic of coastal systems. Seedling and juvenile stages may be especially sensitive to harsh physical stresses (Maun 1994). In the seedling stage, soil moisture, sand movement, salt spray, and temperature are the most limiting environmental factors in coastal systems (Van der Valk 1974; Maun 1994). Thus, environmental extremes have been considered primary factors influencing coastal community dynamics. Nevertheless, in harsh environments biotic interactions may be just as important.

Indeed, positive interactions have been associated with severe environments (Niering et al. 1963; Bertness 1989; Bertness and Shumway 1993; Bertness and Callaway 1994; Bertness and Hacker 1994; Maun 1994). Physical stresses are often ameliorated by plant cover, facilitating colonization and establishment (Niering et al. 1963; Bertness 1992). Substratum shading reduced evaporative water loss and soil salinity in coastal marsh and the marsh/upland interface (Bertness 1991; Bertness and Callaway 1994; Callaway 1994), and reduced water loss and soil temperatures in desert systems (Franco and Nobel 1985; Valiente-Banuet and Ezcurra 1991), thus facilitating establishment. Many woody species common to coastal systems are sensitive to both water and salt stress. Mitigation of these factors by substratum shading may positively influence seedling establishment. Thus, substratum shading by grasses may facilitate woody seedling establishment during the grass seral stage of coastal systems.

Inhibitory mechanisms of competition and herbivory may also be factors influencing succession processes. When environmental stress was reduced in a coastal marsh, a previously net facilitative effect was replaced by a net inhibitory effect (Bertness and Hacker 1994). Additionally, removal of potential competitors altered relative species dominance in a swale on a North Carolina barrier island (Silander and Antonovics 1982), while competition for water and soil nutrients limited woody seedling invasion and growth in old fields and grasslands (Gill and Marks 1991).

Herbivory has been demonstrated to have a negative impact on several coastal species (Ehrenfeld 1990). Insect herbivory reduced growth rates and mortality of _Salix cordata_, a sand dune species (Bach 1994). Additionally, insect herbivory reduced height and caused significant defoliation of _Baccharis_ species (Kraft and Denno 1982; Lara and Fernandes 1994). Further, insect herbivory influenced plant successional patterns in a sand dune sere (Bach 1994).

Facilitation, competition, herbivory, and abiotic factors interact, potentially altering successional processes. Neighbor vegetation enhanced emergence and survival of seedlings in secondary succession, but subsequent seedling growth was inhibited (DeStevens 1991; Berkowitz 1995). Herbivory can alter competitive outcome, while competition can influence susceptibiltiy to herbivore attack (Louda et al. 1990). Variation in intensity of competition has been related to physical factors in a variety of habitats (Berkowitz et al. 1995). Increased stress also can magnify the negative effects of herbivory (Parker and Slazman 1985), as well as reduce compensatory growth (Louda et al. 1990). As a result, the relationships among biotic and abiotic mechanisms may be particularly important in harsh and resource limited environments, such as coastal systems.

Few studies have examined the influence of interactions among potential underlying mechanisms (e.g. facilitation, competition, herbivory, and abiotic factors) on the rate and progression of primary succession (Ehrenfeld 1990; Bach 1994). Further, virtually no studies have examined these interactions and their impact on coastal successional processes. Indeed, interrelationships among biotic mechanisms have received limited attention in coastal systems, especially in upland woody communities. Yet, the results from my preliminary experiments during the 1995 field season on a Virginia barrier island suggest that interactions among biotic mechanisms may indeed be key factors influencing successional processes during the transition from grass seral stage to shrub thicket stage in these harsh environments. Elucidating the relative importance and interrelationships among mechanisms influencing the establishment of woody species is essential for understanding community dynamics and successional processes in coastal systems.

Accreting barrier islands are particularly well suited to examining the interplay among potential underlying mechanisms influencing primary succession in coastal environments. Barrier islands are highly dynamic systems with extreme spatial and temporal variability (Barbour et al. 1985; Crawford 1989; Ehrenfeld 1990). Whereas environmental gradients are gradual, vegetation zonation is distinct and discrete, suggesting a potential role for biotic interactions. Thus, the potential interrelationships among environmental factors and biotic interactions, coupled with a soil chronosequence due to island accretion patterns, make accreting barrier islands an ideal location to study mechanisms influencing the progression of early primary succession in coastal systems.

The goal of this research was to ascertain biotic mechanisms influencing woody seedling establishment during the transition from the grass seral stage to woody shrub thicket seral stage on an accreting barrier island. The central hypothesis was two-fold: first, that grasses facilitate the establishment of woody seedlings by ameliorating microsite environmental extremes; and second, that grasses facilitate insect herbivory of shrubs, influencing competitive responses of shrubs with grasses (Fig. 1).

There were five primary objectives. The first was to examine the relative intensity of facilitation and inhibition of grasses on shrub seedling establishment by manipulating grass canopy cover and root distribution. The second, was to examine the relative impact of insect herbivory on seedling establishment using insect exclosures, as well as to examine the effect of canopy cover on the occurrence and intensity of herbivory. The third, was to examine the effect of grass canopy manipulation on microsite environmental factors, and the potential relationships between differences in environmental factors and corresponding variations in physiological and growth responses of shrubs among treatments. The fourth, was to examine potential protection offered by surrounding small dunes on edaphic characteristics and shrub mortality and biomass. The Fifth, was to examine shrub occurrence within the swale in relation to distance from the ocean, grass cover, and several potentially limiting environmental factors.

METHODS

Field site and focal species.

Experimental sites were located on the northern accreting end of Hog Island (371401N, 751401W) of the Virginia Coast Reserve (VCR), a long-term ecological research site (LTER). Hog Island is 1,177 ha, approximately 10 km in length, and 2.4 km at the widest point. Field experiments were conducted in an area of early shrub colonization within an existing soil chronosequence (Hayden et al. 1991). This "colonizing site" is within a grass dominated swale preceding the primary dune ridge. The focal species were *Myrica cerifera*, a dominant shrub on Atlantic Coast barrier islands, and *Baccharis halimifolia*, a common shrub with many overlapping physical tolerances with *Myrica cerifera*. Experimental plots within the study site were followed during 1995 and 1996. Additional examination of natural density effects and environmental gradients as well as Myrica occurrence along transects across the study site were included in 1996.

Experimental plots

1995 Experimental design - neighbor removal and site protection. To examine the relative facilitation, inhibition, and relative site protection on woody seedling establishment, a full factorial treatment design with three factors was employed. The three factors were grass canopy manipulation, manipulation of root distribution, and site protection. Each factor contained two levels: canopy presence/absence, root exclosure presence/absence, and small dune presence/absence, respectively. Two experimental sites were selected within the colonizing site. Site A was located with adjacent small dunes that could potentially provide physical protection from prevailing winds along with associated aeolian salt and sand scouring and deposition. Site B was located without adjacent dunes. Additionally, sites were selected so that elevation of plots within sites A and B did not vary by more than ± 5 cm (Trimble Navigation 4000 SE laser survey system). Forty ¼ m^2 plots were established within each site (A and B). Vegetation in half the plots within sites A and B was clipped to within 2 cm of the soil surface. Within each plot, two seedlings of each species were fitted with root collars. Seedlings of each species were randomly assigned to each of the 8 treatments (total n=20).

1996 Experimental design - neighbor removal and herbivory. Because of the observed effects of herbivory on both Myrica and Baccharis in 1995, herbivore exclosure was added as a factor, replacing the site factor. The relative importance of facilitation, inhibition, and herbivory as potential mechanisms influencing woody seedling establishment were thus examined. A full factorial treatment design with three factors was employed, using ten replicate paired 1x2 m^2 plots (total plots = 20) randomly distributed within the swale. Plots of each pair were separated by 1/2 m to minimize edge effects. The three factors, grass canopy manipulation, root exclosure, and insect herbivore exclosure, each contained two levels: canopy presence/absence, root exclosure presence/absence, and insect exclosure presence/absence. Established vegetation in one plot of each pair was clipped to within 2 cm of the soil surface. Within each of the paired plots, half of the seedlings were fitted with root collars.

Insect exclosures of tight weave no-see-um mosquito netting were placed on half of the seedlings receiving root collars, and on half of the seedlings without root collars. Two seedlings of each species were randomly assigned to each of the 8 treatments within the paired plots (total n=20).

Seedling and treatment application. In May of 1995 and 1996, seedlings from field grown populations were obtained from the colonizing site on Hog Island and immediately transplanted into the plots (Height: Myrica 19.3 cm ± 0.9, Baccharis 19.7 cm ± 0.7). Clipped treatments consisted of clipping all vegetation in the plot to approximately 2 cm above ground level. Plots were clipped every 10 - 14 days during the growing season. Clipped vegetation was removed from the plots to minimize nutrient input from clippings. Root exclosures consisted of PVC pipe (7.5 cm diameter, 30 cm length) with open ends. Based on soil core data from the 1995 field season, grass roots did not extend deeper than the root exclosures (unpublished data, K.S. Tolliver). In 1996, insect exclosures consisted of sacs (40cm x 30 cm) made from tight weave no-see-um mosquito netting, placed over individual plants and fastened at the base with twist ties.

Density plots

The effect of grass density on growth and mortality of woody seedlings, as well as potential differences in herbivory with variation in grass density were examined in 1996. A single factor (density) design with three levels of density (low, medium, and high) was used. Five replicate quadrats (1 x 2 m^2) of low, medium, and high naturally grass occurring densities were established within the swale preceding the foredune. Two seedlings of each shrub species from field grown populations were transplanted into each quadrat (n=10). Mortality and environmental variables were monitored and biomass quantified as detailed for removal experiments.

Neighbor density, species, and root depth

Average grass density of the unclipped plots was determined by counting the number of live stems in a randomly selected 0.10 m^2 area of each unclipped plot (n=10). Grass density was quantified once in June, 1996.

To verify that grass roots did not extend deeper than the 30 cm root exclosures, average root depth of grasses was determined once in June, 1995, from soil cores (n=5) located adjacent to the experimental plots. Dominant species in unaltered plots were determined by field identification and number of individuals present. Plots were censused in June and August.

Shrub response

Physiological response. The response of _Myrica_ and _Baccharis_ to variations in environmental and edaphic factors in individual treatments was determined by quantifying net photosynthesis, stomatal conductance, and midday xylem pressure potential in 1995. Physiological response was quantified only in 1995 due to inclement weather and flooded site conditions. Seedlings were acclimated to the treatments for a minimum of two weeks prior to beginning physiological measurements. Physiological measurements (n=5) were obtained monthly in 1995 (June through September) for both species, on relatively cloud-free days. Current year leaves (_M. cerifera_) were used for all physiological measurements. Midday xylem pressure potential was measured between 1100 -

1400 h (solar time) with a pressure chamber (Model 650, Plant Moisture Stress, Corvallis, OR, USA). Due to logistical considerations, pre-dawn xylem pressure potential was not measured. Net photosynthesis and stomatal conductance were quantified at midday with a portable photosynthesis system (Li-Cor LI-6200, Corvallis, OR, USA). Measurements were taken only when the photosynthetic photon flux density (PPFD) above the grass canopy was in excess of 500 1mol $m^{-2}s^{-1}$.

Mortality and Biomass. In addition to physiological measures of treatment effects, mortality and biomass were integrated over the growing season. The initial and final height of each seedling was recorded in May and September, 1996 only. To quantify biomass, seedlings of both species (1995: n=10, 1996: n=20) were harvested in September, then oven dried for 72 h at 80 °C.▪ Root and shoot dry mass (g) were measured.

Herbivory

A damage index was utilized to examine potential variation in the occurrence and intensity of herbivore damage between clipped and unclipped treatments over the course of the growing season. The damage category of all seedlings in treatments without insect herbivore exclosures or root collars was recorded bimonthly. The damage category was subjectively assigned, based on estimated damage to above ground tissue, as follows: 0 = 0% leaf area removed, 1 = 1-5%, 2 = 6-25%, 3 = 26-50%, 4 = 51-75%, and 5 = 76-100% leaf area removed.

Meteorological and edaphic characteristics

Because grasses may alter microclimate and edaphic characteristics in a manner that may facilitate shrub seedling establishment, the following environmental factors were quantified. Due to inclement weather and flooded conditions in 1996, July and August measurements of temperature, PPFD, and edaphic factors were not obtained.

Mean precipitation. Average monthly precipitation was obtained from meteorological stations (MET) in close proximity to Hog Island. MET stations were located on north Hog Island, Brownsville, and in Oyster.

Depth to groundwater and groundwater chlorides. Depth to groundwater (n=5) and groundwater chloride content (n=5) were obtained monthly in 1995, from temporary wells established with an hand auger adjacent to plot locations.

Chloride content was measured with a conductivity meter (Model 33, YSI, Yellow Springs, OH, USA).

Temperature and incident PPFD. Air temperature (1C) and incident photosynthetic photon flux density (PPFD 1mol $m^{-2}s^{-1}$) were monitored monthly at midday for both clipped and unclipped plots (n=5) in conjunction with the physiological measurements. Incident PPFD (Li-Cor LI-1000, Lincoln, NE, USA) was measured at two heights: above the grass canopy and at seedling height in both clipped and unclipped plots. Atmospheric and soil temperatures were quantified above the grass canopy, at seedling height, and at the soil surface in both clipped and unclipped plots, using copper and constantine thermocouples attached to a microvoltmeter (Wescor HR-33T Logan, UT).

Diurnal microclimate. To characterize general diurnal fluctuations in microclimate parameters specific to the summer field season, incident PPFD and both atmospheric and soil temperatures were quantified as described for monthly measurements, every h (0800-1500 solar time) on a clear day in June, 1995 and 1996. Additionally, to determine insect exclosure effects on microclimate, PPFD and temperature were followed diurnally within the insect exclosures (n=5).

Soil water content and chlorides. Soil samples from the root zone of both clipped and unclipped plots (n=5) were obtained for gravimetric analysis of soil water content. Random samples were placed in separate ziploc bags in the field for transport back to the laboratory for further analysis. Soil samples were obtained from clipped and unclipped plots (n=5). Total soil chlorides were determined with a chloride electrode after water extraction (Young et al. 1994). Soil samples for both water content and chlorides were obtained bimonthly, June through September.

Plot size effects. To examine the effect of plot size on microsite environmental variables and growth, incident PPFD and temperature were quantified as detailed for experimental plots, within 4 replicate plots of four size classes (0.25, 0.5, 1.0 and 2.0 m^2). Myrica seedlings (n=8) were transplanted into the size plots in May from field grown populations, and harvested in September to obtain root, shoot, and total weight.

Transects and Myrica occurrence.

Natural shrub establishment in relation to distance from the ocean and environmental factors was examined within the swale preceding the primary dune. Five transects (approximatly 150 m) were established perpendicular to the shore, from the hi-tide line to the primary dune. Circular sample plots (1 m radius) were placed every 25 m along the transects. Random samples (n=5) were obtained and analysed in June for soil chlorides, water content, and pH, as detailed previously. Additionally, *Myrica* shrub occurrence was recorded at each 25 m mark along the transects within the 1 m radius plots.

Statistical analysis.

Assumptions. Normal probability plots, Kolmogorov-Smirnov, Levene, Cochran's, and Bartlett's Box tests were utilized to examine the assumptions of normality and equality of variance prior to using any parametric tests (Sokal and Rohlf 1981; Zar 1984). Growth data from experimental plots were $\log_{10}$ transformed prior to analysis to normalize the data. Each species was analysed separately.

Physiological variables and biomass. A three factor analysis of variance (ANOVA) was used to analyze data from experimental plots for each sample date, and repeated for each dependant variable (net photosynthesis, stomatal conductance, xylem pressure potential, root weight, shoot weight, and total weight). A single factor analysis of variance was utilized for the density plots and for the plot size analysis. Tukey multiple comparison test for single or multiple analysis (Zar 1984) was utilized to determine where significant differences occurred among treatment means. Data were pooled when no significant interaction was indicated, and subsequently analyzed using a two factor or single factor analysis of variance with Tukey multiple comparison tests, as appropriate. In the case of unequal sample sizes, the Scheffé multiple comparison test was used (Zar 1984).

Herbivory between clipped/unclipped plots and mortality. A 2 x 4 chi-square analysis was used to test for association between canopy manipulation and damage category. In order to examine cumulative damage over the growing season, frequency of occurrence in each of the damage categories in September was utilized for this analysis. Categories one (1-5%) and two (6-25%) were combined for analysis. Mortality was analysed using a 2 X

4 chi-square analysis to test for association between treatment and survival outcome.

Meteorological and edaphic characteristics. Student’s t-test was used to independently examine differences between clipped and unclipped treatment means for the dependent variables (PPFD, temperature, soil water content, soil chlorides) on each date. Single factor analysis of variance was used to analyze differences among density plot (low, medium, high) means for the dependent variables.

Transect analysis. Linear regression was used to examine soil chlorides, water content, pH, and Myrica occurrence in relation to distance from the ocean. Additionally, step multiple regression procedures were utilized to examine the linear relationship between Myrica seedling occurrence and the edaphic characteristics, soil salinity, water content, and pH as well as distance from the ocean. Rules governing inclusion and elimination during the step procedure were F=0.05 for inclusion, and F=0.10 for elimination. All variables were examined for compliance with the assumptions of normality, linearity, and homogeneity of variance. Data were transformed as necessary for compliance with the assumptions. Samples from all five transects were combined for analysis.

RESULTS

In 1996, precipitation levels were unusually high during the field season relative to the preceding five years. This resulted in flooding of the experimental and density plots over the summer. Due to the inclement weather, physiological and meteorological sampling were restricted to the month of June in 1996.

Shrub response

Myrica physiological response-experimental plots. No consistent pattern was exhibited in June, 1995 for net photosynthesis (Fig. 2). In comparison, July and August values for net photosynthesis were consistently higher in treatments with root exclosures (Fig. 2). Stomatal conductance exhibited a general increase over the summer, but did not vary significantly among the treatments, except for significantly greater stomatal conductance in unclipped relative to clipped plots in August (not shown). Mid-day xylem pressure potential declined to a low in late July (Fig. 2). At this low point, mean mid-day xylem pressure potential was lower in clipped (-1.56 MPa) relative to unclipped plots (-1.18 MPa), though not significantly.

Baccharis physiological response - experimental plots. No discernable trends were detected for Baccharis net photosynthesis early in the field season (Fig. 3). In contrast, net photosynthesis was significantly higher in clipped plots in August ($p=0.04$, 2 August (Fig. 3). Similarly, no significant trends were exhibited for stomatal conductance until August, when stomatal conductance was higher in clipped relative to unclipped plots (not shown). Midday xylem pressure potentials decreased from June (-1.0 - (-1.3)) to July (-1.4 - (-1.6)), though no significant differences were detected (not shown). Tissue loss due to herbivory was significant during late July and August. As a result, undamaged leaf tissue was insufficient to allow reliable sampling of midday xylem pressure potentials in August.

Myrica biomass - experimental plots. No significant interaction among factors was exhibited in either 1995 or 1996 (Fig. 4). Significant differences ($p<0.02$) among treatment means occurred for both neighbor and root exclosure presence/absence in 1995. No significant difference was detected between Site A and Site B. Because there was no interaction, data were pooled for subsequent separate analysis of neighbor and root exclosure treatments.

Shoot, root, and total biomass were significantly (p<0.01) greater in clipped treatments in 1995 (Fig. 4). In this relatively dry year, a significant difference (p=0.02) in mean root biomass between root exclosure presence/absence treatments was indicated in the three factor ANOVA (Fig. 4). When data were pooled, no significant difference was detected (p>0.05).

Though not significant, results from 1996 exhibited the same trend as in 1995 (Fig. 4), with greater biomass occurring in clipped treatments. In contrast to the greater root biomass seen in 1995 with root exclosures, there was no discernable difference in root biomass between treatments in 1996 , the high precipitation year (Fig. 4).

Baccharis biomass - experimental plots. In 1995, shoot biomass was greater with canopy grasses present (Fig. 5). This difference between above-ground clipping treatments was significant (p=0.04) in the three factor analysis of variance. When data were pooled due to no significant interaction, the difference between clipped and unclipped treatment means was still statistically significant ($p=0.05$). A significant interaction ($p=0.04$) between root distribution (roots within root exclosure/roots not within root exlosure) and site (protected/not protected) was detected. This interaction was not significant ($p>0.05$) in subsequent analysis using a two factor ANOVA with only exclosure and site factors. In contrast to *Myrica* where no difference between sites was indicated, both *Baccharis* root and total biomass were significantly greater ($p<0.01$) in site A compared to site B in 1995.

In 1996, no significant interactions were detected. The net effect of grasses on *Baccharis* was opposite 1995 results in this high precipitation year. Root biomass was significantly greater ($p=0.03$) in clipped treatments (Fig. 5). Total biomass was also greater in clipped treatments, but the increase in biomass was not statistically significant. Corresponding with 1995 results, no discernable difference between means for root exclosure presence/absence was detected.

Biomass - density plots. There were significant differences ($p=0.02$) among treatment means for *Myrica*.

Mean root biomass in the low density treatment was significantly ($p=0.05$) greater than root biomass in the high density treatment (Fig. 6). No discernable trend was exhibited for *Baccharis*.

Mortality - experimental plots. No mortality occurred in 1995 for *Myrica*; however, mortality occurred for *Myrica* seedlings in 1996, the high precipitation year (Fig. 7). In contrast, mortality of *Baccharis* seedlings was greater in both 1995 and 1996 in clipped relative to unclipped treatments (Fig. 7). *Baccharis* mortality was also greater in site A compared to site B in 1995. Yet, based on the chi-square test of independence (*Myrica*: $x^2 = 1.53$, *Baccharis* $x^2 = 5.63$, d.f. = 3, $\propto = 0.05$) there was no dependence between survival category (dead, alive) and treatment for either species.

Mean stem density. Mean stem density of grasses (mean number of grass stems/m^2) differed significantly ($p<0.001$) among the three density levels, with high density (6840 ± 361 m^2) significantly ($p=0.05$) greater than medium (4460 ± 211 m^2) or low (3340 ± 307 m^2) density plots. Mean stem density of unclipped plots in the neighbor removal experiment was between the means for medium and high density plots (5160 ± 601 m^2). Primary species naturally occurring in the experimental and density plots were Spartina patens, Scirpus americana, Andropogan virginicus, Panicum amarum, and Juncaceae species.

Mortality - density plots. Myrica mortality did not differ between low and medium density; however, mortality was three times higher in the high density plots than in the low and medium density plots(Fig. 7). No specific density related pattern was detected for Baccharis, with mortality higher in medium density relative to both low and high density.

Herbivory

Both Myrica and Baccharis seedlings exhibited significant above ground tissue damage in 1995. The percentage of above ground damage to Myrica seedlings in upper damage categories (51-75 and 76-100) was greater in treatments with grasses present (Fig. 8). This was supported by the chi-square test for independence, which indicated a dependence between damage category and treatment for Myrica seedlings.

In contrast, the number of Baccharis seedlings in each damage category varied little for treatments with grasses present (Fig. 8); however, when grasses were removed there was an increasing number of seedlings in higher damage categories. This suggested greater tissue loss with grass canopy removal, though dependence between damage category and treatment was not supported for Baccharis seedlings by the chi-square test. In contrast to 1995, in 1996 all seedlings of both species were within the 0-25% damage category.

Meteorological and edaphic characteristics

Precipitation. Mean monthly precipitation for the summer remained below 50 mm in 1995. In contrast, the 1996 field season was 200% higher. Further, the 1996 mean monthly precipitation was high relative to the previous five years (Fig. 9). This resulted in flooded conditions over much of the summer field season, with soils seldom leaving a saturated state. Due to the flooding and inclement weather, temperature, PPFD, and edaphic factors were not measured in July or August. Thus, references to 1996 meteorological and edaphic characteristics are based only on June sampling.

Groundwater depth and salinity of colonizing site. Depth to groundwater increased over the course of the summer to a maximum of 50 cm in August, 1995 (Fig. 10). Depth to groundwater in 1996 was greater in June relative to 1995 values; however, for the remainder of the season the colonizing site had standing water or saturated soils on sampling dates. Groundwater salinity remained < 1 ppt in both 1995 and 1996.

PPFD and temperature - experimental plots. Midday incident PPFD was significantly ($p<0.001$) reduced at seedling height in unclipped relative to clipped treatments in both 1995 (Fig. 11) and 1996. In contrast, no significant differences in PPFD were observed between above canopy and seedling height in clipped treatments.

Temperature at the soil surface in clipped treatments was significantly (1995: $p<0.01$, 1996: $p=0.04$) higher than unclipped treatments in both 1995 (Fig. 11) and 1996. Within unclipped treatments, temperatures above the canopy were reduced relative to seedling height and soil surface temperatures, though significant differences ($p=0.01$) were observed only in June, 1996.

PPFD and temperature - density plots. Midday incident PPFD was significantly ($p<0.002$) reduced at seedling height in all three density treatments for the single sampling date in June (not shown). Incident PPFD at seedling height under both medium and high density conditions was significantly ($p=0.05$) reduced relative to low density. Correspondingly, mean soil temperature was significantly ($p=0.05$) higher in low density treatment relative to both medium and high density treatments. Within medium and high density treatments, temperature at seeding height was significantly ($p<0.01$) greater than either soil or above canopy temperatures. Within low density, soil temperature was significantly ($p<0.01$) greater than either seedling height or above canopy temperatures.

Diurnal PPFD and temperature. Representative, individual values indicated the following trends. In experimental plots, incident PPFD at seedling height was lowest in the presence of grasses (Fig. 12) in both 1995 and 1996. No discernable difference between above canopy and seedling height PPFD was observed in low density plots; however, PPFD was reduced at seedling height in both medium and high density plots, with the lowest values occurring after midday in high density plots (Fig. 12).

No discernible trends in temperature were identified between above canopy and seedling height regardless of grass canopy (i.e. clipped versus unclipped) (Fig. 13); however, temperatures at the soil surface and at -10 cm were reduced with the grass canopy intact (Fig. 13). Highest temperatures occurred at the soil surface in clipped treatments, while temperatures at -10 cm below the soil surface were lowest over the course of the day when grasses were present.

Temperatures at seedling height in medium and high density plots were higher relative to above canopy temperatures (Fig. 14). Additionally, temperatures at soil surface and -10 cm below the soil surface were highest at low density (Fig. 14).

Soil water content and soil chlorides - experiment plots. In 1995, there was no significant interaction between site and above ground clipping treatments for soil water content, with the exception of 2 August ($p=0.01$). Thus, except for 2 August, data were pooled for subsequent analysis. Water content (g) was significantly ($p=0.01$)

higher in unclipped plots relative to clipped on the 6 July, 1995 sampling date (Fig. 15). No significant differences between clipped and unclipped treatments were detected for the remainder of the summer. Water content in all plots decreased over the summer to a low of 7.7 % on 2 August (Fig. 15), corresponding with the reduced precipitation over the summer. Soils remained saturated or flooded on sampling dates in 1996, with no significant difference in soil water content between clipped and unclipped treatments.

Due to flooding, soil chlorides were examined only in 1995. No significant interaction between treatment and site was exhibited, nor was there a significant difference in soil chlorides between treatments; however, there was a significant difference ($p<0.03$) in soil chlorides between site A and site B on all sampling dates (Table 1). Soil chlorides were greater in site A relative to site B except for the final sampling date, September 16, when site B soil chlorides were greater than site A. Additionally, on 16 September, both _Myrica_ and _Baccharis_ seedlings in site B exhibited considerable leaf chlorosis.

Plot size

No significant difference in biomass (root, shoot, total) was exhibited among the different plot size classes for Myrica seedlings.

Transects and Myrica occurrence

Variation in both soil chlorides (μmol/g soil) and water content (%) exhibited a trend of patchy distribution (Table 2), with significant differences ($p<0.001$) among means of sampling locations along the transects (Table 2); however, the low r^2 values suggest that distance from the ocean only partially explains the observed trends. A weak linear relationship was also indicated between pH and distance from the ocean (Table 3), with pH decreasing with increasing distance (Table 2). There was a very weak linear relationship ($r^2=0.07$) between Myrica occurrence and distance from ocean (Table 3). Stepwise regression suggested distance and pH as contributing to Myrica occurrence along the transects (Table 3). The linear equation best predicting Myrica occurrence ($F<0.001$) was $y = -2.68 + 0.007x_1 + 0.305x_2$, where x_1 and x_2 represent distance and pH, respectively (not shown). The low r^2 value suggested that occurrence of Myrica seedlings was only partially explained by distance and pH. Further, Myrica seedlings never occurred on dunes, only in swales and along the sides of dunes (Table 2).

DISCUSSION

The central hypothesis was two-fold. First, grasses facilitate the establishment of woody seedlings by ameliorating microsite environmental extremes. Second, grasses facilitate insect herbivory of shrubs, influencing competitive responses of shrubs with grasses. The facilitation portion of the hypothesis was only partially supported for Baccharis under dry conditions, with a net inhibitory effect on Myrica in both years. Further, Myrica above ground tissue loss was greater within the grass canopy, supporting the inhibitory portion of the hypothesis; however, Baccharis tissue loss was greater with the grass canopy removed. Thus, the indirect effects of herbivory may differentially influence competitive responses of these two species with grasses. The precipitation regime during the growth season further mediated shrub response and the intensity of herbivory.

Relative intensity of faciliation and inhibition

Myrica - low precipitation year. The grass canopy had an inhibitory effect on Myrica seedling growth. Increased growth combined with increased net photosynthesis in July and August of 1995 for treatments with above-ground clipping and root exclosures, indicated that competitive interactions between grasses and *Myrica* for soil resources may be a causal mechanism.

Sandy soils characterizing swales have low water holding capacity, leading to reduced soil water content and plant moisture stress (Young 1992; Shao et al. 1993). In general, shading did not affect soil water content in experimental plots, though soil water content increased in medium and high density plots. Regardless, overall soil water content and depth to ground water were lowest during July and August, corresponding with reduced midday xylem pressure potentials in July. Unexpectedly high XPP measurements in August may have been due to a recent rain event or reduced vapor pressure deficit specific to this sampling date. *Myrica* is sensitive to moisture stress (Young 1992). Thus, water may well be the limiting resource underlying the competitive interaction.

Additionally, observed temperatures during July and August were near optimal (30 C) for *Myrica* photosynthesis (Young 1992) in all treatments. Further, midday incident PPFD was not reduced below the photosynthetic light saturation point (400 μmol $m^{-2}s^{-1}$) for Myrica (Young 1992) even when shaded by grasses. Thus, it is unlikely that either competition for light or reduced microclimate temperatures through shading were critical factors differentially influencing growth for Myrica in this study.

High temperatures are considered a limiting factor for seedlings in coastal environments, and amelioration of temperature extremes has facilitated seedling establishment, (Van der Valk 1974; Maun 1994). Additional experiments are needed to determine if grasses facilitate survival of newly emergent shrub seedlings as a result of decreased soil temperatures. Further, competition for light might be a factor, if for example, the reduction in incident PPFD observed during early morning and late afternoon with grasses was sufficient to affect cumulative net carbon gain over the season, thus impacting growth.

Baccharis - low precipitation year. In contrast to Myrica, the grass canopy had a net positive effect on Baccharis seedlings. Net photosynthesis followed a similar pattern to Myrica, with higher values occurring early in the season, but these values shifted to the clipped treatments in August. None the less, overall facilitation by grasses dominated in the dry year, with both increased biomass and decreased mortality in the presence of grasses.

Unlike Myrica, the reduction in midday xylem pressure potential was not significant, nor was a significant difference exhibited for root exclosure treatments; however, due to the extensive above ground tissue damage due to herbivory, XPP was not measured in August when plant stress is most likely to occur during a dry year. Competition for soil resources does not appear to explain the differences in growth among treatments.

Shading by the grass canopy may have facilitated seeding growth by reducing incident PPFD and soil temperatures. Relatively constant mortality rates in clipped relative to unclipped plots for both dry and wet years supports a possible role for facilitation through shading. However, the temperature optimum and light saturation point for Baccharis need to be identified to clarify the role of shading.

Myrica - high precipitation year. The net inhibitory effect on growth appears to be related to a direct negative impact of flooding over the course of the growing season. Because no significant differences between root exclosure treatments were apparent, competition for soil resources may not be a primary factor influencing Myrica growth and establishment.

No mortality over the dry year for Myrica, coupled with little to no herbivory in the wet year, indicates that the frequent flooding experienced over the growing season may have contributed to mortality of shrub seedlings in 1996. Myrica tolerated short term (30d) freshwater flooding in a glass house (Tolliver et al. 1997). Cumulative effects from frequent and prolonged anoxic soil conditions over the season may have contributed to overall mortality. Further, prolonged flooding is known to reduce net photosynthesis and growth in many species (Levitt 1980; Hale and Orcutt 1987).

Baccharis - high precipitation year. Baccharis was also sensitive to freshwater flooding (Tolliver, et al. 1997). Thus, flooding may have influenced plant performance. Yet, mortality varied little between the dry (1995) and wet (1996) years for Baccharis, so flooding is probably not the dominant factor leading to mortality for this species.

Herbivory

Herbivory influenced mortality and growth rates of coastal sand dune plant species (Bach 1994). Further, mortality from defoliation was higher for the seedling and juvenile life history stages in an arid environment (Parker 1985). In the present study, herbivore damage resulted in a significant loss of above-ground tissue to both species in 1995, but herbivory was negligible or non-existent in 1996, the high precipitation year. Grass cover directly affected herbivore activity in a desert ecosystem (Burger and Louda 1994). On Hog Island, grass cover appeared to have a direct effect on the intensity of insect herbivore feeding activity on these two shrubs. Herbivore activity on Myrica seedlings was reduced in clipped plots, but increased for Baccharis, indicating differential effects of grasses on the different herbivore species. Thus, herbivory indirectly affected plant performance.

Mortality and herbivory need to be followed over several cycles of wet/dry years to determine if observed associations between mortality, herbivory, and precipitation are indeed consistent patterns. Additionally, because the insect exclosure data from this study could not be included in the analysis due to flooding interactions with the nets, future studies must incorporate insect exclosures to determine predation intensity. Further, the individual herbivore species feeding on the shrub seedlings need to be identified, and the effect of drought and flooding on these species determined, as well as any positive associational benefits between grasses and these herbivore species.

Site protection and Myrica occurrence along transects

Only Baccharis seedlings exhibited significant differences in growth and mortality between sites, with increased growth and decreased mortality in the more protected site (A). In contrast to previous studies in a New England saltmarsh (Bertness 1991; Hacker and Bertness 1995), shading did not reduce soil salinity among treatments except on 2 August. However, soil chlorides were the only microsite environmental variable that differed significantly between sites A and B, with higher soil chlorides in site A. Myrica is sensitive to soil chlorides (Sande and Young 1992; Young, Erickson, and Semones 1994). Yet, Myrica exhibited no difference in growth or mortality between sites. Thus, the statistical difference was not ecologically significant and a direct effect of soil chlorides on seedling growth is unlikely to be the causal factor in observed differences between these sites.

Additionally, storm overwash may lead to flooding in swales, with increased salinity of flood waters (Ehrenfeld 1990; Young et al. 1995). After the harvest date, a storm event in September resulted in chlorosis of leaf tissues in seedlings in the less protected site (B). In contrast, the protected site (A) exhibited no leaf chlorosis. Soil chlorides in site B also rose to three times the level of site A after this event. Myrica and Baccharis are both sensitive to salt water flooding, with reduced stomatal conductance and midday xylem pressure potentials, and at higher salinities, the onset of mortality (Tolliver et al. 1997). Thus, establishment of both Myrica and Baccharis seedlings may be facilitated through microtopographic protection from increases in soil chlorides or salt water flooding during the primary growth season.

Distance from the ocean and pH only partially explained Myrica occurrence along the transects. Myrica seedling establishment occurred within swales or along the sides of dunes, where depth to groundwater was reduced.

Establishment may be restricted to these areas due to Myrica sensitivity to moisture stress. However, because grasses also establish in these areas and have a greater root density relative to these two shrubs, soil water may be a limiting resource in competitive interactions between grasses and Myrica seedlings.

Conclusions/synthesis

The results suggest the possible importance of biotic interactions in this harsh coastal environment. Yet, environmental factors interacted with and mediated biotic interactions. That abiotic and biotic factors interacted in a manner that influenced plant performance, indicates the potential impact on the progression of this coastal sere, from grasses to shrub thicket. Further, the effects are species specific. These findings are consistent with modern successional theories that view community change as a process of individual replacement due to changing interrelationships between abiotic and biotic factors, as well as life history traits (Walker and Chapin 1986; Huston and Smith 1987; Picket et al. 1987; Chapin et al. 1994).

Physical factors may dominate in determining safe sites for initial shrub colonization and establishment.

Shrub establishment along transects was related to distance from the ocean, and in the case of Myrica, site characteristics that favored soil water availability. Establishment is further facilitated by microtopographic protection from storm induced innundation and salt spray, which are both known factors limiting the seedling stage (Van der Valk 1974; Maun 1994).

Though physical factors may dominate distributional limits (Ehrenfeld 1990; Stalter and Odum 1993), once safe sites are encountered the interrelationships among biotic interactions and physical factors appeared to play a greater role in plant performance. Inhibition dominated in both wet and dry years for Myrica. The present study indicated that competition for water and indirect inhibitory effects of insect herbivores may well be the predominant underlying mechanisms influencing seedling performance in the dry year (Fig. 16). Competitive interactions with grasses for soil resources as well as environmentally induced stress may have increased susceptibility to herbivore attack (Louda et al. 1990). The grass canopy may also exert a positive effect on insect herbivores preying on Myrica, compounding the inhibitory effect. Thus, biotic interactions of competition (grasses with shrubs) and facilitation (grasses toward herbivores) may have interacted to produce the net inhibitory effect under limited soil water conditions.

Flooding is a major factor influencing the distribution of coastal species (Bertness et al. 1992; Pennings and Callaway 1992; Studer-Ehrensberger et al. 1993); however, when physcial stress is reduced, competitive interactions often dominate (Pennings and Callaway 1992; Studer-Ehrensberger 1993; Bertness and Shumway 1993; Bertness and Hacker 1994). In the wet year, flooding was a contributor to mortality of Myrica seedlings regardless of canopy manipulation. Yet, flooding induced stress was consistent regardless of canopy manipulation (Fig. 16). Thus, competitive interactions between grasses and shrubs during periods of reduced stress may explain the decreased growth and increased mortality with the grass canopy intact.

Baccharis response to the presence of grasses was variable, with inhibition dominating in the wet year, and facilitation in the dry year. In contrast to Myrica, the grass canopy may have facilitated Baccharis establishment via both direct (shading) and indirect (effect on herbivores) effects in the dry year (Fig. 17). Although expected, there was no indication of fungal pathogens in this wet year. Underlying inhibitory mechanisms in the wet year were not as clearly defined, and further studies are necessary to elucidate the predominant mechanisms influencing Baccharis seedling performance.

Finally, biotic mechanisms influence succession in this coastal sere, yet precipitation leading to consistent flooding or limited soil water availability over the growing season mediates the intensity and type of biotic mechanisms at work. Thus, interrelationships among environmental factors and biotic mechanisms (i.e. facilitation, competition, herbivory), may impact small-scale distribution patterns. Perhaps more importantly, these interrelationships may impact coastal succession by influencing shrub performance in general, as well as differentially by species.

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Table 1. Soil chlorides (μg/g) for a site protected by small dunes (A) and a site without small dune protection (B) on a Virginia barrier island. Values are means ± 1 SE.

	Soil Chlorides			
Date:	Site A	(SE)	Site B	(SE)
21-Jul	74.8	10.2	16.9	1.2
2-Aug	109.4	14.2	23.3	3
25-Aug	185.2	48.3	68.2	18.1
9-Sept.	242.1	45.4	1099.7	138.3

Table 2. Mean chlorides (µg/g), soil water content, pH, and *Myrica* occurrence (#) along a distance gradient from the ocean on a Virginia barrier island. Elevation for each sampling location is indicated by type (B=beach, s=swale, d=dune, sd=side of dune). ANOVA was used to analyse differences among distances from the ocean for the dependant variables (mean chlorides, soil water content, and pH, n=5 transects).

							Distance						ANOVA
		0	25	50	75	100	125	150	175	200	225	250	Sig. P
Elevation type:		b	d,sd	d,sd	d	s,d	s,d	s,sd,d	s,sd	s,d	sd,d	s	
Chlorides: (µg/g)	mean	141	26	7	11	15	16	388	930	2	3	12075	p<0.001
	SE	35	10	1	1	4	4	236	348	0.4	0.2	2001	
Water content: (%)	mean	2.6	3.5	2.5	8.6	9.3	10.9	8.1	4.7	2.6	1.3	16.7	p<0.001
	SE	0.7	0.6	0.5	2.3	2.3	2.9	2.3	1.3	1.4	0.2	3	
pH:	mean	8.1	8.1	8	7.4	7.8	7.1	7	6.9	7.2	6.6	7.8	p<0.001
	SE	0.2	0.2	0.2	0.2	0.3	0.3	0.4	0.4	0.2	0.3	0.4	
Myrica #:		0	0	0	0	10	0	0	11	0	0	4	

Table 3. Linear regression equations providing best fit for chloride, water content, pH, and Myrica occurrence along a distance gradient from the ocean on a Virginia barrier island.

		Regression	
	r^2	Sig. t	Equation
Chlorides:	0.196	t=0.027	(log)y = -1047.51 + 16.99x
Water content:	0.051	t=0.358	(log)y = 4.065 + 0.022x
pH:	0.118	t<0.001	y = 8.09 - 5.45x
Myrica #:	0.071	t<0.001	y = 7.65 + 4.846x

FIGURE LEGEND

Figure 1. Conceptual diagram of potential interrelationships among biotic interactions of facilitiation, inhibition, and herbivory on shrub establishment in a coastal sere.

Figure 2. Net photosynthesis (A) and midday xylem pressure potential (ψ) for Myrica cerifera in response to four treatments in 1995: grass canopy removal by clipping (❍), clipping and root exclosure ( ), intact canopy with root exclosure (■), and control with no manipulation (●). Means are ± 1 SE. Asterisks indicate dates with significant differences.

Figure 3. Net photosynthesis (A) for Baccharis halimifolia in response to four treatments in 1995: canopy removal by clipping (❍), clipping and root exclosure ( ), intact canopy with root exclosure (■), and control with no manipulation (●). Means are ± 1 SE. Asterisks indicate dates with significant differences.

Figure 4. Shoot and root dry mass (g) for Myrica cerifera in 1995 and 1996 experimental plots, in response to two factors, canopy and root manipulation: grass canopy removal by clipping (open), no grass canopy manipulation (shaded), root exclosure (open), and no root exclosure (shaded). Because there were no significant interactions between canopy and root manipulation treatments, data were pooled for each factor. Means are ± 1 SE. Asterisk indicates a significant difference in total biomass, whereas alpha characters indicate significant differences between treatments for shoot or root dry mass.

Figure 5. Shoot and root dry mass (g) for Baccharis halimifolia in 1995 and 1996 experimental plots, in response to two factors, canopy and root manipulation: grass canopy removal by clipping (open), no grass canopy manipulation (shaded), root exclosure (open), and no root exclosure (shaded). Because there were no significant interactions between canopy and root manipulation treatments, data were pooled for each factor. Means are ± 1 SE. Asterisk indicates a significant difference in

total biomass, whereas alpha characters indicate significant differences between treatments for shoot or root dry mass.

Figure 6. Shoot and root dry mass (g) for Myrica cerifera and Baccharis halimifolia in 1996 density plots in response to three densities of the naturally occurring grass canopy: low (3340 ± 307), medium (4460 ± 211), and high (6840 ± 361). Means are ± 1 SE. Alpha characters indicate significant differences between treatments for shoot or root dry mass.

Figure 7. Percent mortality for Myrica cerifera (open) and Baccharis halimifolia (shaded) in 1995 (A) and 1996 (B) in response to grass canopy removal by clipping and no canopy manipulation. Percent mortality for Myrica cerifera (open) and Baccharis halimifolia (shaded) in 1996 in response to three densities of the naturally occurring grass canopy: low, medium, and high.

Figure 8. Percent occurrence for Myrica cerifera and Baccharis halimifolia seedlings in four damage categories in response to above-ground insect herbivory for the clipped (open) and unclipped (shaded) grass canopy treatments.

Figure 9. Precipitation (mm) in summer months for years 1992 - 1996, obtained from nearby meteorological (MET) stations.

Figure 10. Depth to groundwater (cm) within the Hog Island swale study site over the summer field season, 1995.

Figure 11. (A) Incident PPFD (μmol m^{-2}s^{-1}) measured in 1995 above the grass canopy (—) and at seedling height ( ), for treatments with the grass canopy intact (open) and clipped (closed). (B) Ambient air temperature (C) above the grass canopy (—), at seedling height ( ), and at soil surface (Δ), for treatments with the grass canopy intact (open) and clipped (closed). Means are ± 1 SE. Asterisks indicate significant differences between means for clipped and unclipped treatments.

Figure 12. Diurnal incident PPFD (μmol m^{-2}s^{-1}) measured in 1995 (A) and 1996 (B) experimental plots and in 1996 density plots (C). Measurements were made above the grass canopy (—) and at seedling

height ( ), for treatments with the grass canopy intact (open) and clipped (closed). Incident PPFD was measured in 1996 (C) at seedling height for the low (❍), medium (■), and high (Δ) density plots.

Figure 13. Diurnal ambient air temperature (C) in 1995 and 1996 experimental plots. Panel A and B: above the grass canopy (—) and at seedling height ( ) for treatments with the grass canopy intact (open) and clipped (closed). Panel C and D: soil surface (Δ) and at -10 cm (∇), for treatments with the grass canopy intact (shaded) and clipped (open).

Figure 14. Diurnal ambient air temperature (C) in 1996 density plots. (A) Above the grass canopy (—), and at seedling height ( ) for low density (—), medium density (…), and high density (-..-). (B) At the soil surface (▲) and at -10 cm (∇) for low (—), medium (. . .) and high (-..-) density plots.

Figure 15. Percent soil water content in 1995 for two treatments: grass canopy removed by clipping (open), and grass canopy intact (shaded).

Figure 16. Interrelationships among biotic mechanisms influencing Myrica seedling establishment, as mediated by the precipitation and soil moisture gradients over a two-year study period on a Virginia barrier island. Increased growth (*) and increased mortality (**) are specific to each quadrant of the diagram. Inhibitory (-) and positive (+) effects are indicated. I and F indicate net inhibition or facilitation, respectively.

Figure 17. Interrelationships among biotic mechanisms influencing Baccharis seedling establishment, as mediated by the precipitation and soil moisture gradients over a two-year study period on a Virginia barrier island. Increased growth (*) and increased mortality (**) are specific to each quadrant of the diagram. Inhibitory (-) and positive (+) effects are indicated. I and F indicate net inhibition or facilitation, respectively.

NOTE – FIGURES ARE OMITTED FROM THIS COPY