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**ENVIRONMENTAL INFLUENCES ON SEX RATIO AND SPATIAL DISTRIBUTION
OF DIOECIOUS MORELLA CERIFERA L. ON A VIRGINIA BARRIER ISLAND.**

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

by

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Table of Contents

Title page.....	ii
Acknowledgements.....	iii
List of Tables.....	v
List of Figures.....	vii
Abstract.....	1
Introduction.....	2
Materials and Methods.....	7
Results.....	10
Discussion.....	14
References.....	20
Tables.....	25
Figures.....	36
Vitae.....	43

List of Tables

Table 1. Sex ratios of the Chronosequence on Hog Island, including distance to ocean shoreline. The ratios are shown by percent female, associated with the transects within the region of the Chronosequence, see Figure 3.....	25
Table 2. Sex ratios of the Accreting region of Hog Island, shown by percent female, associated with the tagged female in which the transect of sexed plants is located, see Figure 4.	26
Table 3. Sex ratios of the South region on Hog Island, divided into Sa, Sb, and Sc. Distance to shoreline of tagged female, associated with ratio (%female) is given, see Figure 5.....	27
Table 4. Spearman's ρ analysis across Hog Island, using all male and female data and associated %female (top). As well as only female data shown at the bottom. Only significant correlations are presented in this stacked table (in bold); no significant relationships were found with sex.....	29
Table 5. One factor ANOVA, mean \pm SE for environmental variables as well as range for distance to shoreline and elevation compared across three different spatial scales of Hog Island. The southern region is missing spring data, due to field constraints.....	30
Table 6. Spearman's ρ analysis across the Chronosequence using male and female data (top). Analysis using female data, on the Chronosequence (bottom). Only significant correlations are presented in this stacked table (in bold).....	31
Table 7. Spearman's ρ analysis of the Accreting region of male and female data (top). Analysis of females only in Accreting region (bottom). Only significant correlations are presented in this stacked table (in bold).....	32
Table 8. Spearman's ρ analysis across the South region using male and female data (top). Analysis of only female data in the South region (bottom). Only significant correlations are presented in this stacked table (in bold).....	33

Table 9. New shoot growth (g) means \pm SE are given ($P \leq 0.05$), by sex and island region: Chronosequence (C), Accreting end (N), and South (S). ANOVA results are presented in the bottom portion of the table. Letters denote similarity between island regions.....34

Table 10. Values of mean \pm SE for female berry production (of fruit/shrub) for three regions of Hog Island.....35

List of Figures

Figure 1. Hog Island, within the Virginia barrier island system, of the Delmarva Peninsula.....	36
Figure 2. Sex ratios determined by X^2 analysis, for Hog Island Chronosequence, Accreting End, and South Hog	37
Figure 3. Chronosequence on Hog Island, containing eight transects (C01-C08) each on the leading edge of a swale. Chronosequence (C) C01-C08 represent the transect coordinates as well as the location for sampled individuals.....	38
Figure 4. The Accreting section of Hog Island, containing 12 transects (N01-N12) situated along the primary dune of the north accreting end.....	39
Figure 5. The South region of Hog Island stretch, ~5 km north to south, spanning 200-500 m in width. The islands southernmost reaches with transects denoted as Sa (top left), then Sb (top right) span southward toward transects Sc along the spit (bottom frame).....	40
Figure 6. Multivariate scatterplot matrix of Spearman's ρ comparing distance to shoreline in meters (Distance), elevation, new shoot growth of females (ShootG), and soil characteristics to female ratios (%female).....	41
Figure 7. Multivariate scatterplot matrix of Spearman's ρ comparing all female environmental and reproductive measurements. Including distance to shoreline (Distance), elevation, new shoot growth of females (ShootG), berry set (fruit/female) and soil characteristics.....	42

Abstract

ENVIRONMENTAL INFLUENCES ON SEX RATIO AND SPATIAL DISTRIBUTION OF DIOECIOUS MORELLA CERIFERA L. ON A VIRGINIA BARRIER ISLAND.

By Molly Margaret Hokkanen, B.S.

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

Virginia Commonwealth University, 2013

Major Advisor: Donald R. Young, PhD
Professor and Chair, Department of Biology

For dioecious plant species, sex ratios within a population depend on multiple environmental and life history characteristics. Sex ratio is an indicator of population health and can be a predictor for genetic bottlenecks. My study established the previously unknown sex ratio for the shrub, *Morella cerifera*, on a Virginia barrier island. The ratio was compared with multiple environmental and reproductive traits to determine their potential influence on sex determination and/or distribution of male and female plants. Multivariate analyses were used to identify relationships between sex, sex ratio and environmental drivers. The sex ratio for *M. cerifera* changed depending on scale. The entire island ratio did not vary significantly from 50:50, based on a Chi-squared analysis. Different spatial scales resulted in different and more variable sex ratios. The environmental variables measured did not suggest any relationships with sex or sex ratio. Future studies with a focus at multiple spatial scales may elucidate the connection between environment and sex ratios for *M. cerifera*.

Introduction

Most plants are monoecious; however, a small subset has evolved dioecy, a reproductive mechanism with distinct male and female plants (Sinclair et al. 2012). Functioning sex ratios of dioecious plant populations have been studied in multiple habitats (Freeman et al. 1980, Lloyd 1980, Bierzychudek and Eckhart 1988, Krischik and Denno 1990, Korpelainen 1998, Ainsworth 2000, Espírito-Santo et al. 2003, Varga and Kytöviita 2011, Mizuki et al. 2012, Sinclair et al. 2012, Pickup and Barrett 2013). This is particularly important in economically significant crops, where ratios can determine pollination success and consequently crop yield. Similarly, for native plant populations like *Morella cerifera* on Atlantic coast barrier islands, sex ratio may influence community ecological processes, as well as population expansion and population genetics (Erickson et al. 2004). A biased sex ratio (i.e. not 50:50) may lead to food source decreases, genetic bottlenecks with decreased pollination sources (Mizuki et al. 2012, Pickup and Barrett 2013), barrier island geomorphology alterations via recolonization (Wolner et al. 2013), and reduced swale microhabitats (Bawa 1980, Sinclair et al. 2012).

Morella cerifera is a common, nitrogen fixing, evergreen shrub along the Atlantic coast from New Jersey southward into Florida (Young et al. 2007). Virginia barrier islands represent a dynamic landscape of perpetually changing shorelines, with highly adapted vegetation, dominated by expanding populations of *M. cerifera*. Depending on location within the Virginia barrier island system, shorelines migrate as much as 13 m per year (Young et al. 2007). Thus, *M. cerifera* shrubs experience constantly changing distance to shoreline, and changes in exposure to abiotic perturbations. One of the most pressing perturbations is sea level rise which along the Virginia coast, is three to four times the rate of normal sea level rise (Sallenger et al. 2012), estimated at an accelerated 3.8 mm per year on the Eastern Shore of Virginia (Emery and Aubrey

1991). Mechanisms associated with *M. cerifera* expansion, including variation and roles of sex ratio patterns, on Virginia islands have not been thoroughly investigated.

Hog Island, Virginia is dominated by thickets of *M. cerifera*, which influence geomorphological processes and ecological succession (Crawford and Young 1998, Young et al. 2007). The island includes a varied matrix of soils and vegetation, as well as a range of environmental gradients, including salinity that fluctuates along a cross-island chronosequence (Hayden et al. 1991, Young et al. 1994). The chronosequence has formed by new sediments which are deposited on the northeastern edge of Hog Island over time. The sediments have resulted in a series of dune and swale bands from the west (now marsh) to the current shoreline on the east. Over this 1200 m cross island space for time substitution, there are bands of soil and plant age, where age increases with distance from current ocean shoreline. Thus, the associated ages and environmental gradients provide opportunities to examine ecological processes across coastal landscapes. New shrub and thicket expansion on Hog Island has been attributed to soil age and time since shrub establishment (Young et al. 1995). Shrub expansion in these habitats is initiated in protected swales, establishing through dune grasses, and quickly forming dense thickets. Thicket expansion on the island has been increasing over time, although island area has been decreasing, this suggests a beneficial underlying mechanism. The success of these thickets across barrier islands could be explained in part by community sex ratio of the shrub.

Spatial variations of sex ratios for *Morella cerifera* have not been quantified or related to environmental variations. However, sex ratio theories suggest that these environmental alterations should change the functioning sex ratio over time (Freeman et al. 1980, Lloyd 1980, Bierzychudek and Eckhart 1988, Krischik and Denno 1990, Korpelainen 1998, Ainsworth 2000, Espírito-Santo et al. 2003, Varga and Kytöviita 2011, Mizuki et al. 2012, Sinclair et al. 2012,

Pickup and Barrett 2013). Understanding the sex ratio of this dominant species across Hog Island will define a functional gender of individuals, perhaps in relation to an environmental trigger (Korpelainen 1998). This will also provide insight toward understanding potential mechanisms of shrub expansion on barrier islands.

Sex ratios may vary with individual plant or population age but may be related to abiotic effects. Korpelainen (1998) proposed that seedling mortality is the driving cause of sex ratios. Seedling survivorship will produce a ratio which is dependent on the local environments, and is often subject to change over time and plant life stages. For adult plants, the sex ratio may be further complicated by the ability of a dioecious plant to change sex (i.e. sexual lability) seasonally in response to nutrient requirements of the current sex and photoassimilate availability (Korpelainen 1998). Sex changes can occur over longer periods of time, or at certain life, and size stages (Korpelainen 1998). For example, wind pollinated plants differ in sex with size. It is optimal for males to be tall and slender, while females are optimized with a short and thick life form, like the herb, *Arisaema triphyllum* (Bierzychudek 1984). Along the spatial and temporal gradients of Hog Island, *Morella cerifera* individuals are expected to change from one expressed sex to the other, being optimized for location and, perhaps, by sexual lability of individual shrubs. Regardless of sexual lability, a functioning sex ratio can be established for *M. cerifera* in the barrier island environment.

In temperate environments such as the Virginia barrier islands, many of the dioecious species are wind pollinated, producing fleshy animal-dispersed fruits (Bawa 1980). In the case of *M. cerifera* flowers and catkins are produced in early spring and fruits are dispersed in the autumn by migratory birds (Young et al. 1994). Among the populations of *M. cerifera* on Hog Island, functioning sex ratio is further complicated by clonal growth, in which ramets cannot be

easily distinguished from the parent plant without invasive methods. Clonal plants replicate from the parent plant and are genetically identical to the parent, producing a multi-stemmed cluster (Erickson and Hamrick 2003). Interestingly, Erickson and Hamrick (2003) observed little allelic diversity of *M. cerifera* along the chronosequence of Hog Island, thus, clonal growth may have little impact on island scale sex ratio for *M. cerifera*.

Storm and overwash events, changing coastlines, and vulnerability to sea spray may increase salinity, and possibly mortality of *M. cerifera* across an island landscape (Young et al. 2007). High salinity events that increase salt stress may alter the active sex ratio, changing spatial distributions of flowering plants and influencing future productivity and pollination patterns (Erickson et al. 2004). Male individuals of dioecious species have higher survival rates in lower quality environments than their female counterparts (Bawa 1980, Bierzychudek and Eckhard 1988, Krischik and Denno 1990, Gehring and Monson 1994, Korpelainen 1998, Varga and Kytöviita 2011, Sinclair et al. 2012, Tognetti 2012, Vaughton and Ramsey 2012). Local, primary environmental drivers can be easily observed and quantified on Hog Island. The north and south portions of Hog Island provide two distinctly different geomorphic regions, and soil salinity levels (Young et al. 1994). Establishing locations for identifying sex ratios of the salt sensitive *M. cerifera*, in relation to salinity levels is a primary concern in determining environmental connections to functioning sex ratios. The north end has an established chronosequence of shrub thickening, with varying levels of salinity and abiotic exposure. The southern portion of Hog Island represents less established, new shrub thicket with little variation in distance to shoreline, and age of thicket (Zinnert et al. 2011).

The objectives of my study were to (1) quantify a functioning sex ratio for *Morella cerifera* in a native population on Hog Island, (2) determine differences in sex ratio,

corresponding to spatial scales, soil salinities, and shoot production, and (3) identify environmental, growth and reproductive differences between male and female *M. cerifera* shrubs across on the Hog Island landscape. I hypothesized that the male to female ratio will favor male plants in more stressful, higher salinity environments. *Morella cerifera* is considered salt sensitive (Sande and Young 1992, Young 1992, Young et al. 1994, Young et al. 1995, Young et al. 2007), and my hypothesis suggests that flowering male plants are more tolerant of salinity than flowering females, regardless of seedling predisposition. This may result in a spatial segregation of the sexes on Hog Island, with a higher composition of female shrubs on the more protected leeward side of the north end, while habitats in close proximity to the ocean side, will have a higher ratio of males due to greater environmental stress.

Methods

Site Description

Spatial variation in *Morella cerifera* sex ratios were quantified on Hog Island, North Hampton County, Virginia. Hog Island (37° 40'N, 17° 40'W) is located along the Eastern Shore of the Delmarva Peninsula within the Virginia Coast Reserve, Long Term Ecological Research (LTER) site (Figure 1). The island is 11 km long with the widest point (1.6 km) at the northern tip. Across the accreting north end, the soils have created a chronosequence (Hayden et al. 1991), with the newest soils and plant growth on the ocean side of the island.

Transects were arranged across the island landscape in three different regions (Figure 2). The northern end of Hog Island consisted of two regions with transects, the Chronosequence (Figure 3) and the Accreting region at the extreme northern end (Figure 4). The South region of the island represents an area of new shrub expansion (Zinnert et al. 2011), so multiple transects were established within this region (Figure 5). Forty one transects in total with multiple georeferenced plants using GPS (Garmin GPSMAP 60CSx) were created among these three regions of the island. These forty one transects differed in exposure and distance to the ocean. The survey included sex determination for all individuals along transects from western thicket edge, to the easternmost thicket edge. Individuals were identified for sampling along transects at increments of 50 m, from the western sound side to the eastern ocean side for the Chronosequence and along the dune ridge of the Accreting end. Transects in the South region were sampled from west to east following a bearing, with exception to the southernmost transects, which flanked the secondary dune ridge. For all sampling points, recent elevation (2010) and distance to shoreline (2011) was determined by overlaying the georeferenced points to LiDAR-based Digital Elevation Model for Hog Island, from the VCR LTER database

(<http://tropical.iternet.edu:8080/knb/metacat?action=read&qformat=lter&insertTemplate=0&docid=knb-lter-vcr.202.7>).

Sampling Methods

Along each transect, flowers on every individual were examined in order to determine a functioning sex ratio during the flowering season of 2012. There is no significant difference in genotype across Hog Island; relatively few multi-stemmed clusters of *Morella cerifera* were composed of a single genotype (Erickson and Hamrick 2003). For these reasons, flowering ramets were counted individually (Pickup and Barrett 2013). Plants without floral structures were considered as juveniles (Espírito-Santo et al. 2003, Mizuki et al. 2012). Every 50 m along each transect, a male and female shrub were identified and permanently marked with an aluminum tag. Soil samples were collected from these plants to determine variations in soil salinity and pH (Young et al. 1994). Soils were sampled in the reproductively significant months of September, 2012 (n=82) for females representing post fruit set, and prior to flowering on both males and females in March 2013 (n=75). Soils were collected (150 g bags) from both east and west aspects of individual plants. Sub samples (50 g) were oven dried at 105°C for 72 hr, combined with 200 mL of deionized water and pH was measured (Eutech Instruments, EC Tester 11+, Conductivity Waterproof Pocket tester). Four mL of 5 M NaNO₃ was added to each sample as an ion equalizer, and total chlorides were measured with a chloride electrode (Model 96176 Orion Boston, MA USA; Young et al. 1994).

To determine fruit production, a subset of 82 females was sampled across the three regions in September, 2012. These individuals were sampled for allometric measures. Each plant was sampled for fruit set per stem, and then branch divisions were multiplied across fruit set for an estimate of total plant fruit set. Thus, dimensional measurements of the branches,

representative plant fruit yield and new shoot growth (as a relative measure of productivity per plant, Espírito-Santo et al. 2003, Varga and Kytöviita 2011) were extrapolated to represent the entire individual, and compared with environmental variables. Shoot growth for both male and female plants (n=76, Young 2006), were collected, dried at 80°C, and weighed (g).

Data Analysis

Spatial variations in sex ratio (i.e. %female) among transects were compared using Chi-squared analysis (χ^2). Sex ratios were related to soil Cl⁻ measurements, pH, elevation and distance to shoreline, growth and reproductive characteristics using Spearman's ρ with JMP software. Spatial variations of fruit yield were analyzed using one-factor ANOVA at two scales; the whole island, and the three regions of the island. Potential variations in new shoot growth were quantified between males and females as well as among the above mentioned regions using two-factor ANOVA. Variations in sex ratio in relation to soil chlorides, soil pH, elevation, and distance to the shoreline as well as to new shoot growth and fruit yield were examined using Spearman's ρ for nonparametric correlation.

Results

Sex Ratios

Morella cerifera began flowering in early March of 2012, the resulting ratios were calculated by using the 2012 survey. Across the Hog Island landscape, there was no difference in sex ratio, with 1423 individuals surveyed (48% female), $\chi^2=5.869$, $P=0.2091$. On a regional scale the Chronosequence contained 46.3% females, the Accreting end community contained 51.1% females, and the South region of Hog island was 48.3% female (Figure 2). These ratios did not vary significantly from 50:50 ($\chi^2=9.27$, $P>0.05$).

Along the Chronosequence the ratio did depart from 50:50 ($\chi^2=91.548$, $df=14$, $P<0.0001$). 529 individuals were sexed, with extreme bay and ocean sides of the chronosequence being male biased, 37.5% female on the bay side of the chronosequence and 0% female on the ocean side. From west to east across the island, the female ratios were 52.6, 57.0, 32.1, 50.0, 49.3 and 41.1% respectively (Table 1). The two sites with female ratios above 50% were located near island interior freshwater marshes (C02 and C03, Figure 3). In comparison, the Accreting region of northern Hog Island there was no significant variation in sex ratio ($\chi^2=33.170$, $P=0.0595$, Table 2, Figure 4) of the 341 shrubs surveyed, resulting in 174 females, 166 males and one juvenile.

The South region had multiple transects from ocean to sound side (Sa, Sb and Sc, from north to south), including 267 females, 275 males and 11 juveniles that significantly differed from a 50:50 ratio ($N=553$, $\chi^2=99.964$, $P<0.0001$). The northernmost cross island transect in the South region (Sa), was comprised of 113 individuals, and was 34% female ($\chi^2=29.595$, $P=0.0002$, Table 3, Figure 5). Transects Sc05-Sc07 were established west to east, located along the southernmost edge of expansion ($N=50$), resulting in a female biases of 56.3, 61.1 and

56.3%, but they did not differ significantly from 50:50 ($df=4$, $X^2=2.259$, $P=0.6883$, Figure 5).

The leading edges of thicket expansion were examined in two short transects ($N=71$) on the west and east side of the forming secondary dune with X^2 of 5.330 ($P=0.5022$). Transects Sc08 and Sc09 were located on the leeward side of the secondary dune showing 40.7 and 57.9% female (Figure 5). Sc10 and Sc11 were located between the primary and secondary dune, resulting in 71.4 and 55.6% female dominant ratios.

Potential Environmental Influences

On each transect used for sex ratios, male and female reference plants were tagged and spaced no less than 50 m from the next set of reference plants. Distance to shoreline and elevation were determined by the georeferenced region, while soils below reference plants were sampled for chlorides and pH, as a potential predictor for sex. Across the entire island, there was no correlation of sex to an environmental predictor based on Spearman's ρ (Table 4, Figure 6, $P>0.05$). These independent variables included distance to shoreline, elevation, chlorides and pH. Using a one factor ANOVA, soil chlorides differed across the regions in autumn but not in spring. In large part this was due to sampling methods of autumn chlorides, being only female. Similarly, soil pH differed among the three regions in autumn but not in spring sampling (Table 5). Mean elevation was slightly less than 5 m above sea level, was least variable along the Chronosequence, and most variable at the South region ranging from less than 2.5 to greater than 9.0 m (Table 5). The Accreting northern end elevation range was between the chronosequence and south end range. Similarly distance to the shoreline for sampled *M. cerifera* varied by 1,000 m across the Chronosequence. Whereas distance to shoreline for the Accreting and Southern ends varied by about 300 m (Table 5).

Along the northern Chronosequence environmental factors and plant growth were compared to the ratio (%female) using ANOVA and Spearman's ρ analysis shown on the sections of transect, coordinating to representative female plant environmental measurements (Figure 3). No significant relationships between the sexes and distance to shoreline, autumn chlorides, autumn pH, spring chlorides, or spring pH were observed along chronosequence ($P>0.05$, Table 6). The Accreting end had similarly low observations. Distance to shoreline, autumn chlorides, autumn pH, spring chlorides, spring pH and shoot growth all had $P>0.05$ using Spearman's ρ analysis with relation to the sexes (Table 7). The South region yielded no significant differences between environmental drivers and sex ratio (Table 8).

Plant growth and reproduction

New shoot growth (both male and female) was compared across Hog Island and was related to elevation (Table 4). New shoot growth was also compared among the three regions and between the sexes (Table 9). The two factor ANOVA indicated a difference between regions ($F=4.0165$, $P=0.0228$), but similarities occurred between shoot growth on the Chronosequence and Accreting region, as well as between the Accreting and South regions. In addition, there was no significant difference in shoot growth between males and females. There was no interaction between shoot growth, region and sex. Further analysis of female shoot growth using Spearman's ρ across the entire island, revealed no other significant relationships to female plant growth or reproduction ($P>0.05$), using distance to shoreline, soil chlorides and pH (Figure 6, Figure 7).

Berry set, a measure of female reproductive health, was compared among the three island regions. Berry set did not differ among the Chronosequence, Accreting end and South region of

Hog Island (Table 10, $F=0.0855$, $P=0.42$). None of the measured environmental parameters showed a relationship with berry set, at any scale ($P>0.05$, Table 10, Figure 7).

When comparisons were limited to female plants, Spearman's ρ analysis indicated a significant relationship with elevation at multiple spatial scales. Elevation was related to autumn pH at the island scale (Table 4), and both autumn chlorides and pH on the Chronosequence (Table 6).

Discussion

The objectives of my study were to (1) quantify a functioning sex ratio for *Morella cerifera* in a native population on Hog Island, (2) determine changes in sex ratio, corresponding to spatial scales, soil salinities, and shoot production, and (3) identify environmental, growth and reproductive differences between male and female *M. cerifera* across a population on Hog Island. I hypothesized that the ratios would favor males, particularly in high stress environments, when across Island gradients.

Interestingly, functioning sex ratio on Hog Island showed no significant variation from 50:50 at the island scale, but varied at smaller scales across the island landscape. Significant variability was found within the northern Chronosequence, with a tendency toward a male bias. This suggests that while including the farthest distance to shoreline exposure, a slight male bias is present. The Accreting region represents the most exposure to salt deposition and stress, but showed no significant variation from 50:50, which would suggest a tolerance to the exposure. The South region significantly varied from a 50:50 ratio, with a male bias. Even with a large primary dune ridge which would provide a barrier to wind deposition of salts, the regions was still male biased within the protected region, despite distance to shoreline. Among the three regions on Hog Island, there were no relationships of the observed sex ratios to any tested variables, including distance to shoreline, elevation, aspect, soil chlorides or pH of the region. This supports the conclusion that exposure to resources and elements needed to produce a sex ratio cannot be described using the above tested variables. Shoot or berry growth of the sampled individuals demonstrated no clear relationships with sex ratio. The sexes showed no significant variation from 50:50, on the region or island scale, within the parameters measured.

When compared with other species of Myricaceae, the sex ratios of *Morella cerifera* were dissimilar. *Myrica gale* has male ratios between 59-100% (Mizuki et al. 2012), compared to *Morella cerifera*'s range in this study of 16-100% males, with little significant variation from 50:50 across multiple site scales. *Morella cerifera*, as well as other members of the Myricaceae family have associations with nitrogen fixing bacterium, negating nutrient availability as a limiting factor and influence on sex ratio biases. Dioecious sex ratios are difficult to predict because of life history traits in conjunction with demography (Field et al. 2013, Pickup and Barrett 2013), supporting the lack of consistency and predictability seen by both *Myrica* and *Morella*.

In the Field et al. (2013) review, sex ratios of 243 species were examined and only 48% deviated significantly from 50:50, suggesting that at the island scale, the *Morella cerifera* ratio is typical of dioecious sex ratios. Examination of sex ratios of *M. cerifera* at multiple scales within the island, revealed spatial variations caused by island geomorphology and subsequent exposure to salinity. In comparison, the ratios for *Myrica gale* were observed at a much smaller spatial scale (40 m²-100 m²), and across the entire country of Japan. As observed on Hog Island, region and microhabitat scales revealed more biases from 50:50, than at the island scale. The differences in scale can account for large changes in sex ratio and should be accounted for when comparing to or analyzing other studies.

Lower elevations on barrier islands provide plants with access to the freshwater lens, and may moderate the influences of salt stresses and ecological processes. But, these lower elevations are more likely to flood and may accumulate salts (Hayden et al. 1995, Young et al. 2011), without dilution from the freshwater lens. Elevation did not impact sex ratio significantly, and could be a result of hydrological interaction as well as a narrow range of tolerance to

flooding and drought in *M. cerifera* (Young et al. 2011). Drought and salt stress both contribute to osmotic stresses, and are particularly hard to tease apart (Munns 2002). Drought has been observed as the key environmental factor in *Myrica gale* female biased sex lability (Davey and Gibson 1917). Transects on the South region of the island, had highly male trends in ratio on transect Sa and Sb, with a female bias close to ocean exposure. The transects within the South region, closest to the southern tip of the island (Sc 05-07) presented female bias as well, but insignificantly from 50:50. Although drought was not apparent during this project some of the trends seen in male biased transects may be explained by their occurrence on salt flats on the marsh side, not apparent in the elevation or soil chloride data and low primary dunes. Similar results were found on the northern end of the island, with just one female biased ratio on the chronosequence. This transect is the only transect which is flooded to varying depth year around.

Hog Island did have an observed higher composition of female shrubs on the more protected leeward side of thickets on the north end, while there were significant male ratios on the marsh and ocean side of the Chronosequence, but no correlation was found with distance to shoreline. My hypothesis that the sex ratio would favor male plants in more stressful, higher saline environments, was not consistently supported. The two female biased transects on the Chronosequence were situated in a swale which is a relatively protected, or a less stressful environment. Female ratios in the South region, showed trends of being located in swales as well. Spatial segregation was found on a microhabitat scale in other studies (Tognetti 2012). Males are more common in low resource sites (Bawa 1980, Gehring and Monson 1994, Korpelainen 1998, Varga and Kytöviita 2011, Sinclair et al. 2012, Tognetti 2012, Vaughton and Ramsey 2012), and future studies of other nutrient resources would better quantify the presence of stress in microhabitats on Hog Island.

Small scale distribution patterns are closely coupled with salinity levels in coastal systems (Oosting and Billings 1942, Hayden et al. 1991, Hayden et al. 1995, Young et al. 2011). Soil chloride measurements along the chronosequence should be related to distance to shoreline and elevation (Young et al. 2011). All plants and soils sampled occurred behind the primary dune, minimizing the variability of measurements (Ehrenfeld 1990). The island configuration reduced sampling of varying distance to shoreline observations. Chlorides also fluctuate with rainfall, overwash and storm events causing time sensitive measurements, and so may not reflect the influences on sex ratio properly. Hog Island has a large overwash fan located on the junction of the northern and southern sections of the island. The overwash fan could be acting as a conduit for salt water inundations, which could be contributing to the variability determined along the Chronosequence region.

The Hog Island chronosequence provides a soil age series represented by dates of ocean shoreline migration. As the island has shifted over the past 200 years, it has left distinctly aged soils and subsequent age classes of *Morella cerifera* thickets (Young et al. 2007). Shifts in sex can occur over long periods of time, or at certain life, and size stages (Korpelainen 1998). Across the Chronosequence, there was a mix of sex ratios, with no apparent relationship of soil or stand age suggested by the chronosequence morphology. Based on my results it was not possible to determine the state of sexual lability, age or island characteristics which may promote sexual bias on Hog Island.

Shoot growth for *Morella cerifera* did not reflect differences in investment of the sexes, yet for many species female individuals invest less in vegetative growth (Gehring and Monson 1994, Espírito-Santo et al. 2003). Berry set was variable across the island with no observed trends. Female plants with no fruit were salt burned and lacked vegetation (personal

observation). Within the extreme environmental zones, it would be beneficial to have had more representative females for comparison.

Spatial segregation of the sexes has been associated with microhabitat differences in dioecious woody species (Beirzychudek and Eckhart 1988, Tognetti 2012), reflected in the scale differences in my observations of *Morella cerifera*. In other studies, sexual lability and current expression were explained by environment, or plant age and size (Varga and Kytöviita 2011). The environmental factors examined in this paper alone, cannot rule out environment as the cause for lability or functioning sex ratio in *M. cerifera*. Males and females of many dioecious species differ in photosynthetic performance, water use, herbivory tolerance (Tognetti 2012), and density (Pickup and Barrett 2013). Freeman et al. (1980) found that in a sampling of wind pollinated species, there was sex differentiation based on soil moisture. Studying a new suite of environmental variables, such as island freshwater lens characteristics, may provide insight towards understanding spatial segregation of the sexes for *Morella cerifera* on barrier islands. It would also be beneficial to conduct the study over a longer time period, with more focus on the chronosequence or, perhaps, island versus mainland populations.

Variations of sex ratio across scales changed in my study, suggesting that microhabitats play a significant role. At the island scale, the sex ratio was 50:50, and was similar to other species in other environments. However, at smaller scales variations from that ratio were either significant or suggested by trends in the data. Regardless of whether *Morella cerifera* is sexually labile, differential seedling establishment occurs or environmental influences impact the adult sex of the plants, further detailed sampling could reveal these environmental variations across the island landscape, relative to current shrub expansion patterns and sex ratio. Differential microhabitats between the sexes could facilitate shrub expansion. If higher resource

environments are dominated by females, and low resource environments are dominated by males, then assuming no limitations in pollen dispersal this strategy could enhance reproductive success and contribute to shrub expansion.

Most future climate change scenarios predict continued rise in sea level as well as increased frequency and intensity in storms (Sallenger et al. 2012). Although the effects of climate change on barrier island geomorphology are quite complex, *M. cerifera* should be able to continue to colonize new habitats and expand as long as protected habitats remain available for shrub colonization and expansion. In the presence of protected microhabitats, and access to the freshwater lens, sex ratio response may contribute to maintenance of productive populations even in the presence of normal barrier island environmental perturbations.

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Table 1. Sex ratios of the Chronosequence on Hog Island, including distance to ocean shoreline. The ratios are shown by percent female, associated with the transects within the region of the Chronosequence, see Figure 3.

Chronosequence (C) Transects	Distance to Shoreline (m)	%female
C01	1060	37.5
C02	838	52.6
C03	590	57.0
C04	490	32.1
C05	334	50.0
C06	306	49.3
C07	201	41.0
C08	160	0.0

Table 2. Sex ratios of the Accreting region of Hog Island, shown by percent female, associated with the tagged female in which the transect of sexed plants is located, see Figure 4.

Accreting End (N) Transects	Distance to shoreline (m)	%female
N01	356	46.8
N02	336	42.9
N03	307	63.3
N04	472	57.9
N05	413	53.3
N06	346	75.9
N07	290	57.1
N08	288	69.2
N09	288	23.2
N10	269	58.6
N11	270	43.3
N12	259	50.0

Table 3. Sex ratios of the South region on Hog Island, divided into Sa, Sb, and Sc. Distance to shoreline of tagged female, associated with ratio (%female) is given, see Figure 5.

South (Sa) Transects	Distance to shoreline (m)	%female
Sa01	312.8	38.5
Sa02	284.3	36.8
Sa03	207.9	28.6
Sa04	165.7	36.4
Sa05	115.2	38.9
<hr/>		
South (Sb) Transects	Distance to shoreline (m)	%female
Sb01	335	84.2
Sb02	256	52.9
Sb03	222	36.4
Sb04	155	66.7
Sb05	118	61.3

South (Sc) transect	Distance to shoreline (m)	%female
Sc01	235	50.0
Sc02	184	47.8
Sc03	137	66.7
Sc04	110	33.3
Sc05	255	56.3
Sc06	214	61.1
Sc07	115	56.3
Sc08	229	40.7
Sc09	220	57.9
Sc10	130	71.4
Sc11	138	55.6

Table 4. Spearman's ρ analysis across Hog Island, using all male and female data and associated %female (top). As well as only female data shown at the bottom. Only significant correlations are presented in this stacked table (in bold); no significant relationships were found with sex.

Variable	by Variable	Spearman's ρ	P
ShootGrowth	Elevation (m)	0.3527	0.0026
pH _{autumn}	Elevation (m)	-0.3721	0.0254
Cl ⁻ _{autumn} ($\mu\text{g/g}$)	pH _{autumn}	0.6336	<.0001
pH _{spring}	pH _{autumn}	0.8427	<.0001
Cl ⁻ _{spring} ($\mu\text{g/g}$)	Elevation (m)	-0.3549	0.0246
Cl ⁻ _{spring} ($\mu\text{g/g}$)	pH _{autumn}	0.5498	0.0120
Cl ⁻ _{spring} ($\mu\text{g/g}$)	pH _{spring}	0.4836	0.0016
Variable	by Variable	Spearman's ρ	P
pH _{autumn}	Elevation (m)	-0.3864	0.0218
Cl ⁻ _{autumn} ($\mu\text{g/g}$)	pH _{autumn}	0.6722	<.0001
pH _{spring}	pH _{autumn}	0.8850	<.0001
Cl ⁻ _{spring} ($\mu\text{g/g}$)	pH _{autumn}	0.5520	0.0143
Cl ⁻ _{spring} ($\mu\text{g/g}$)	pH _{spring}	0.5186	0.0229

Table 5. One factor ANOVA, mean \pm SE for environmental variables as well as range for distance to shoreline and elevation compared across three different spatial scales of Hog Island.

The southern region is missing spring data, due to field constraints.

	Accreting	Chronosequence	South	ANOVA	Island Level
Distance to shoreline (m)	249-472	160-1060	110-479	F=20.37 <i>P</i><0.0001	302.76 \pm 23.08
Elevation (m)	4.12-8.00	3.80-6.64	2.46-9.18	F=0.99 <i>P</i> =0.38	4.83 \pm 0.15
Cl ⁻ _{autumn} (μ g/g)	4.19 \pm 0.81	45.67 \pm 51.0	22.75 \pm 7.00	F=5.25 <i>P</i>=0.01	22.16 \pm 30.70
Cl ⁻ _{spring} (μ g/g)	17.16 \pm 3.68	16.17 \pm 2.82	—	F=0.04 <i>P</i> =0.85	16.75 \pm 15.20
pH _{autumn}	5.65 \pm 0.11	5.93 \pm 0.40	6.21 \pm 0.11	F=5.24 <i>P</i>=0.01	5.97 \pm 0.48
pH _{spring}	5.19 \pm 0.19	5.18 \pm 0.20	—	F=0.0002 <i>P</i> =0.98	5.19 \pm 0.14

Table 6. Spearman's ρ analysis across the Chronosequence using male and female data (top).
 Analysis using female data, on the Chronosequence (bottom). Only significant correlations are
 presented in this stacked table (in bold).

Variable	by Variable	Spearman's ρ	P
Elevation (m)	Distance	-0.6511	0.0086
ShootGrowth	Elevation (m)	0.5290	0.0426
pH _{autumn}	Elevation (m)	-0.8929	0.0068
Cl _{autumn}	Elevation (m)	-0.9286	0.0025
Cl _{autumn}	pH _{autumn}	0.8214	0.0234
pH _{spring}	Elevation (m)	-0.7048	0.0033
pH _{spring}	pH _{autumn}	0.9550	0.0008
pH _{spring}	Cl _{autumn}	0.9370	0.0019
Variable	by Variable	Spearman ρ	P
pH _{autumn}	Elevation (m)	-0.8929	0.0068
Cl _{autumn}	Elevation (m)	-0.9286	0.0025
Cl _{autumn}	pH _{autumn}	0.8214	0.0234
pH _{spring}	Elevation (m)	-0.9950	0.0008
pH _{spring}	pH _{autumn}	0.9550	0.0008
pH _{spring}	Cl _{autumn}	0.9370	0.0019

Table 7. Spearman's ρ analysis of the Accreting region of male and female data (top). Analysis of females only in Accreting region (bottom). Only significant correlations are presented in this stacked table (in bold).

Variable	By Variable	Spearman's ρ	P
pH _{spring}	pH _{autumn}	0.8862	0.0001
Cl ⁻ _{spring}	Distance	-0.6994	0.0001
Cl ⁻ _{spring}	Elevation (m)	-0.4144	0.0441
Cl ⁻ _{spring}	pH _{spring}	0.4548	0.0256
Variable	By Variable	Spearman's ρ	P
pH _{spring}	pH _{autumn}	0.8862	0.0001
Cl ⁻ _{spring}	Distance	-0.6200	0.0315
Elevation (m)	Distance	0.5849	0.0457

Table 8. Spearman's ρ analysis across the South region using male and female data (top).

Analysis of only female data in the South region (bottom). Only significant correlations are presented in this stacked table (in bold).

Variable	by Variable	Spearman's ρ	P
Shoot Growth	Distance	-0.4891	0.0045
CI_{autumn}	Distance	0.5353	0.0326
CI_{autumn}	Berry set	0.5022	0.0474
Variable	by Variable	Spearman's ρ	P
CI_{autumn}	Distance	0.5252	0.0326
CI_{autumn}	Berry set	0.5022	0.0474

Table 9. New shoot growth (g) means \pm SE are given ($P \leq 0.05$), by sex and island region: Chronosequence (C), Accreting end (N), and South (S). ANOVA results are presented in the bottom portion of the table. Letters denote similarity between island regions.

	Male	Female	Shoot growth by scale
Accreting	3.27 \pm 0.55	0.94 \pm 0.57	2.15 \pm 0.40 AB
Chronosequence	2.68 \pm .67	2.96 \pm 0.67	2.82 \pm 0.47 A
South	1.23 \pm 0.49	1.17 \pm 0.49	1.21 \pm 0.35 B
Total Island	2.39 \pm 0.33	1.69 \pm 0.34	1.85 \pm 0.24

Shoot Growth	DF	SS	F	<i>P</i>
N/C/S	2	28.96	4.0165	0.0228
Sex	1	7.96	2.2086	0.1422
N/C/S *Sex	2	22.11	3.0664	0.0536

Table 10. Values of mean \pm SE for female berry production (of fruit/shrub) for three regions of Hog Island.

Regions	Berry Production
Accreting	98403 \pm 93955
Chronosequence	275128 \pm 132872
South	238646 \pm 72777

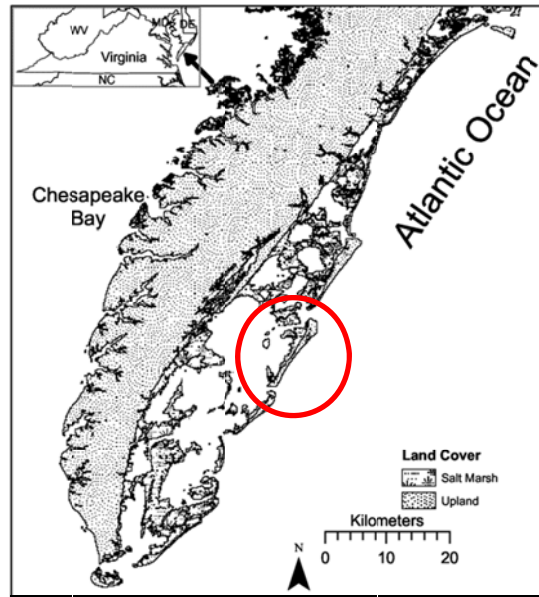


Figure 1. Hog Island, within the Virginia barrier island system, of the Delmarva Peninsula.

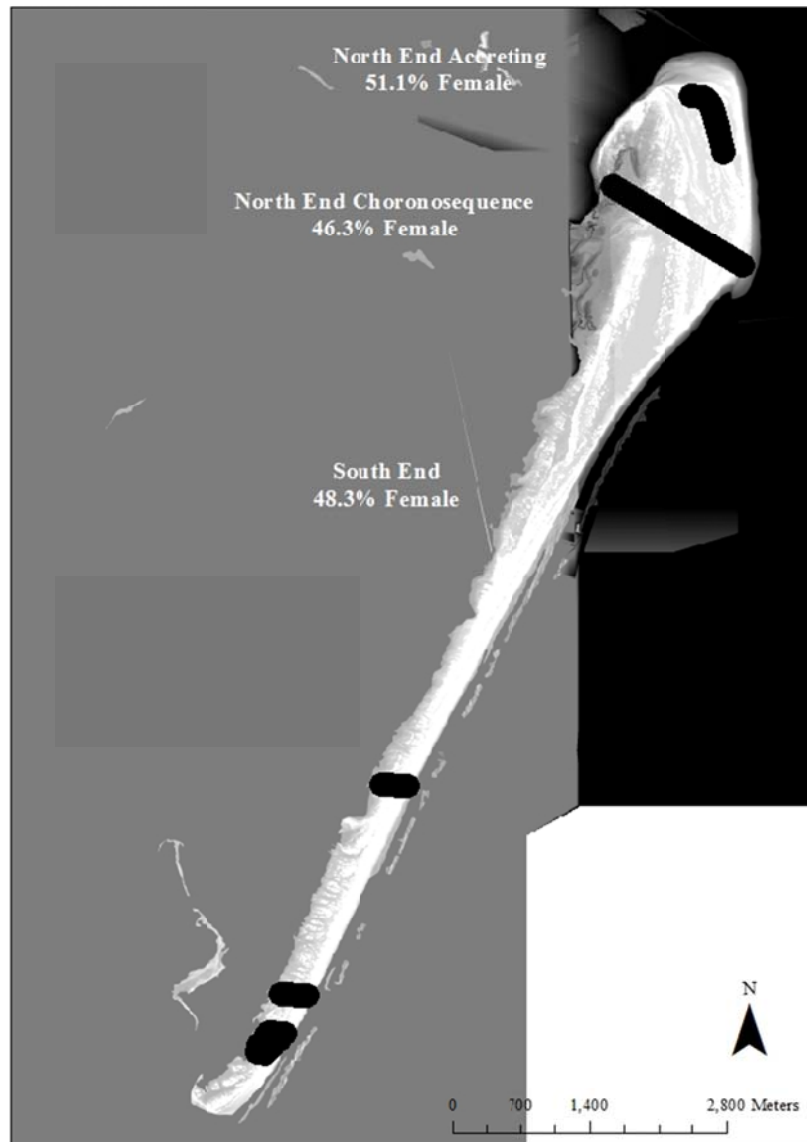


Figure 2. Sex ratios determined by X^2 analyses, for Hog Island Chronosequence, Accreting End, and South Hog.

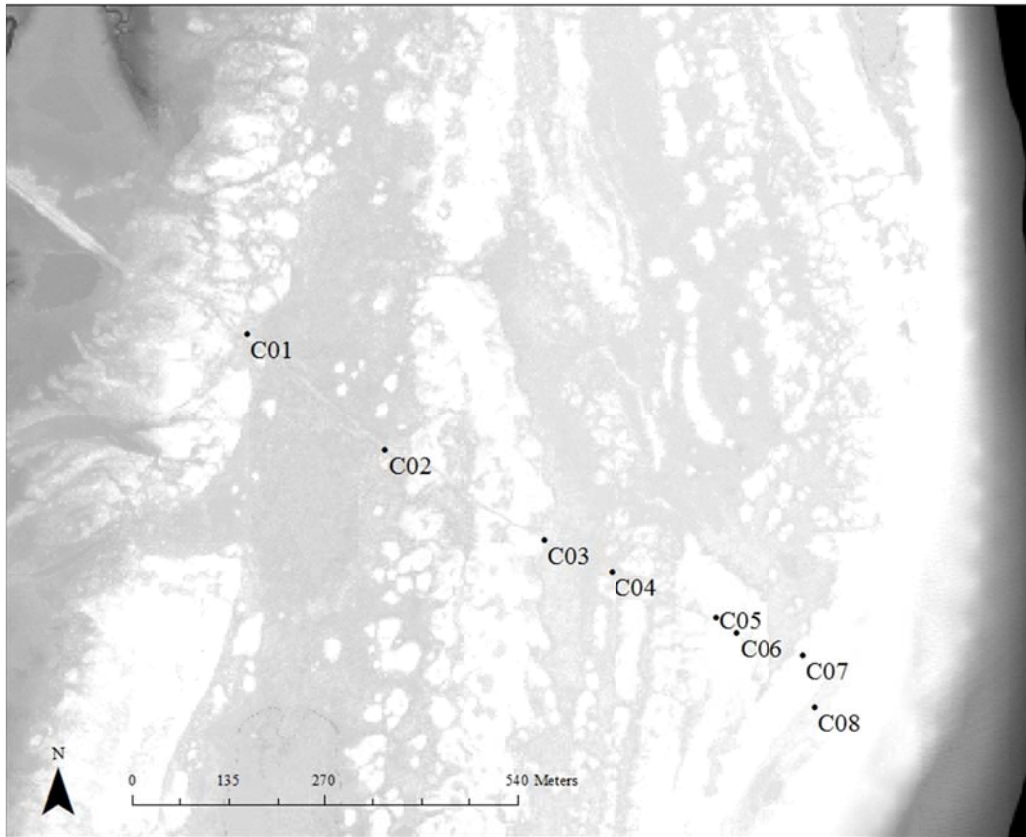


Figure 3. Chronosequence on Hog Island, containing eight transects (C01-C08) each on the leading edge of a swale. Chronosequence (C) C01-C08 represent the transect coordinates as well as the location for sampled individuals.

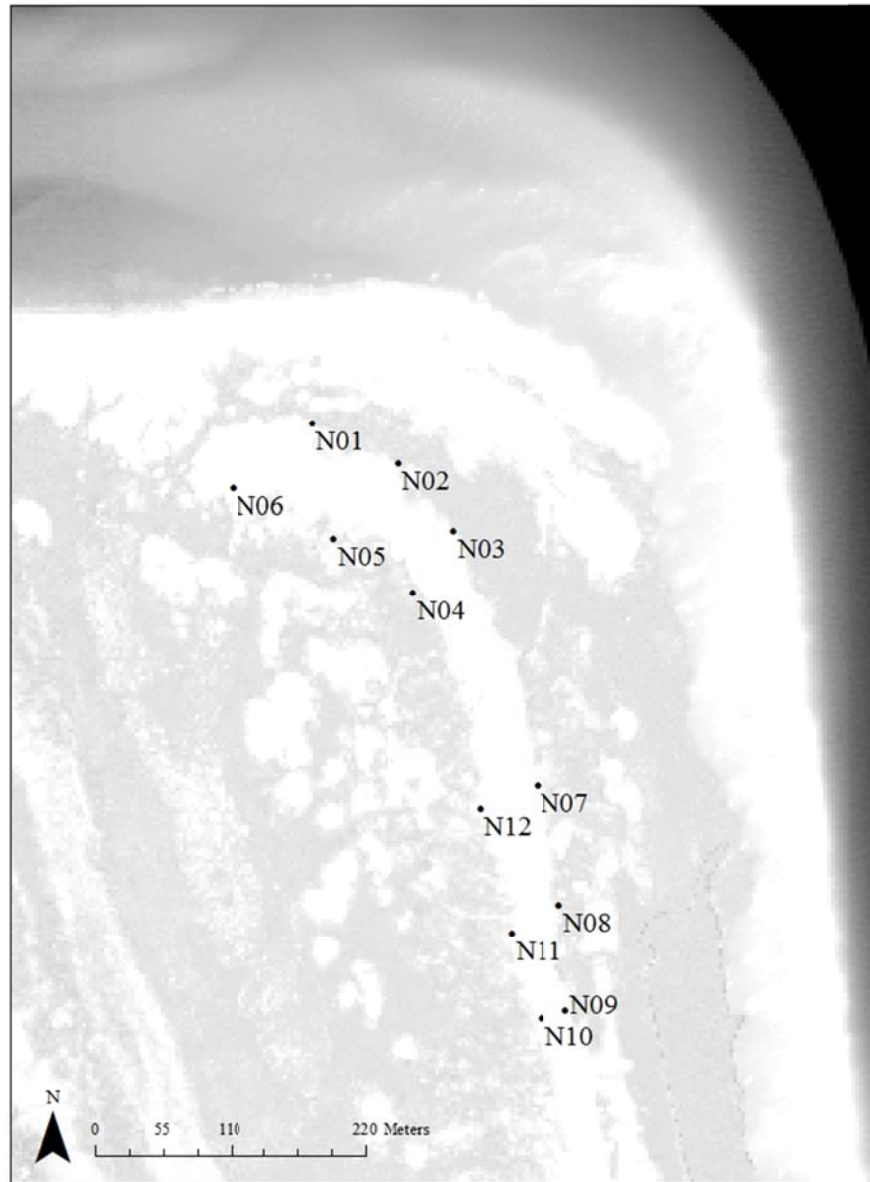


Figure 4. The Accreting section of Hog Island, containing 12 transects (N01-N12) situated along the primary dune of the north accreting end.

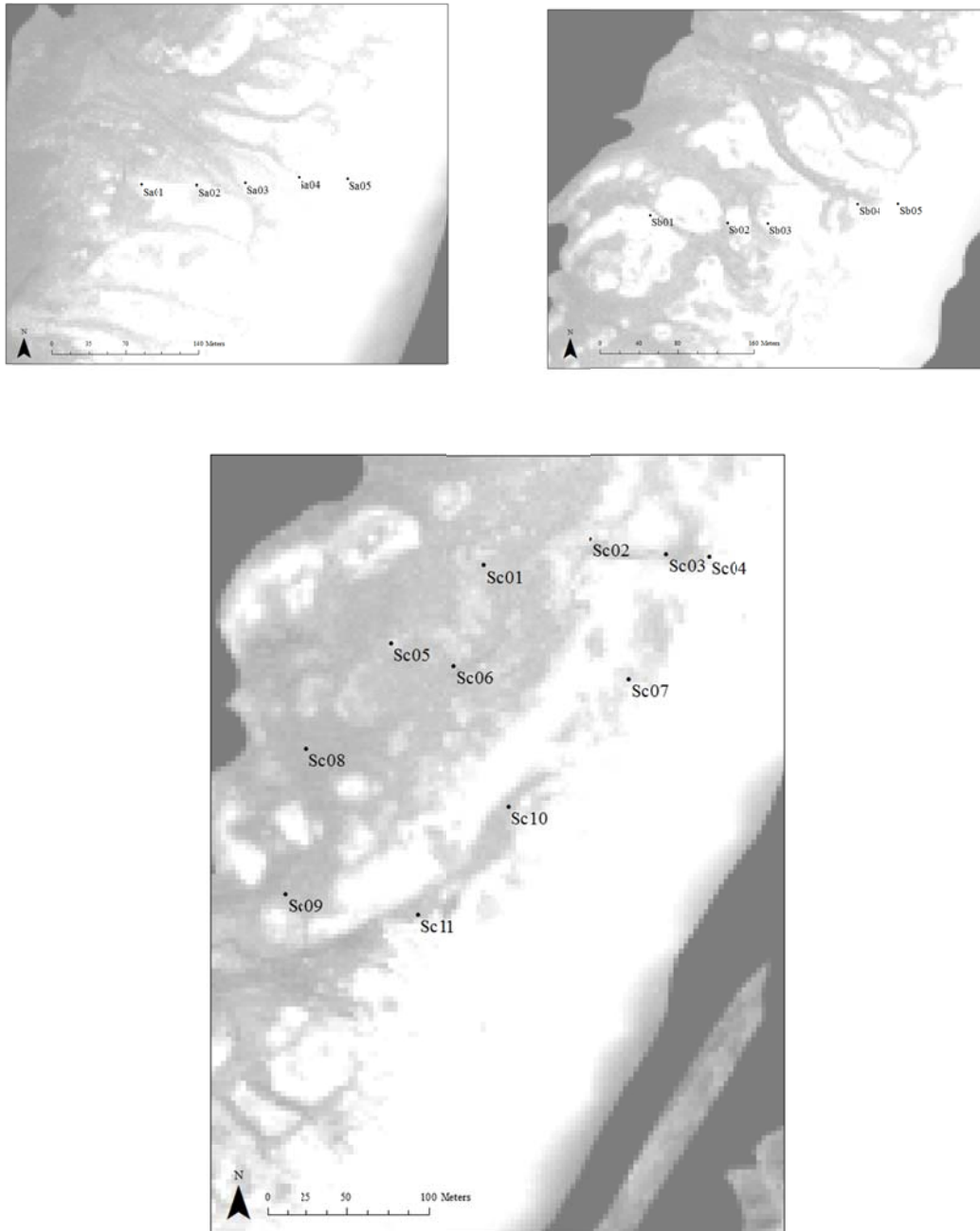


Figure 5. The South region of Hog Island stretch, ~5 km north to south, spanning 200-500 m in width. The islands southernmost reaches with transects denoted as Sa (top left), then Sb (top right) span southward toward transects Sc along the spit (bottom frame).

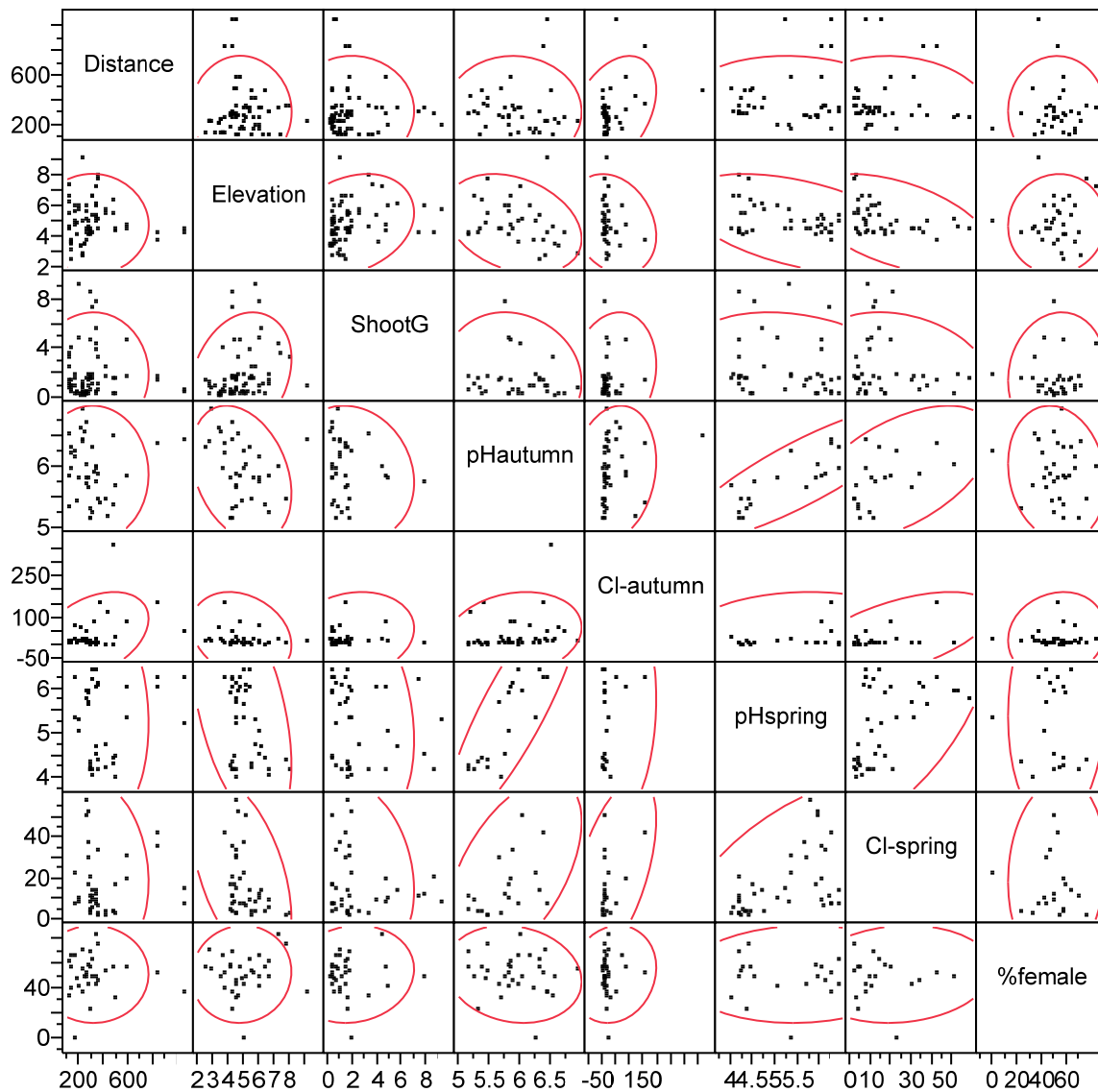


Figure 6. Multivariate scatterplot matrix of Spearman's ρ comparing distance to shoreline in meters (Distance), elevation, new shoot growth of females (ShootG), and soil characteristics to female ratios (%female).

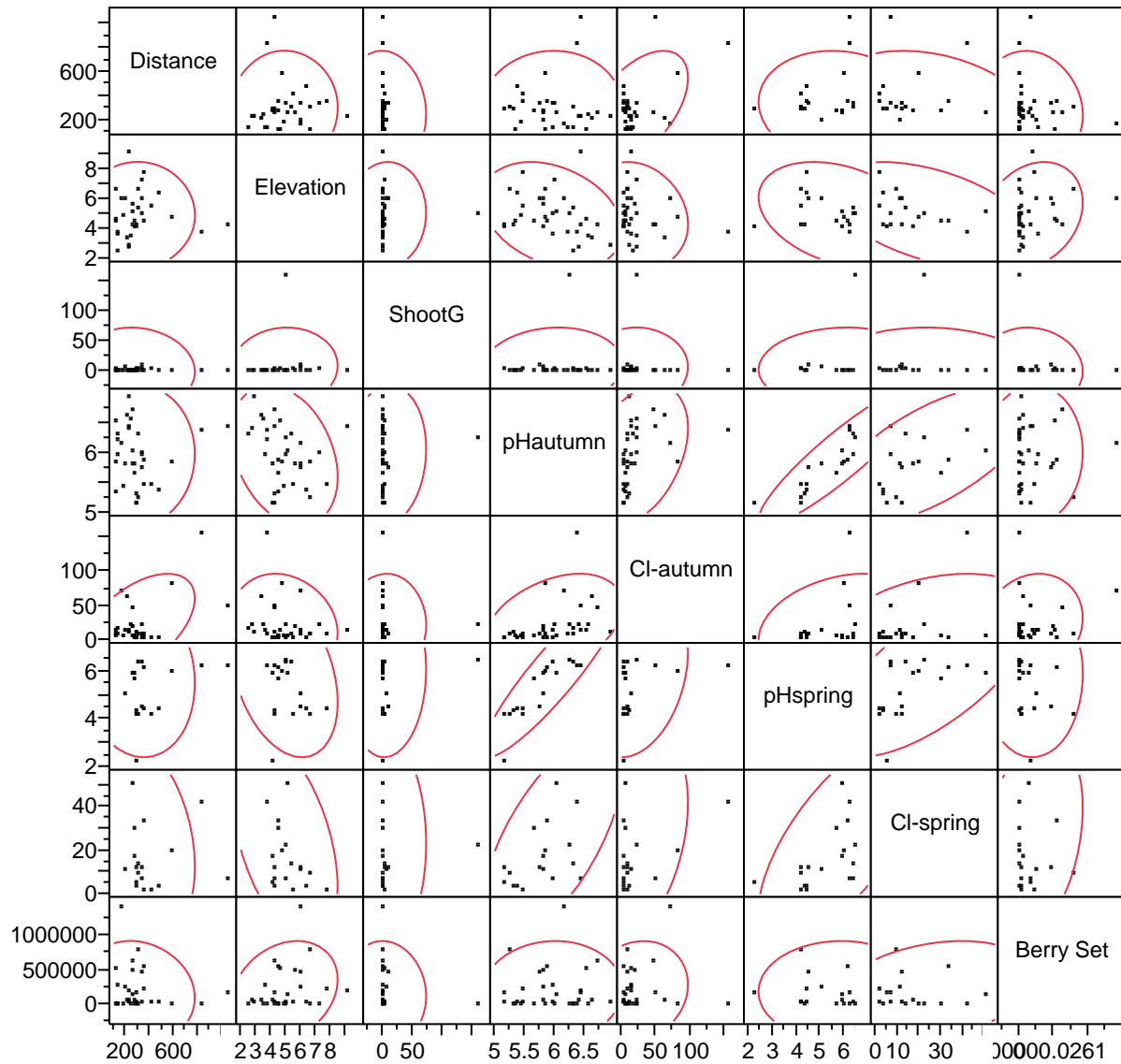


Figure 7. Multivariate scatterplot matrix of Spearman's ρ comparing all female environmental and reproductive measurements. Including distance to shoreline (Distance), elevation, shoot growth of females (ShootG), berry set (fruit/female) and soil characteristics.

VITAE

Molly Hokkanen received her B.S in Environmental Management from South Dakota State University in 2009 with a minor in Botany and Cow Tipping. The following summer was spent in the Alleghenies as a forest ecology intern for Carnegie Natural History Museums satellite site, Powdermill Nature Reserve. That winter she pressed east toward Front Royal, Virginia interning with The Smithsonian Conservation Biology Institute. There, she spent a year frolicking in the Blue Ridge Mountains, wrestling deer and counting a disturbing amount of spice bush. With a few adventures under her belt and a taste for southern Barbeque, she moseyed down to Richmond in hot pursuit of further education, and this here thesis. After her defense is wrapped up, she will be teaching 6th grade Earth Science at The Bullis School, in Potomac, MD.