

Cass A. Wigent. HABITAT AND THE EFFECTS OF ELEVATION, SALINITY, AND DROUGHT ON *Amaranthus pumilus* RAFINESQUE (AMARANTHACEAE)
(Under the direction of Dr. Claudia L. Jolls), Department of Biology, April 2006.

Habitat loss causes most species extinctions; to preserve a species' habitat, the species' ecological limiting factors must be defined. I used field transplants, salinity and water growth chamber experiments, and geographic information systems (GIS) to assess maritime strand habitat of the threatened annual *Amaranthus pumilus*, at Cape Lookout and Cape Hatteras National Seashores. At elevations below 0.7 m relative to mean high water, only 10 % of the transplants survived. Yet, these plants grew twice as much as plants in the 0.7 and 2.0 m elevation range. The transplant data suggest overwash disturbance and physiological stress may restrict distributions of *A. pumilus* at low and high elevations, respectively. Final growth chamber germination was $\leq 12\%$ in salinities ≥ 10 ppt. Half of the plants survived the most extreme salinity and water treatments, yet essentially no growth occurred in salinities ≥ 20 parts per thousand (ppt) or in watering regimes ≥ 3 days without water. Thus, salinity and water availability may be able to influence germination, survival, and growth of *A. pumilus*. Naturally occurring plants were highly clumped. Habitat area and area/shoreline at Cape Hatteras were half that at Cape Lookout and, therefore, may be variable, at least at this larger scale. This habitat analysis provides another example of the utility and challenges in application of remotely sensed data and GIS to ecological questions. Information provided here about relationships among elevation and plant success, salinity and drought tolerance, and GIS habitat analysis may be used by resource managers in identification and preservation of the highly dynamic habitat of *A. pumilus* and other threatened maritime dune species.

HABITAT AND THE EFFECTS OF ELEVATION, SALINITY AND DROUGHT ON

Amaranthus pumilus RAFINESQUE (AMARANTHACEAE)

A thesis

Presented to

the Faculty of the Department of Biology

East Carolina University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science in Biology

by

Cass A. Wigent

April 2006

HABITAT AND THE EFFECTS OF ELEVATION, SALINITY, AND DROUGHT ON

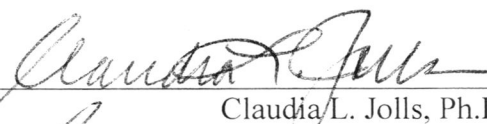
Amaranthus pumilus RAFINESQUE (AMARANTHACEAE)

by

Cass A. Wigent

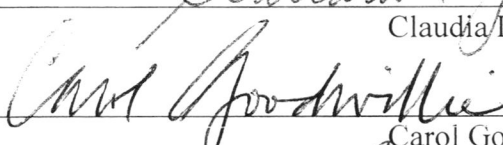
APPROVED BY:

DIRECTOR OF THESIS



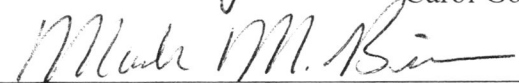
Claudia L. Jolls, Ph.D.

COMMITTEE MEMBER



Carol Goodwillie, Ph.D.

COMMITTEE MEMBER



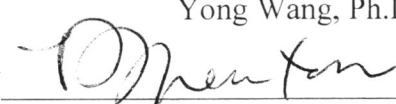
Mark M. Brinson, Ph.D.

COMMITTEE MEMBER



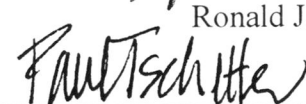
Yong Wang, Ph.D.

CHAIR OF THE DEPARTMENT OF BIOLOGY



Ronald J. Newton, Ph.D.

DEAN OF THE GRADUATE SCHOOL



Paul Tschetter, Ph.D.

ACKNOWLEDGEMENTS

First and foremost I wish to thank Dr. Claudia Jolls for her patience, persistence and unfailing support of my endeavor; her inherent ability to see and relay to me the larger significance of this work and the entirety of the educational process has been truly astounding and inspirational. I thank my wife Amber for her understanding, tolerance, and patience; her encouragement has been my sustaining force. Jon Sellars introduced and patiently trained me in the use of GIS. Jon set an example and provoked in me a higher standard of achievement academically and socially; his assistance is greatly appreciated. Also appreciated, are Sarah Johnson's patient and repeated explanations of statistical procedures and her enthusiastic assistance in the lab and the field. In addition, I thank my thesis committee members for their numerous consultations and guidance.

This work would not have been possible without the patient, encouraging and knowledgeable assistance from ECU Biology department faculty, staff, lab assistants, interns, and fellow graduate students; particularly, Dr. Gerhard Kalmus, Debbie Daniel, Barbara Beltran, Anne McLendon, Karen Trueblood, Emma Hardison, and Bernice Bailes. Tremendous logistical support from the following National Park Service personnel Jeff Cordes, Marcia Lyons, and Michael Rikard is greatly appreciated.

I also thank the Martha N. Jones Scholarship, the James S. McDaniel Scholarship, ECU Department of Biology, and the National Park Service Natural Resources Preservation Program for their support of my work.

TABLE OF CONTENTS

LIST OF FIGURES.....	v
LIST OF TABLES.....	vi
CHAPTER I. INTRODUCTION.....	1
CHAPTER II. INTERACTIONS OF ELEVATION, PLANT SUCCESS AND OVERWASH.....	6
Introduction.....	6
Materials and Methods.....	8
Experimental Design, Transplants, Plots, and Sites.....	8
Response to Protection from Overwash.....	13
Elevation Measurement and Propagation of Transplants.....	14
Transplant Response and Statistical Analyses.....	16
Results.....	17
Transplant Responses at Different Elevations.....	17
Responses to Protection from Overwash.....	19
Discussion.....	19
CHAPTER III. SALINITY AND WATER AVAILABILITY AS FACTORS AFFECTING HABITAT OF SEABEACH AMARANTH.....	28
Introduction.....	28
Materials and Methods.....	34
Salinity and Germination.....	34
Propagation of Test Plants.....	35

Response of Juvenile Plants to Salinity.....	36
Response of Juvenile Plants to Water Availability.....	36
Plant Response and Statistical Analyses.....	38
Results.....	38
Germination Responses to Salinity.....	38
Survival and Growth Responses to Salinity.....	40
Survival and Growth Responses to Water Availability.....	46
Discussion.....	51
CHAPTER IV. PLANT DISPERSION AND HABITAT AREA OF SEABEACH	
AMARANTH AT CAPE LOOKOUT AND CAPE HATTERAS NATIONAL	
SEASHORES.....	57
Introduction.....	57
Materials and Methods.....	60
GIS Modeling of Habitat Area.....	60
Dispersion.....	63
Habitat Area.....	64
Results.....	65
Dispersion.....	65
Habitat Area.....	65
Discussion.....	68
CHAPTER V. CONCLUSIONS.....	
Elevation and Success of Transplants of <i>Amaranthus pumilus</i>	75

Responses to Salinity and Water Availability.....	76
Aggregated Plant Dispersion.....	78
Spatial Extent and Patterns of Habitat Distribution.....	79
General Conclusions.....	80
REFERENCES.....	87

LIST OF FIGURES

1. Transplant plot locations at Cape Hatteras National Seashore (CAHA).....	10
2. Transplant plot locations at Cape Lookout National Seashore (CALO).....	11
3. Locations and elevations of plots at four transplant sites used to test for differences in survival and growth of <i>Amaranthus pumilus</i> at different elevations and exposed to different intended risks of overwash.....	12
4. Configuration of plots at the overwash protection transplant experiment site.....	15
5. Proportion of <i>Amaranthus pumilus</i> transplants surviving at wk 10 at elevations below (LOW-OUT), within (IN), and above (HIGH-OUT) the 0.7 - 2.0 m elevation range described by Sellars (2001).....	18
6. Growth of <i>Amaranthus pumilus</i> transplants at wk 10 at elevations below (LOW- OUT), within (IN), and above (HIGH-OUT) the 0.7 - 2.1 m elevation range described by Sellars (2001).....	20
7. Scatterplot showing transplant diameter vs. elevation.....	22
8. Water table profile of Bodie Island, NC (Whittecar and Emry 1992).....	32
9. Survival of <i>Amaranthus pumilus</i> watered with saline solutions of 0, 2, 5, 10, 20, and 30 ppt for 8 wk; 31 plants were grown in each treatment.....	42
10. Mean leaf number of <i>Amaranthus pumilus</i> plants grown at six salinities.....	43
11. Mean number of nodes of <i>Amaranthus pumilus</i> plants grown at six salinities.....	44
12. Mean crown diameters of <i>Amaranthus pumilus</i> plants grown at six salinities.....	45
13. Survival of <i>Amaranthus pumilus</i> plants grown at five watering regimes.....	47
14. Mean leaf numbers of <i>Amaranthus pumilus</i> grown at five watering regimes.....	48
15. Mean number of nodes of <i>Amaranthus pumilus</i> grown at five watering regimes....	49
16. Mean crown diameters of <i>Amaranthus pumilus</i> grown at five watering regimes....	50
17. GIS data Tiles at two North Carolina national seashores.....	62

LIST OF TABLES

1. Coefficients for the regression of transplant diameter ratio with elevation (m)..... 21
2. Chi-square comparisons between proportions of seabeach amaranth seeds
germinating in pairs of salinity treatments after 6 d..... 39
3. Chi-square comparisons between proportions of seabeach amaranth seeds
germinating in pairs of salinity treatments after 30 d..... 41
4. Holgate's Index of Dispersion and the number of naturally-occurring
Amaranthus pumilus plants used in calculation of the index at Cape
Hatteras and Cape Lookout National Seashores for the years 2000 – 2003..... 66
5. Hectares of suitable seabeach amaranth habitat, kilometers of shoreline length,
and the ratio of suitable habitat to shoreline length at Cape Hatteras and
Cape Lookout National Seashores for the years 1997 – 1999..... 67
6. Hectares of suitable seabeach amaranth habitat, kilometers of shoreline,
habitat area adjusted to shoreline (Ratio) for each year, and each Tile at
Cape Hatteras and Cape Lookout National Seashore, respectively..... 73

CHAPTER I

INTRODUCTION

Loss of habitat is widely accepted as the single largest cause of species extinctions (Meffe and Carroll 1997, Chapin *et al.* 1997, Vitousek *et al.* 1997). Wilson (1992) estimated global rates of species extinction to be 100,000 times higher than the normal, pre-human background rate estimated by Raup (1991). Many species are dependent on specific habitats (Baskauf and Eickmeier 1994). When species' specific habitats are destroyed, fragmented, or significantly altered, those species may be forever lost to extinction (Zedler *et al.* 2001, Vitousek *et al.* 1997). Species endemic to habitats with small ranges are particularly at risk of extinction (Kruckeberg and Rabinowitz 1985). Therefore, there is a need for ecologists and conservation biologists to identify and define threatened habitats so that conservation goals can be outlined and procedures can be implemented.

Knowledge of habitat characteristics and general species biology are prerequisites for the conservation of individual species and their habitats (Kruckeberg and Rabinowitz 1985, Chapin *et al.* 1996, Wiser *et al.* 1998). Creating a working definition of habitat is complex; multiple factors must be sampled over large areas (Velazquez 1996). While large scale forest or other habitat conversion is easily recognized, less conspicuous forms of habitat loss are sometimes recognized only by studying, defining, and/or modeling the habitat of those species threatened by declining distributions. The minimum and maximum boundaries of certain abiotic and most commonly edaphic parameters are often included in habitat definitions (Kruckeberg and Rabinowitz 1985). Ecologists, therefore,

are faced with a difficult task; simultaneously define or describe the specific threatened habitat using a rare species from that habitat, in the midst of loss of that habitat.

Habitat definition and modeling may be especially important for maritime strand species. Maritime strands are the narrow beach ecotones located between ocean shorelines and upland terrestrial habitats. Beach renourishment, seawalls, beach hardening structures, and commercial development along the Atlantic seaboard have resulted in large scale losses of strand habitats (Pilkey and Neal 1992). Characteristics common to strand species such as short life cycles, high habitat specificity or patchy habitat availability increase the risk of extinction (Karr 1982, Pimm 1988, Quintana-Ascencio and Menges 1996, Turner *et al.* 1996, Fisher and Stocklin 1997). Marine strands are among the most temporally and spatially variable habitats (Ignaciuk and Lee 1980, Ehrenfeld 1990, Hayden *et al.* 1991). In US Atlantic coast maritime strands, lack of shade results in high summertime sand surface temperatures, and proximity to the ocean results in high annual disturbance from hurricanes and nor'easters. At one extreme, nearshore habitat can be completely removed and then deposited again in a single storm (Ignaciuk and Lee 1980, pers. obs.); at the other extreme, sandy soils with little organic matter can be left without nutrient input from storm overwash for years on end (Gagne and Houle 2002). Many maritime strand species have been described as fugitives in this environment (Seneca 1969, van der Valk 1974, Barbour *et al.* 1985, and Crawford 1989). Fugitives rely on regular disturbance to create and provide constant availability of large areas of new, open habitat (Bazzaz 1979). Conservation of strand species can be improved through determination of the biotic and abiotic parameters

limiting distribution and abundance as well as temporal and spatial variability in these variables and habitats.

This thesis investigates the habitat parameters of seabeach amaranth (*Amaranthus pumilus* Raf., Amaranthaceae), an annual maritime strand fugitive endemic to disturbed open-sand areas in coastal barrier island ecosystems of the eastern US (Bücher and Weakley 1990). It was federally listed as threatened in 1993; at that time, it had been extirpated from nearly three-fourths of its historic range (USFWS 1993). Seabeach amaranth plants in North Carolina numbered in the thousands historically (Bücher and Weakly 1990), but census counts since 1985 have ranged from 16,530 individuals in 1988 to as few as 11 individuals in 1999 (Sellars 2001). Populations at Cape Lookout and Cape Hatteras National Seashores ranged from 22 individuals in 2000 to 1614 in 2003 (pers. obs.) while hundreds of plants grew on Bogue Banks in 2002 and 2003 (estimated from pers. obs). Habitat loss due to dune stabilization and beach hardening is the primary reason for population reductions in seabeach amaranth (Bücher and Weakley 1990). An improved understanding of *Amaranthus pumilus* biology and knowledge of what biotic and abiotic parameters constitute seabeach amaranth habitat are critical for this species' preservation and recovery.

Bücher and Weakly (1990) reported that seabeach amaranth habitat occupies a narrow range of elevations within the maritime strand environment. Sellars (2001) and Jolls and Sellars (2000) used GIS techniques to define the elevation range of seabeach amaranth as between 0.77 m and 2.0 m above mean high water (MHW). The National Ocean Service defines MHW as mean of the maximum heights reached by rising tides.

Preliminary research also suggests that larger plants are associated with lower elevations (Wigent *et al.* 2002). This thesis further examines seabeach amaranth's habitat elevation range and attempts to determine some of the mechanisms restricting seabeach amaranth habitat to this range.

Chapter II of my thesis takes a closer look at the interactions of elevation, plant success, and overwash. Elevation influences plant distributions through its influence on soil characteristics, disturbance, and other habitat factors. Growth and survival results are reported for plants transplanted to beach sites below, within, and above elevations in Sellars' (2001) model to shed light on factors influencing seabeach amaranth distribution. Growth and survival results also are reported for transplants exposed to low elevations and associated overwash.

In Chapter III of my thesis, the potential of salinity and water availability to restrict the distribution of *Amaranthus pumilus* to its narrow elevation range is examined. In maritime strand habitats, elevations range only on the order of a few meters. Oosting (1954), however, regarded elevation as the primary cause of differences in water availability, inundation, and exposure to salt spray. High salinities can reduce germination (Woodell 1985, Khan 1991, Mariko *et al.* 1992, Clevering 1994, Khan and Rizvi 1994, Ungar 1995, Huang 2003). Salinity also can reduce recruitment, growth, and survival (Larcher 1995, Lambers *et al.* 1998), and has been used to differentiate plant habitat (Migahid 2003). Water availability and salinity are interconnected, especially in maritime strands, because soil salinity reduces soil water potential (Bernstein and Hayward 1958). Substrate water availability alone has been shown to influence plant

species distributions at all stages of development (Clevering 1994, Walmsley and Davy 1997, Bram and Quinn 2000). Differing species' tolerances to salinity and drought along with varying osmotic potential throughout environments can result in different plant distribution patterns (Naidoo and Naicker 1993).

Chapter IV uses geographic information systems (GIS) to determine the extent of aggregation of naturally-occurring *Amaranthus pumilus* plants and to quantify habitat area. GIS techniques are used to estimate dispersion in an attempt to improve knowledge of preferences for specific sites and improve definition of suitable habitat. Sellars' (2001) and Jolls and Sellars' (2000) habitat delineation methods are applied to several years of habitat data for several sites to make general estimates of differences in habitat availability through time and between sites.

This thesis focused on the four following questions:

- 1) Do seabeach amaranth plants grown *in situ* grow best within the elevation range (0.77 to 2.0 meters above mean high water) suggested by Sellars (2001) and Jolls and Sellars (2000)?
- 2) Could the narrow elevation distribution of seabeach amaranth be associated with its tolerance of salinity and drought?
- 3) What is the dispersion of naturally-occurring seabeach amaranth plants?
- 4) What is spatial extent of seabeach amaranth habitat at Cape Lookout and Cape Hatteras National Seashores, and can any patterns in spatial or temporal distribution of habitat be detected?

CHAPTER II

INTERACTIONS OF ELEVATION, PLANT SUCCESS, AND OVERWASH

Introduction

Elevation has been used to describe plant distribution, abundance, and fitness (Clausen, Keck and Heisey 1940, Lawrence 1945), and to model plant habitat (Austin and Meyers 1996, Sperduto and Congleton 1996, McGraw *et al.* 2003). Upper and lower elevation boundaries of species distributions, however, are not inherent in the elevations themselves; rather, they result from the influence of topography on disturbance, radiation, soil water content, temperature, or other biotic or abiotic factors (Austin and Meyers 1996). Many studies of plant distribution along elevation gradients have been in habitats with elevations ranging on the order of tens or hundreds of meters (Clausen, Keck and Heisey 1940, Lawrence 1945, Austin and Meyers 1996, Sperduto and Congleton 1996, McGraw *et al.* 2003). In maritime strands, however, elevations range only on the order of one to a few meters; yet, elevation has long been regarded as the primary cause of differences in water availability, inundation, and salt spray exposure in maritime strands (Oosting 1954). Porous sand substrates may exaggerate the influence of small elevation changes through rapid percolation of water from higher to lower microsites (Whittecarr and Emry 1992). Proximity of maritime strand habitat to the shoreline can also exaggerate the influence of elevation on abiotic habitat variables such as overwash disturbance (Ignaciuk and Lee 1980, pers. obs.), salinity, and water availability (Martin 1959, Van der Valk 1974, Whittecarr and Emry 1992, and Ullman *et al.* 2003).

Bücher and Weakly (1990) described the elevation range of *Amaranthus pumilus*

as about 1.3 m from the lowest to the highest elevations. Sellars (2001) and Jolls and Sellars (2000) more specifically defined *A. pumilus* habitat using GPS positions of naturally-occurring plants in conjunction with remotely sensed elevation data and monochromatic reflectance photos of Shackleford Banks North Carolina; the authors bracketed the elevation range of seabeach amaranth between 0.70 m and 2.0 m above mean high water. In a pilot study, Wigent *et al.* (2002) divided seabeach amaranth's suitable habitat elevation range into elevation sub-ranges and found plants were larger at lower elevations. The authors also found that the distribution of plants decreased more abruptly at the low end of the elevation range than at the high end.

The upper and lower extents of seabeach amaranth's elevation range may be limited by different environmental factors, each with its own gradient of stress and distinct plant distribution. Overwash, for example, can create a steep disturbance gradient, strongly affecting one site while leaving nearby sites untouched (Ignaciuk and Lee 1980, pers. obs.). Payne and Maun (1984), examining seedling emergence, survival, and growth in the lakeshore annual, *Cakile edentula*, found that survival at low elevations was determined by the extent of overwash disturbance and that water availability was the primary factor limiting growth and survival at higher elevations. Reduced survival due to overwash could have caused the pattern of distribution observed by Wigent *et al.* (2002) study and may in part determine the lower end of *A. pumilus*' habitat range. Measuring plant size and survival of *A. pumilus* transplanted into the field at sites in close proximity but differing elevations could aid identification of variables restricting habitat as well as the relative importance of those variables. This chapter reports on growth and survival of

transplants at beach sites of different elevations to test the effect of elevation on seabeach amaranth.

Assessment of the potential suitability of low elevation inlet habitat protected and unprotected from overwash was attempted. Bücher and Weakley (1990) include island ends in a list of important habitat sites for seabeach amaranth; I, too, have observed relatively large aggregations of plants at inlets. Yet, most of the wide, flat beach area at accreting (and some eroding) island ends is lower than Sellars' model defines as suitable habitat (pers. obs). Although there have been several studies of habitat gradients from the shore to the dune line, I am not aware of any studies of habitat variability from one end of an island to the other or comparing inlets to island mid sections. A transplant experiment was devised to test if overwash disturbance frequency or magnitude may be reduced at island ends allowing for increased success of *A. pumilus* at lower elevations.

I asked two questions in this portion of my thesis. 1) Do transplants grow to different sizes and/or have different survival at different elevations? and 2) does overwash disturbance determine the lower elevation boundary of seabeach amaranth's habitat range? If the former were true, then significant differences in the response of transplants (e.g., mean size and survival) should be observed for plants grown at different elevations. If the latter were true, transplants at low elevations protected from overwash disturbance would be more likely to survive than those at unprotected sites.

Materials and Methods

Experimental Design, Transplants, Plots, and Sites. Plant response to elevation and protection from overwash were tested in a single field experiment using 690

transplants of *A. pumilus*. The study was conducted summer 2002 at Cape Hatteras (CAHA) and Cape Lookout (CALO) National Seashores, in Dare, Hyde and Carteret Counties, NC. Juvenile plants were planted in the field in plots at different elevations to test for responses to elevation. Test plots were 10 X 12 m, each containing 20 or 30 plants following the methods of Jolls *et al.* (2004). Based on Sellars (2001), the elevation range 0.77 m and 2.00 m above mean high water will be referred to as IN. Elevations below this range will be referred to as LOW-OUT and elevations above will be referred to as HIGH-OUT. IN elevations were separated into LOW-IN and HIGH-IN when they were below and above 1.35 m, respectively.

Four sites were established. Two sites were located at CAHA: 1) on the west-facing beach, north of the point (DRAIN) and 2) on east-facing Loran Beach (LORAN) (Figure 1). Two sites were located at CALO: 1) on the west-facing beach south of the spit (SOUTH SPIT) and 2) near the northern tip of the spit (NORTH SPIT) (Figure 2). DRAIN and SOUTH SPIT were chosen 1) so that six plots could be situated at each site and 2) so that each plot would have one of six different elevations at each site. Thus, DRAIN and SOUTH SPIT each had a group of six plots that spanned the elevation range from HIGH-IN to LOW-OUT. LORAN was chosen so that three plots could be established at three similar IN elevations and three plots could be established at three similar HIGH-OUT elevations (Figure 3). Each site in this experiment represents elevations ranging from either LOW-OUT to IN, or elevations ranging from IN to HIGH-OUT. No sites represented the entire elevation range from LOW-OUT to HIGH-OUT.

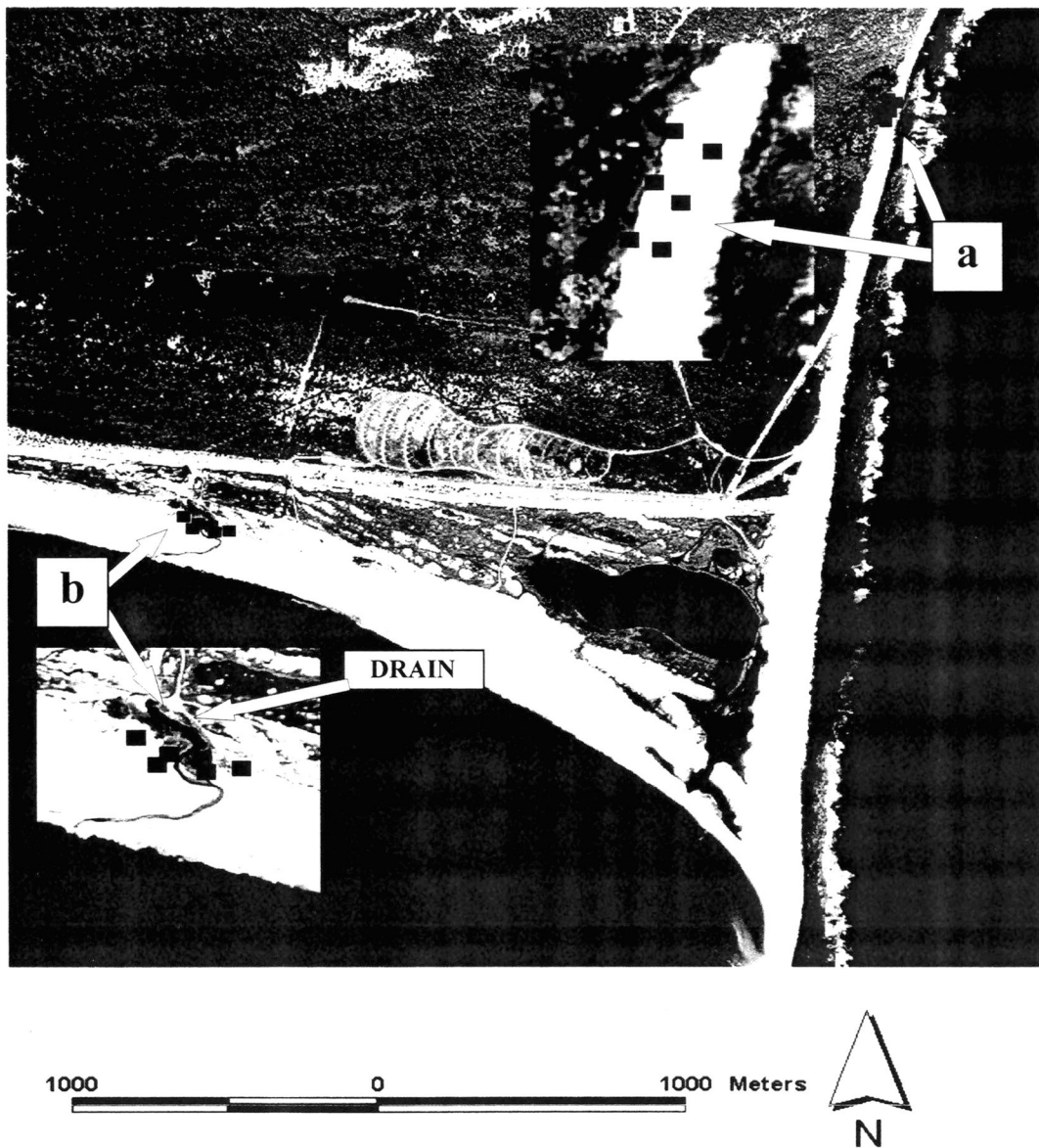


Figure 1. Transplant plot locations at Cape Hatteras National Seashore. Plots are depicted as black rectangles. Transplants to Loran Beach (LORAN) plots (a) were at IN (0.7 – 2.0 m) and HIGH-OUT (> 2.0 m) elevations. Transplants in DRAIN plots (b) spanned an elevation range from 0.5 to 1.8 m (LOW-OUT through IN).

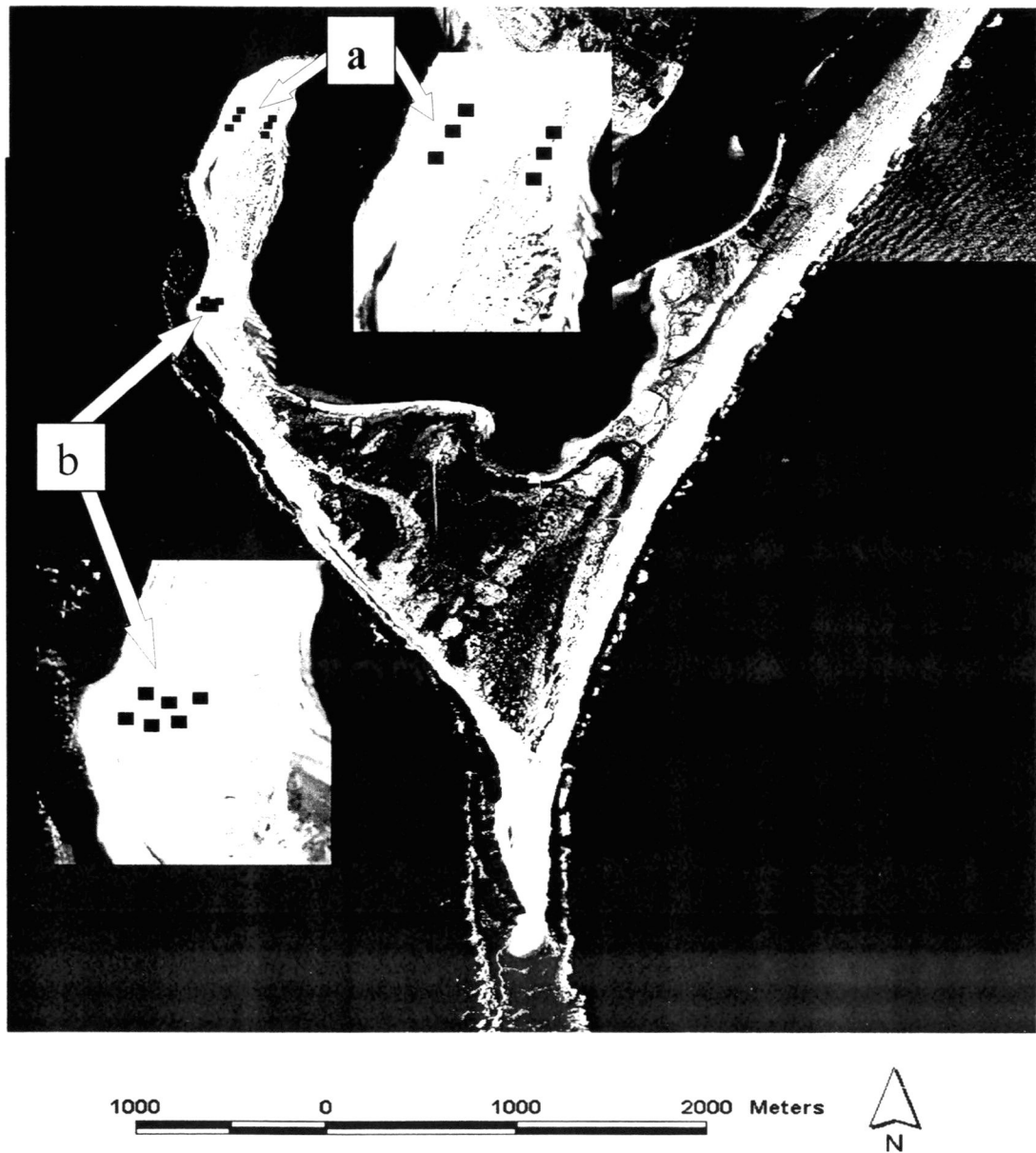


Figure 2. Transplant plot locations at Cape Lookout National Seashore. Plots are depicted as black rectangles. NORTH SPIT plots (a), used to test the effect of protection from overwash disturbance, were on the unprotected west side and the protected east side of the spit. SOUTH SPIT plots (b), used to test the effect of elevation on transplant success, spanned an elevation range from 0.5 to 1.8 m (LOW-OUT through IN).

	LOW-OUT (below 0.77 m)	LOW-IN (0.78 - 1.34. m)	HIGH-IN (1.35 – 1.99 m)	HIGH-OUT (above 2.0 m)
CAHA (Loran Beach)			30 30 30	30 30 30
CAHA (Drain Site)		30 30 30	30 30 30	
CALO (south spit)		30 30 30	30 30 30	
CALO (north spit)	30 30 30 20 20 20	← PROTECTED ← UNPROTECTED		

Figure 3. Locations and elevations of plots at four transplant sites used to test for differences in survival and growth of *Amaranthus pumilus* at different elevations and exposed to different intended risks of overwash. Plots are represented by black rectangles. The number inside each rectangle represents the number of plants in each plot. Plots used to test for responses to varying risk of overwash are labeled as protected and unprotected, respectively.

Response to Protection from Overwash. Plots at NORTH SPIT, at CALO (Figure 2), were all planted in similar LOW-OUT elevation areas, one assumed to be protected and the other assumed to be unprotected from overwash to test if the suitable habitat model (Sellars 2001) should be extended to include LOW-OUT but protected areas. In this experiment, overwash was distinguished from inundation to include high energy movement of water and a higher potential for mechanical abrasion and disturbance. It was assumed that ocean side or ocean facing beaches have greater overwash based on their proximity to larger open-ocean waves. Protected and unprotected plot locations were selected based on evidence of disturbance, lack of established perennial vegetation, rack lines, and on each beach's aspect to open ocean. The six plots at NORTH SPIT were arranged in two groups of three plots per group: one protected and one unprotected. The sound side beach, on the east side of NORTH SPIT, was presumed to have relatively low wave energy. East of NORTH SPIT is Core Sound and to the west is the Atlantic Ocean; it was assumed that the shorter distance across the sound relative to open-ocean would limit the wind's ability to build waves. The east side of NORTH SPIT was, therefore, used to establish the group of three protected plots. The group of unprotected plots in this experiment was located on the ocean facing beach on the west side of NORTH SPIT (Figure 2). Groups were arranged with the closest possible proximity to minimize potential variability of uncontrollable abiotic characteristics such as rainfall, wind speed, and wind direction. Protection from overwash disturbance was afforded by a ridge of high ground separating the protected east side of the site from the unprotected west side (Figure 4.).

Elevation Measurement and Propagation of Transplants. Elevation values were acquired at the base of each transplant used in this experiment to enable comparisons of transplant responses and their elevation. An RL-50A laser-level (Topcon™, Paramus, NJ) was used to survey from USGS elevation benchmarks. Locations and elevations of benchmarks were found at the North Carolina Geodetic Survey (NCGS) website. Two additional temporary benchmarks were established at each site to use as references for surveying elevations of nearby transplants. Estimated accuracy for the elevation values was 10 cm or less; sites furthest from the benchmarks required the most laser-leveling and thus possessed errors closest to 10 cm. Elevations were obtained for 16 locations at CAHA and 16 locations at CALO to aid initial site selection. Site selection was made through collaboration with NPS staff at CAHA and CALO to minimize conflicts with ongoing park activities and management practices.

Transplants were reared from approximately 2000 seeds initially cold stratified for 3 mo (Sellars 2001). Seeds had two general lineages: 1) Agricultural Research Service-Germplasm Resources Information Network (ARS-GRIN) from David Brenner, Plant Introduction Station, Iowa State University Ames, IA, and 2) from field collections authorized by the North Carolina Plant Conservation Program and the National Park Service (NPS). Seeds were germinated in groups of <100 seeds in a Conviron® growth chamber (Winnipeg, Manitoba, Canada), using a 30/20 °C thermoperiod, and a 16 h light/8 h dark photoperiod. Seeds were placed in 10 cm pots filled with 200 mL of autoclaved field collected beach sand and watered daily with deionized water.

As germination occurred, each seedling was transplanted to a Conetainer®

Protected from Overwash (sound side) LOW-OUT (elev. 0.5 m)		Unprotected from Overwash (ocean side) LOW-OUT (elev. 0.5 m)
	High Dune Ridge	
1 plot of 30 plants	blocks overwash from high energy beach	1 plot of 20 plants
1 plot of 30 plants		1 plot of 20 plants
1 plot of 30 plants		1 plot of 20 plants

Figure 4. Configuration of plots at the overwash protection transplant experiment site.

All plots were at NORTH SPIT at Cape Lookout National Seashore, within the LOW-OUT elevation range, and each plot contained either 20 or 30 plants. Close proximity of plots was possible because a high dune ridge separated the three plots protected from overwash from the three plots unprotected from overwash.

(Steuwe and Sons, Inc., Corvallis, OR). Growth media was a 50-50 mixture of autoclaved field-collected beach sand and sifted, Black Cow[®] composted manure (Black Gold Composting Co. Oxford, FL). Plants were grown in the growth chamber for approximately 3 mo., using methods developed by Sellars (2001).

Plants were transplanted to sites at CAHA and CALO in April of 2002. Plots were prepared in advance and transplant holes were dug just before planting. Plants were watered thoroughly, placed in plastic wash-tubs, and transported to their respective sites using automobile, boat, and/or four-wheeler. Plants were then watered a second time, removed from their containers, and planted in holes in the field such that the soil from the container was even with the sand surface. Planted transplants were watered with approximately 3 liters of water immediately after watering and again the next morning.

Transplant Response and Statistical Analyses. Plant success was measured twice monthly throughout the growing season as survival and size of plants. Chi-square goodness of fit was used to identify significant differences in survival among elevation groups. The number of leaves on each plant was counted before plot assignments were made and plants were assigned to plots to achieve a high similarity of plant sizes per plot. Mean leaf numbers were not significantly different among plots ($F_{23, 666} = 3.103$, $P < 0.000$). Plant diameter can predict fecundity in the field (Wigent *et al.* 2001) and was the only practical response measure, so plant diameter was used as the primary indicator of plant size. Diameter at wk 10 was divided by diameter after planting (wk 2) to calculate Diameter Ratio; this provided a measure of growth that controlled for each plant's original size. Differences in mean plant size and Diameter Ratio per elevation were

determined using one-way analysis of variance (ANOVA) in the SPSS 10.1 for Windows (Chicago, IL) software package. The dependent variable, Diameter Ratio, was transformed to meet the assumptions of ANOVA. Tukey's Honestly Significant Differences post-hoc tests were used to determine which elevation groups had significantly different mean Diameter Ratios. Regression was also used to measure correlation between elevation and plant diameter (Diameter Ratio) within and among sites. For regression analysis NORTH SPIT and SOUTH SPIT sites were combined because they were closely located. Also, the LOW-OUT elevations of the NORTH SPIT plots broadened the total range of elevations represented at the Spit.

Results

Transplant Responses at Different Elevations. Survival among plots differed significantly ($X^2 = 192.422$, $df = 2$, $P < 0.001$). Plant survival was lowest in LOW-OUT (10%), intermediate in IN (63%), and highest in HIGH-OUT (94%) elevation groups (Figure 5). Transplants at LOW-IN elevations had significantly higher survival than plants in the LOW-OUT elevations ($X^2 = 6.651$, $df = 2$, $P < 0.05$) and significantly lower survival than transplants at HIGH-IN elevations ($X^2 = 164.713$, $df = 2$, $P < 0.001$). Survival of transplants in the LOW-OUT elevation category was not significantly different from survival of transplants in the LOW-IN elevation category, when considering only plants unprotected from overwash ($X^2 = 0.428$, $df = 2$, $P > 0.05$). Growth from wk 2 to wk 10, represented as Diameter Ratio (wk 10 diameter/wk 2 diameter), was significantly different among elevation groups ($F_{2,381} = 33.477$, $P < 0.001$, Figure 6). Tukey's post-hoc detected significant differences in mean Diameter Ratio

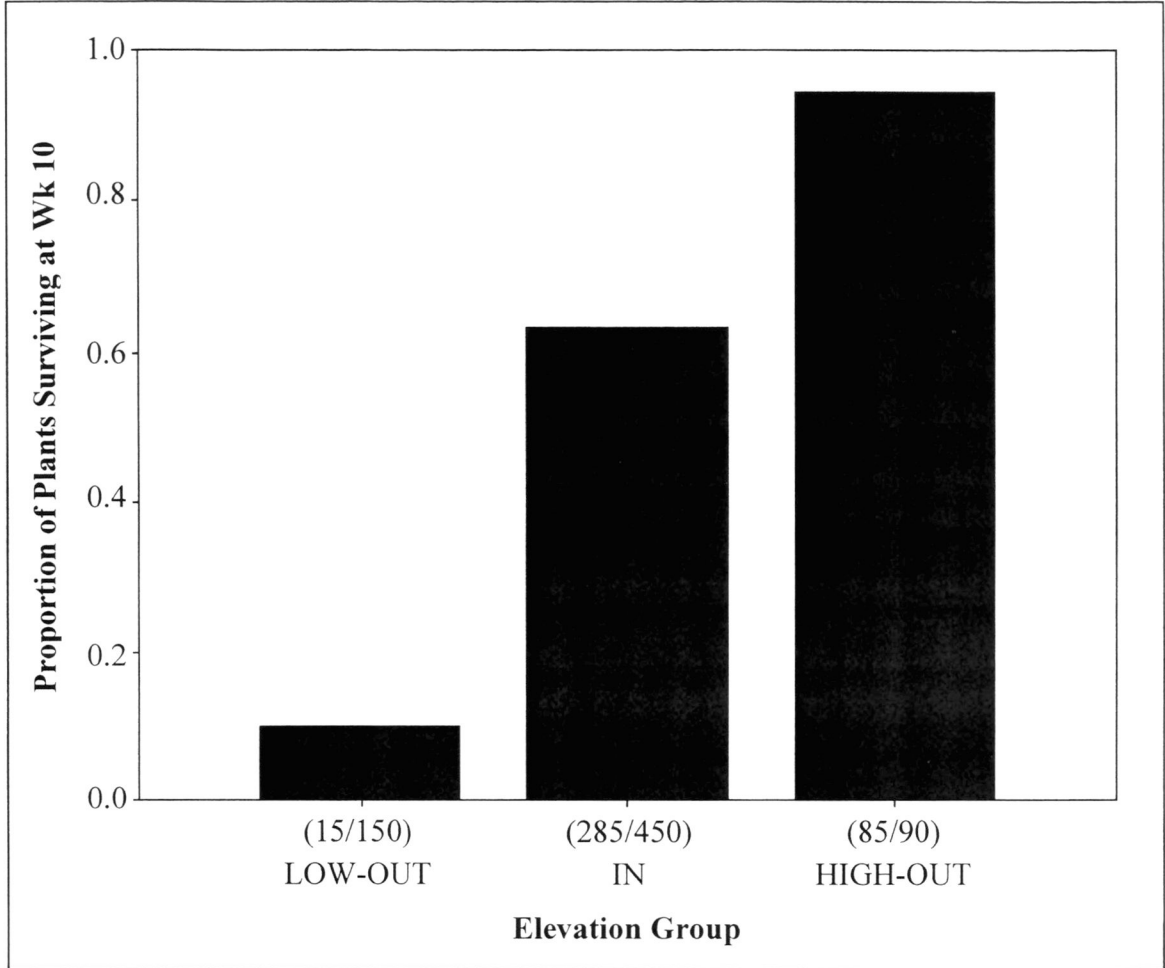


Figure 5. Proportion of *Amaranthus pumilus* transplants surviving at wk 10 at elevations below (LOW-OUT), within (IN), and above (HIGH-OUT) the 0.7 - 2.0 m elevation range described by Sellars (2001). Significant differences in survival were observed ($X^2 = 192.422$, $df = 2$, $P < 0.001$). Number of plants surviving and total number of plants in each group are provided in parentheses.

between LOW and IN ($P < 0.001$), LOW and HIGH ($P < 0.001$), and IN and HIGH ($P < 0.001$) elevation groups. Mean transplant Diameter Ratios were 6.51 ± 0.74 cm (mean $\pm$ SE, $n = 15$) in the LOW-OUT group, 1.78 ± 0.09 cm (mean $\pm$ SE, $n = 284$) in the IN group, and 0.99 ± 0.10 cm (mean $\pm$ SE, $n = 85$) in the HIGH-OUT group. Mean transplant diameters on wk 10 were 21.39 ± 3.07 cm (mean $\pm$ SE, $n = 15$) in the LOW-OUT group, 8.42 ± 0.43 cm (mean $\pm$ SE, $n = 285$) in the IN group, and 4.83 ± 0.49 cm (mean $\pm$ SE, $n = 85$) in the HIGH-OUT group.

Significant but small negative linear relationships were found for growth response to elevation (m) within sites (Table 1). Two sites showed modest negative relationship between plant size and growth (LORAN $r^2 = 0.149$, combined SPIT $r^2 = 0.468$, Figure 7). No relationship was found between plant diameter and elevation at the DRAIN site ($P = 0.310$, Table 1). Combining sites and variable transformations did not improve fit.

Responses to Protection from Overwash. All plants in the overwash protected sound-side site died within 6 wk after planting. Hyperhaline or hypoxic soils are assumed to have been the cause of mortality; yellowing of the plants and loss of leaves were observed at the first census, two weeks after planting. No physical or mechanical removal of plants was noted; plant stems remained after death. At the unprotected site, however, survival within plots was 10%, 25%, and 40%; surviving plants exhibited signs of mechanical abrasion and breakage, and salt hypertrophy.

Discussion

Survival and growth data suggest that mechanical factors associated with overwash (erosion, abrasion, and burial), rather than soil suitability, may determine a low

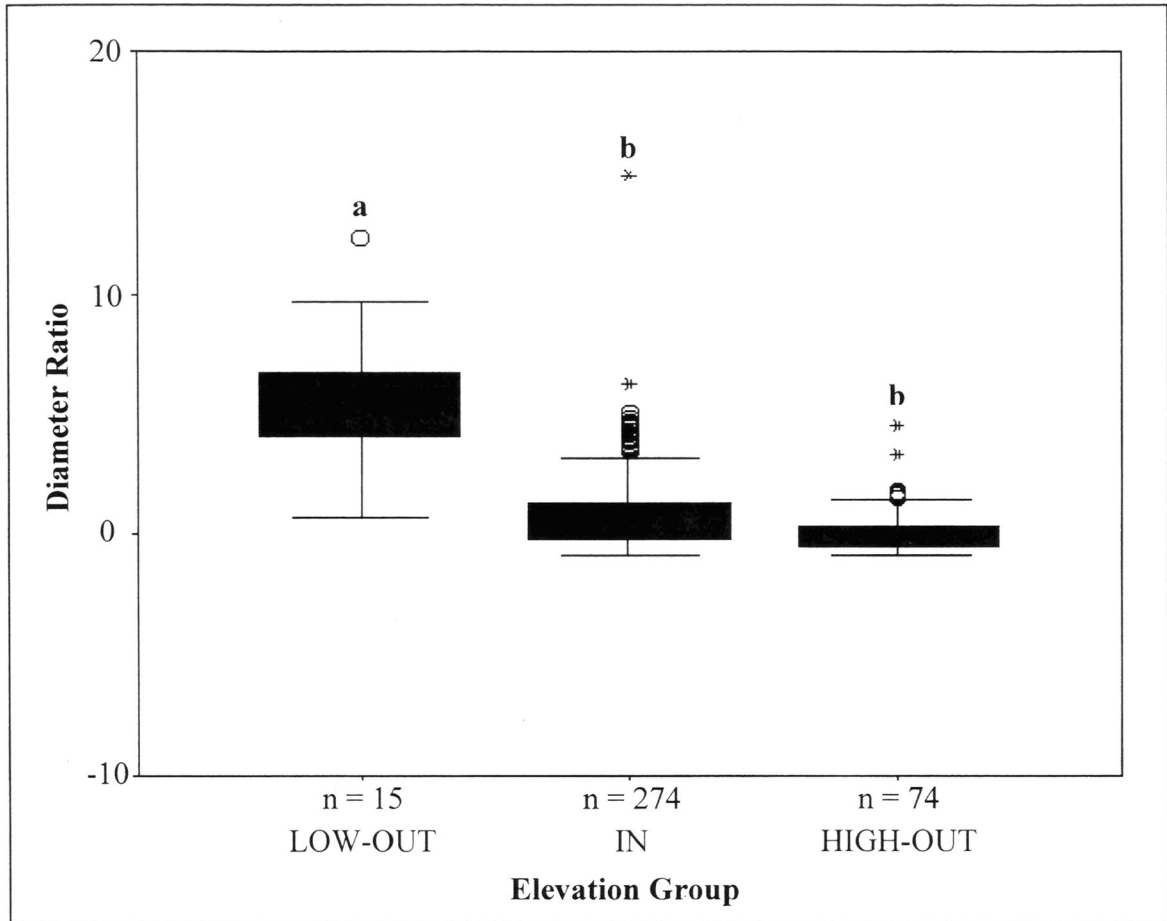


Figure 6. Growth of *Amaranthus pumilus* transplants at wk 10 at elevations below (LOW-OUT), within (IN), and above (HIGH-OUT) the 0.7 - 2.1 m elevation range described by Sellars (2001). Growth is represented as Diameter Ratio (diameter in cm at wk 10/diameter in cm at wk 2). Different superscripts denote significant differences in means ($F_{2,360} = 44.41$, $P < 0.001$). Box plots represent the median, quartiles, outliers, and extreme values for each group.

Table 1. Coefficients for the regression of transplant Diameter Ratio (diameter wk 10/diameter wk 2) with elevation (m). Regression coefficients enable prediction of plant size with elevation at each site. Constant B = y-intercept, elevation B = slope.

Transplant Site	Model	<u>Coefficients</u>			<u>95% CI for B</u>	
		B	t	P	Lower	Upper
CAHA Loran	constant	17.730	8.853	<0.000	13.776	21.683
	elevation	-5.116	-5.429	<0.000	-6.976	-3.256
CAHA Drain	constant	1.909	.264	0.792	-12.503	16.321
	elevation	4.326	1.023	0.310	-4.104	12.755
CALO Combined Spit Sites	constant	31.389	10.434	<0.000	25.440	37.339
	elevation	-15.909	-7.700	<0.000	-19.994	-11.823

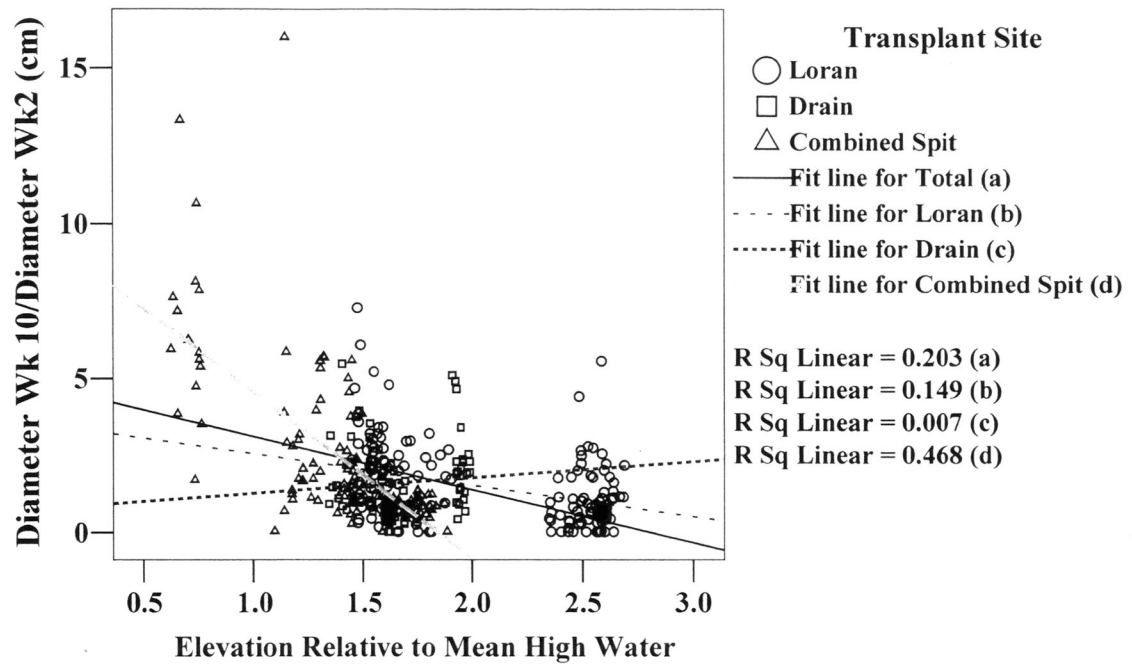


Figure 7. Scatterplot showing changes in transplant size (Diameter Ratio) with elevation. Regression lines show linear relationships between elevation and plant size across (Total a)) and within transplant sites: LORAN (b), DRAIN (c), and combined NORTH SPIT and SOUTH SPIT (Combined Spit (d)). Corresponding fit lines and coefficients of determination (R Sq) are denoted with corresponding lower case letters.

elevation barrier to plant survival. Although the lowest elevation plants, at the site protected from overwash disturbance at CALO, likely died as a result of physiological stress, their elevations were 25 cm below any other plot in the study, and disturbance seems to have influenced plant survival more than physiological stress at all other LOW-OUT and LOW-IN elevation sites. The proportion of transplants surviving at LOW-OUT and LOW-IN elevations was a fourth of that for plants in HIGH-IN and HIGH-OUT elevations. At lower elevations, except at the overwash protected site, plant sizes were much larger, transplants exhibited few signs of physiological stress, and wave overwash was observed at several sites; therefore, the loss of plants at low elevations is presumed to have resulted primarily from physical damage or removal of plants. Physical restriction of habitat by overwash at low elevations has been observed in other near-shore dune species. Barbour *et al.* (1976) studied shoreline plant distributions on 34 California maritime strand sand-substrate beaches and found overwash at the tide line to be the primary factor limiting the seaward distribution extent. Payne and Maun (1984) found overwash limited the low elevation extent of distribution in a lakeshore population of *Cakile edentula* through removal of seedlings. Mechanical disturbance from overwash, therefore, may limit the lower end of seabeach amaranth's habitat range.

Differences in survival between overwash protected and unprotected LOW-OUT elevation sites suggest some additional suitable habitat for seabeach amaranth may exist at elevations below 0.77 m relative to MHW at sites where overwash is reduced. Mean plant growth in surviving plants at the unprotected site was about twice that of plants at higher IN elevations, suggesting some LOW-OUT elevation sites may have a greater

suitability in levels of salinity, water or nutrient availability, or other edaphic characteristics. These data also suggest, however, that physiological factors may begin to influence plants at elevations approaching mean high water. Plots at the overwash protected site were unintentionally situated at elevations roughly 25 cm lower than plots at the unprotected site. Yet, based on observations of overwash, wrack-line deposition and evidence of disturbed sand, the intended overwash pattern occurred, i.e., the unprotected site experienced overwash with higher mechanical energy than the unprotected site. Still, the pattern of the response in the experiment was opposite of what was expected. Some plants in all three nearshore unprotected plots survived while no plants survived in the three protected plots. No plants at the unprotected site were observed to be chlorotic, brown, or desiccated and dead plants were largely missing or broken. Thus, burial, abrasion, and erosion, i.e., mechanical effects of overwash, are assumed to be the primary causes of mortality in the unprotected plants. Unprotected plants, however, did exhibit salt hypertrophy in leaves and stems. Salt hypertrophy occurs after prolonged salinity stress and may be a salt tolerance mechanism (Boyce 1951). So, although physical and physiological stresses may be relatively increased, LOW-OUT elevations may provide other edaphic conditions for greater growth.

Complete and rapid mortality at the sound-side protected site is likely to have resulted primarily from physiological stress. Plants at the protected site were losing leaves as early as the first census; stems were hypertrophic and the color of stems and remaining leaves became pale and/orange-brown. Elevation and topography differences are assumed to have resulted in different overwash frequencies and durations at the

overwash protected and unprotected sites, although, washed sand and wrack lines provided frequent evidence of recent flooding at both sites. Presence of the salt tolerant marsh annual *Salicornia virginica* (Zedler *et al.* 2003) suggests the protected site may have had high soil salinities, long flooding durations, or other edaphic stresses more characteristic of salt flat and marsh habitat (Mitsch and Gosselink 1993). Long duration of flooding was observed at the protected site on two separate occasions and on one occasion inundation was estimated to have lasted as long as two days (Jeff Cordes, National Park Service, pers. comm.). The topography of the ocean-side unprotected site was convex, allowing flood water to flow back toward the ocean, while the protected site was in a concave basin or swale that would pond water. Survival and growth of plants at the unprotected site suggest that there may be some additional suitable *A. pumilus* habitat at elevations lower than 0.7 m above MHW. Identification of low elevation habitat for protection or reintroductions, however, may need to include avoidance of sound-side sites and/or sites inhabited by species more common in marshes.

At HIGH-OUT sites, lower growth suggests that water, nutrients, salinity, or other edaphic factors may have the potential to restrict seabeach amaranth plant distributions. Higher survival suggests that overwash disturbance did not influence HIGH-OUT plants during this season. Transplants at LOW-OUT sites grew three times as much as transplants at IN sites while transplants at HIGH-OUT sites generally did not grow larger than their size at planting. Other researchers have measured changes in soil characteristics with elevation in maritime dunes. Martin (1954) found lower water availability, higher inputs of salt spray, and reduced vegetation cover on a New Jersey

maritime strand at elevations corresponding with HIGH-OUT elevations in this transplant study. In maritime strands, elevation increases with increased distance from shore and decreases in salinity and water availability with increased distance from shore have been widely reported (Wells and Shunk 1938, Oosting and Billings 1942, Boyce 1954, Erickson and Young 1995, Cheplick and Demetri 1999). Increased presence and competition of perennial neighbors may also explain some of the reduced success of seabeach amaranth at higher elevations (USFWS 1996, Johnson 2005). USFWS (2001) states that seabeach amaranth plants are not found more than 1 m above the toe of the dune and cites competition as one possible cause.

Low coefficients of determination (r^2) for growth and elevation at the within-site scale may suggest that site-specific factors other than elevation strongly influence plant growth, or that the relationship is non-linear. It is also possible that the limited elevation ranges represented by each site (e.g., LORAN) contributed to the low r^2 values. CALO SPIT, where the lower three elevation ranges from LOW-OUT to HIGH-IN were represented, had the highest negative linear relationship between elevation and plant growth. Also, low r^2 values at the DRAIN may have resulted from lack of surviving plants grown at low elevations. At the DRAIN site, for example, almost all of the LOW-IN elevation plants were lost when rain water ponded and inundated the lower elevation parts of the site for several days. Regardless, the strength of the regressions between elevation and plant growth was low, even across all sites, suggesting that 1) the relationship between plant growth and elevation is complex and variable across sites and/or 2) factors other than elevation *per se* influenced plant growth in this study.

Ultimately, transplant survival and growth data suggest that seabeach amaranth occupies a narrow range of elevations that closely approximates Sellars' model. Suitability of habitat and the influence of elevation may vary among sites and seashores. These data also support the conclusion that mechanical overwash disturbance and elevation-related edaphic characteristics are among factors restricting *A. pumilus* plant distributions at low and high elevations, respectively.

CHAPTER III

SALINITY AND WATER AVAILABILITY AS FACTORS AFFECTING HABITAT OF SEABEACH AMARANTH

Introduction

Abiotic factors such as soil anoxia, nutrients, salinity, and water availability are known to play a role in shaping plant distribution and abundance. Species that thrive in one site may grow poorly or even perish in nearby sites with different soil characteristics. For example, *Spartina patens* thrives in higher marsh elevations but can not tolerate anoxia in nearby low marsh soils (Bertness 1991). Tzialla *et. al.* (2005) found variation in species composition including complete exclusion of some forb species from sites along a moisture gradient in a Mediterranean pasture. The utility of water availability in defining habitat has been compared to that of light availability and temperature (Kruckeberg and Rabinowitz 1985). Gradients in abiotic factors can also influence plant distribution and abundance through effects on inter- and intraspecific competition (Wilson and Keddy 1985, Bertness 1991, Gaudet and Keddy 1995, Tzialla 2005).

Salinity and water availability also are especially important abiotic factors in marine-influenced environments, strongly influencing plant species distribution and abundance. Saline substrates can reduce germination (Woodell 1985, Khan 1991, Mariko *et al.* 1992, Clevering 1994, Khan and Rizvi 1994, Ungar 1995, Huang 2003), recruitment, growth, and survival (Larcher 1995, Lambers *et al.* 1998), and have been used to differentiate plant habitat (Naidoo and Naicker 1993, Migahid 2003). Salinity can influence water availability by reducing soil water potential (Bernstein and Hayward 1958), and water availability has been used to explain plant distributions at continental

(Bowman and McDonough 1991) and ecosystem scales (Englebrecht and Kursar 2003). Substrate water availability can influence plant species distributions at all stages of development (Clevering 1994, Walmsley and Davy 1997, Bram and Quinn 2000).

Salinity from salt spray has long been identified as a major abiotic contributor to zonation in maritime strands (Wells and Shunk 1938, Oosting and Billings 1942), possibly because salinity is highly variable throughout strand habitat. The salinity of salt spray equals that of seawater (van der Valk 1974, Barbour and DeJong 1977) and most salt spray falls within 90 m of shore (Cheplick and Demetri 1999). Overwash inundates soils with 35 ppt salinity seawater, and soil salinities increase significantly after storms (Erickson and Young 1995). High salinities resulting from salt spray or inundation may quickly be displaced by storm rainwater (Whittecar and Emry 1992), and soil salinity measurements suggest low salinity is common in the dune strand. Boyce (1954) found high salinities on the sand surface and only extremely low soil salinity concentrations 15 cm below ground on a dune strand at Long Beach North Carolina. Martin (1959) measured salinities less than 2 ppt in the foredune. Erickson and Young (1995) reported salinities in the foredune between 1 and 10 ppt, increases in salinity with proximity to shore, and salinities less than 2 ppt in 89% of the root zones of the Virginia dune annual, *Strophostyles umbellata*.

Measured low salinity tolerances in strand plants suggest that high salinities may be restricted both spatially and temporally. Strand species have been categorized as intolerant halophytes (Barbour 1970) or true glycophytes (Oosting 1945, Barbour *et al.* 1985, Christensen 1988) rather than halophytes. Baskin and Baskin (1998) reported that

for seeds of 17 halophytic beach, cliff, and foredune species, the salinities necessary to reduce germination to <10% ranged widely from 3.6 to 36 ppt. Seneca (1972) found significant differences in soil salinity tolerance in four North Carolina dune grasses. Salinities in strand habitats may be low much of the time.

Water availability has also been used to explain zonation of species in coastal dune ecosystems (McLeod and Murphy 1984, Maun 1985, Maun 1994, Ishikawa *et al.* 1995). In maritime strands freshwater may be consistently available in certain microsites. Studies suggest two general patterns of water availability in the field: 1) Soil water content is variable through the habitat, and 2) lower elevation areas, especially in front of the foredune, tend to have more available water. In his field surveys, Martin (1959) found consistently moist sand within a few centimeters of the dune surface and that soil moisture increased noticeably with proximity to water table (e.g., the foredune). Van der Valk (1974) found consistently moist soil at depths of 20 cm or more. On spatial variability, Martin (1959) found the highest water availabilities in the foredune, while van der Valk (1974) found no differences along a landward transect, sampling 20 cm below the surface. Patterns in availability of fresh and saline water seem to be present and may influence plant success and population distributions.

The especially strong influences of elevation on hydrology in dune ecosystems may explain some of the spatial variation in soil salinity and water availability. In sandy barrier island systems like on North Carolina's coast, very little surface runoff occurs; rainwater rapidly percolates through the porous sand and displaces subsurface saltwater (Whittecar and Emry 1992). This leaves relatively low salinity water available to plants

situated close to the water table. Whittecar and Emry (1992) profiled the water table reaching across Bodie Island, NC; the water table profile was lens-shaped, it was meters below the surface of the 6 – 8 m high dune peaks, and it approached the sand surface near the toe of the dunes (Figure 8). At Cape Henlopen, Delaware, Ullman *et al.* (2003) found the water table to be just below the surface of the beach. The authors observed low saline ground water, high in N and P, discharging at and below the shores waterline. Based on ground penetrating radar surveys, Ullman *et al.* (2003) also suggested that higher discharge would occur on barrier island beaches wide enough to support a larger and fresher water table and that some seepage should occur on any beach face. Fresh water discharge near shore would reduce soil salinities by displacing saltwater from tides or overwash, thus, hydrology in a given microsite may be influenced by the site's elevation relative to sea-level, by island width, and by the topography and relative elevation (water storage capacity) of the surrounding dunes. Decreased availability of water at higher elevations and increased availability of water at lower elevations may explain part of the observed relationship between elevation and patterns of distribution in maritime dune vegetation (Oosting and Billings 1942).

Elevation also influences the distribution of salinity from overwash and salt spray. Salt spray (Martin 1959) and overwash frequency (Barbour 1978) both increase with proximity to shore and the associated lower elevations. Salt spray deposition also increases on elevated surfaces such as the faces of primary dunes and clumps of grasses (Martin 1959).

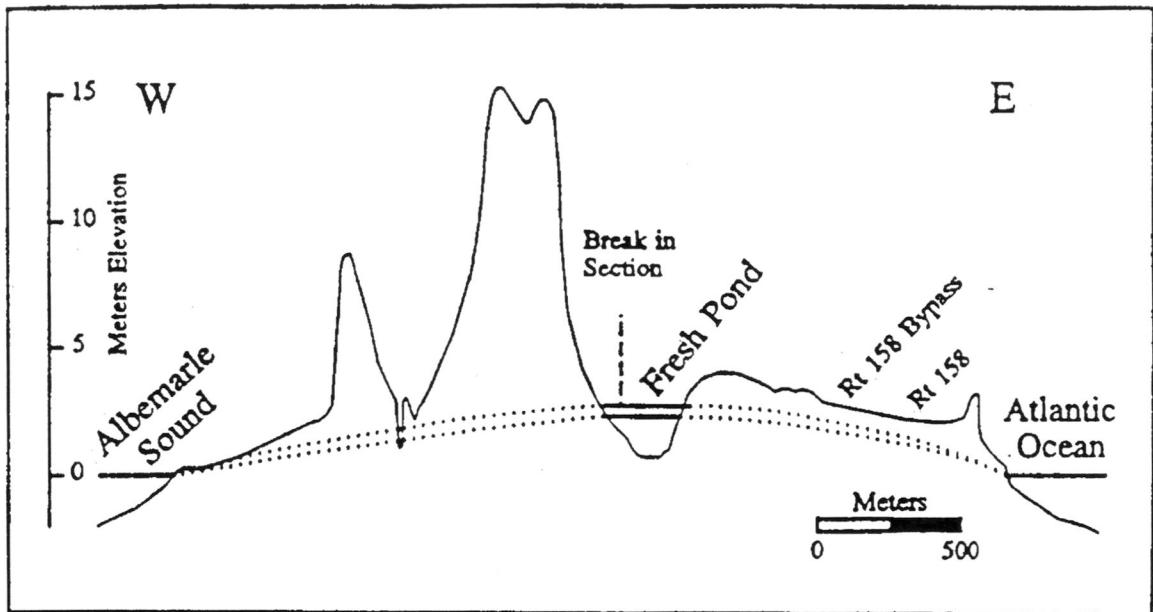


Figure 8. Water table profile of Bodie Island, NC (Whittecar and Emry 1992). Profile has 70 x vertical exaggeration. The water table can be seen breaking the surface at the pond and at a ditch and approaching the sand surface at the Albemarle Sound and Atlantic Ocean shores on each side of the island.

Results in Chapter II suggest that reduced growth in seabeach amaranth at the upper end of its elevation range may be related to increased physiological stress. Intolerance of salinity in germination and/or juvenile stages, if demonstrated, would suggest soil salinity as the potential to be factor restricting plant distributions, particularly for an annual like seabeach amaranth. Germination responses to salinity have been studied in several coastal annuals (Maun 1994, Walmsley and Davy 1997), but germination studies specifically of foredune species are limited in number. There are no known studies of tolerance to salinity or drought in juveniles of seabeach amaranth. Experimentally-induced delays in seed germination or dormancy in substrates with only moderate or low salinities may help explain restriction of seabeach amaranth to microsites, i.e., elevations above 0.77 m above MHW. Significantly reduced survival or growth in lab-grown juvenile or adult seabeach amaranth plants observed after a few days of exposure to high salinities (>20 ppt), or prolonged exposure to moderate or low levels of salinity (>5 - 10 ppt), may also help explain restriction of seabeach amaranth to elevations above 0.77 m above MHW. Similarly, experimentally-induced reductions in survival of seabeach amaranth plants exposed to moderate or low water availabilities also could help explain restriction of seabeach amaranth to lower elevation microsites, i.e., below 2.0 m above MHW.

In this chapter, I ask questions relating to seabeach amaranth success under exposure to varying salinity and water availability regimes. Specifically, how are seabeach amaranth germination, growth, and survival affected by substrate salinity and water availability?

Materials and Methods

I tested germination response of seeds of seabeach amaranth treated with five salinities and the response of laboratory-reared juvenile plants to six soil salinity and five water availability regimes in the controlled conditions of a laboratory growth chamber. I cold stratified seeds for all salinity and water experiments in a refrigerator at 4° C, on moist sand, in petri dishes, for a minimum of 12 wk to break dormancy. Seeds were obtained from two sources: 1) Agricultural Research Service-Germplasm Resources Information Network (ARS-GRIN) from David Brenner, Plant Introduction Station, Iowa State University Ames, IA, and 2) from field collections authorized by the North Carolina Plant Conservation Program and the National Park Service (NPS). I then discarded the flat and obviously dead seeds and subjected the remaining stratified seeds to their respective treatments.

Salinity and Germination. I examined the influence of five soil salinities on germination of seeds of seabeach amaranth experimentally in a growth chamber using the methods of Noe and Zedler (2000). After stratification, I randomly assigned and placed seeds into 20 - 10 cm plastic pots filled with 200 mL of beach sand. Pots were placed in a Conviron[®] model E15 growth chamber (Controlled Environments, Inc., Winnipeg, Manitoba, Canada) to maintain a controlled environment with 16 h light/8 h dark photoperiod and 30/20 °C thermoperiod. I applied saline solutions (0, 2, 5, 10, and 20 ppt) to each of five treatments consisting of four replicates of 47 seeds each. I used Instant Ocean[®] salt (Aquarium Systems Inc., Mentor, OH), and a Leica model Brix30 refractometer (Bannockburn, IL), to create and measure the concentration of the salt

solutions. I used the five saline solutions to maintain moisture in the pots and flushed all the pots thoroughly with daily watering to attempt to maintain the desired substrate salinities. I also covered each pot with a clear plastic lid to prevent water loss and increases in salinity due to evaporation.

I counted and removed all germinated seeds each third day for 30 d. I measured the response to salinity as the proportion of seeds germinating after 6 d and 30 d of treatment to test early and longer term responses. I analyzed differences in the proportion of seeds germinating using Chi-square.

Propagation of Test Plants. I applied six salinity and five water treatments to groups of growth chamber reared, 4 wk old seabeach amaranth plants to assess the effects of salinity and water availability on growth and survival. After stratification, groups of ≤ 100 seeds were placed in 10 cm plastic pots on moist sand to germinate. I used a Conviron[®] model E15 growth chamber (Controlled Environments, Inc., Winnipeg, Manitoba, Canada) to maintain a controlled germination environment with 16 h light/8 h dark photoperiod and 30/20 °C thermoperiod. As germination occurred, I transplanted each seedling to a Conetainer[®] (Steuwe and Sons, Inc., Corvallis, OR) filled with autoclaved beach sand collected from Emerald Isle, North Carolina. Plants were grown in the growth chamber for approximately 4 wk. I watered the plants with a nutrient solution of Fafard[®] 20-20-20 N - P - K, water soluble plant food (Agawam, MA), at a concentration of 15 mL nutrient per 3.8 L tap water.

I assigned plants to treatment groups randomly. I counted the number of nodes and leaves, measured the diameter of each plant treatment, and added all the

measurements to calculate a single index. I then ranked the plants based on the size index and used random sequences from the website <http://www.random.org/sform.html> to assign each plant to a treatment group. All treatment groups contained 31 plants.

Response of Juvenile Plants to Salinity. I applied six salinity treatments to groups of growth chamber reared, 4 wk old seabeach amaranth plants to assess the effects of salinity on growth and survival. I created six treatment solutions in six - 20 L carboys with combination saline and nutrient solutions with which to water plants. I used Instant Ocean[®] (Aquarium Systems Inc., Mentor, OH) to increase NaCl concentrations in five carboys to 2, 5, 10, 20, and 30 ppt. Then, I added water soluble plant food to all six carboys at a ratio of 15 mL nutrient per 3.8 L of solution. I used this method as needed to produce and maintain the solutions used for watering each treatment group. All saline dilutions were performed using a nutrient solution with the same concentration to maintain equal nutrient concentrations among saline solutions. I watered the plants in each of the treatment groups to field capacity, once each day. I subjected the plants to a 7 d long salinity treatment cycle following the methods of Bram and Quinn (2000). This method was chosen to simulate natural rainwater flushing and to decrease salt accumulation. On day 1, treatment groups were saturated with half-strength saline solutions. On days 2 – 4, full-strength solutions were applied and on days 5 – 7, all plants were flushed with a salt-free nutrient solution.

Response of Juvenile Plants to Water Availability. I used a modified version of Gagne and Houle's (2002) and Houle's (1997) water treatment experiments to test the response of *Amaranthus pumilus* to different drought regimes. Gagne and Houle (2002)

applied various watering regimes to two perennial marine foredune taxa (*Honckenya peploides* and *Elymus mollis*). I treated seabeach amaranth plants with five different watering cycles.

Plants were grown in the growth chamber and subjected to treatments of five watering frequencies: 1) once each day (zero days without water, 0 DWW), 2) each second day (one day without water, 1 DWW), 3) each third day (two days without water, 2 DWW), 4) each fourth day (three days without water, 3 DWW) or 5) each fifth day (four days without water, 4 DWW). I fertilized containers using pellets of Osmocote® Vegetable and Bedding Smart Release® Plant Food (The Scotts Company, Marysville, OH), fertilizer analysis 14-14-14 N - P - K, attempting to buffer the varying influence differing soluble fertilizer-based watering regimes may have had on nutrient application. I applied fertilizer pellets based on the manufacturer's recommended volume per soil area: 15 mL/0.3716 m² (3 tablespoons/4 ft²) or about three full size pellets per container.

I estimated the minimum percent field capacities that resulted at the most extreme point of drought in each water treatment by measuring water loss in test Conetainers®. Without plants, these test Containers® were exposed to the water availability experiment's light, temperature, and watering regimes. Percent field capacity for the treatment 4 DWW was extrapolated from a cubic regression line fit to the data because the additional treatment was added after the treatment test. The minimum percent field capacities experienced in each drought cycle were estimated to be 97, 80, 60, 42, and 22 % for 0 – 4 DWW, respectively. I converted the calculated mean percent field capacities to gravimetric water content. I then estimated that the soil water potentials

used in this experimental ranged from field capacity (0.0 MPa) to the permanent wilting point for most herbaceous plants (- 1.5 MPa) (Reynolds *et al.* 2002) based on comparison with a graph of soil water potential versus gravimetric water content.

Plant Response and Statistical Analyses. I measured plant size response to salinity and water treatments three ways: diameter of rosette, number of leaves, and number of nodes. I measured all plants three times: at 0 weeks, 4 weeks, and 8 weeks. I used analysis of variance to compare natural log transformed mean node number, cubed root leaf number, and cubed root diameter among treatments (SPSS vers. 11.0, SASS institute, Cary, NC). I used Tukey's post hoc to detect significant differences in plant size between treatment pairs, and Chi-square analysis to compare germination and survival between and among treatments.

Results

Germination Responses to Salinity. Mean percent germination after 6 d was 83.50 ± 4.41 (mean $\pm$ SE, $n = 47$) in 0 ppt, 61.25 ± 5.12 ($n = 47$), in 2 ppt, 19.75 ± 8.86 ($n = 47$) in 5 ppt, 0.50 ± 0.50 ($n = 47$) in 10 ppt, and 0 ($n = 47$) in 20 ppt salinity treatments. On d 6, significant differences were detected in germination between each possible Chi-square treatment comparison (Table 2). Mean percent germination after 30 d was 91.75 ± 1.49 ($n = 47$) in 0 ppt, 83.50 ± 0.96 ($n = 47$) in 2 ppt, 76.50 ± 2.72 ($n = 47$) in 5 ppt, 11.25 ± 3.33 ($n = 47$) in 10 ppt, and 0 ($n = 47$) in 20 ppt salinity treatments. Final germination on d 30 was not significantly ($n = 47$) in 20 ppt salinity treatments. Final germination on d 30 was not significantly different between 2 and 5 ppt treatment groups; all other possible Chi-square comparisons between treatments showed significant differences in

Table 2. Chi-square comparisons between proportions of seabeach amaranth seeds germinating in pairs of salinity treatments after 6 d.

Comparison	# germinated per treatment in each comparison (n = 188)	X ²	df	Significance
0 ppt vs. 2 ppt	157 vs. 115	23.45	1	$P < 0.001$
0 ppt vs. 5 ppt	157 vs. 37	153.35	1	$P < 0.001$
2 ppt vs. 5 ppt	115 vs. 37	67.187	1	$P < 0.001$
2 ppt vs. 10 ppt	115 vs. 1	162.02	1	$P < 0.001$
5 ppt vs. 10 ppt	37 vs. 1	37.94	1	$P < 0.001$

germination (Table 3).

Survival and Growth Responses to Salinity. Statistically significant differences were detected among salinity treatments in the number of plants surviving ($X^2 = 50.8$, $df = 4$, $P < 0.05$) (Figure 9). Survival was highest in salinities ≤ 10 ppt ($\geq 94\%$), lower after treatment with 20 ppt saline (74%) and lowest in salinities of 30 ppt saline (52%). Analysis of variance detected significant differences among salinity treatments in mean number of leaves ($F = 382.19$, $df = 5, 153$, $P < 0.001$) (Figure 10), mean number of nodes ($F = 652.31$, $df = 5, 153$, $P < 0.001$) (Figure 11), and mean plant diameter ($F = 287.28$, $df = 5, 153$, $P < 0.001$) (Figure 12). Mean leaf number, node number and diameter increased from the 0 ppt to the 2 ppt treatment and then decreased with increased salinity. Plants in the 2 ppt treatment group had the highest mean number of leaves, 133.65 ± 4.00 ($n = 31$), the highest mean number of nodes, 101.06 ± 2.29 ($n = 31$), and the highest mean crown diameter, 22.75 ± 0.47 ($n = 31$). Tukey's post hoc tests showed significantly higher mean number of leaves ($P < 0.001$), mean number of nodes ($P < 0.001$), and mean plant diameter ($p < 0.001$) for plants grown in 2 ppt relative to plants in 0 ppt. Post hoc tests also showed significantly higher mean number of leaves ($P < 0.001$), mean number of nodes ($p < 0.001$), and mean plant diameter ($P < 0.001$) in plants grown in 2 ppt relative to plants in 5 ppt. No significant differences were detected between the 0 ppt and 5 ppt groups. All other pairwise differences in mean leaf number between treatments were significant. Plants in the 30 ppt salinity treatment group had the lowest mean number of leaves, 5.94 ± 0.76 ($n = 16$), number of nodes, 8.19 ± 0.40 ($n = 16$), and smallest crown diameter,

Table 3. Chi-square comparisons between proportions of seabeach amaranth seeds germinating in pairs of salinity treatments after 30 d.

Comparison	# germinated per treatment in each comparison (n = 188)	X ²	df	Significance
0 ppt vs. 2 ppt	173 vs. 157	6.341	1	$P < 0.02$
0 ppt vs. 5 ppt	173 vs. 144	16.91	1	$P < 0.001$
2 ppt vs. 5 ppt	157 vs. 144	2.81	1	$P < 0.10$
2 ppt vs. 10 ppt	157 vs. 21	197.32	1	$P < 0.001$
5 ppt vs. 10 ppt	144 vs. 21	163.39	1	$P < 0.001$

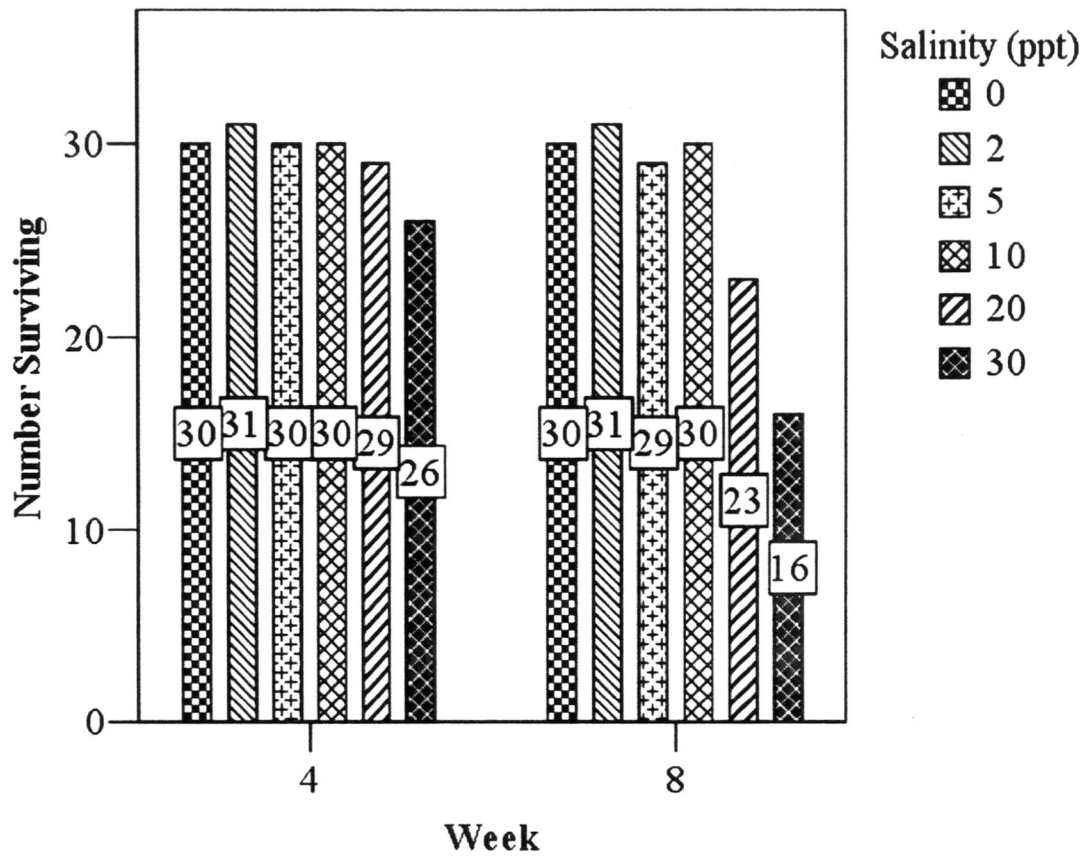


Figure 9. Survival of *Amaranthus pumilus* watered with saline solutions of 0, 2, 5, 10, 20, and 30 ppt for 8 wk; 31 plants were grown in each treatment. Treatments receiving 0 and 10 ppt salinities had the same number of plants surviving at wk 4 and wk 8.

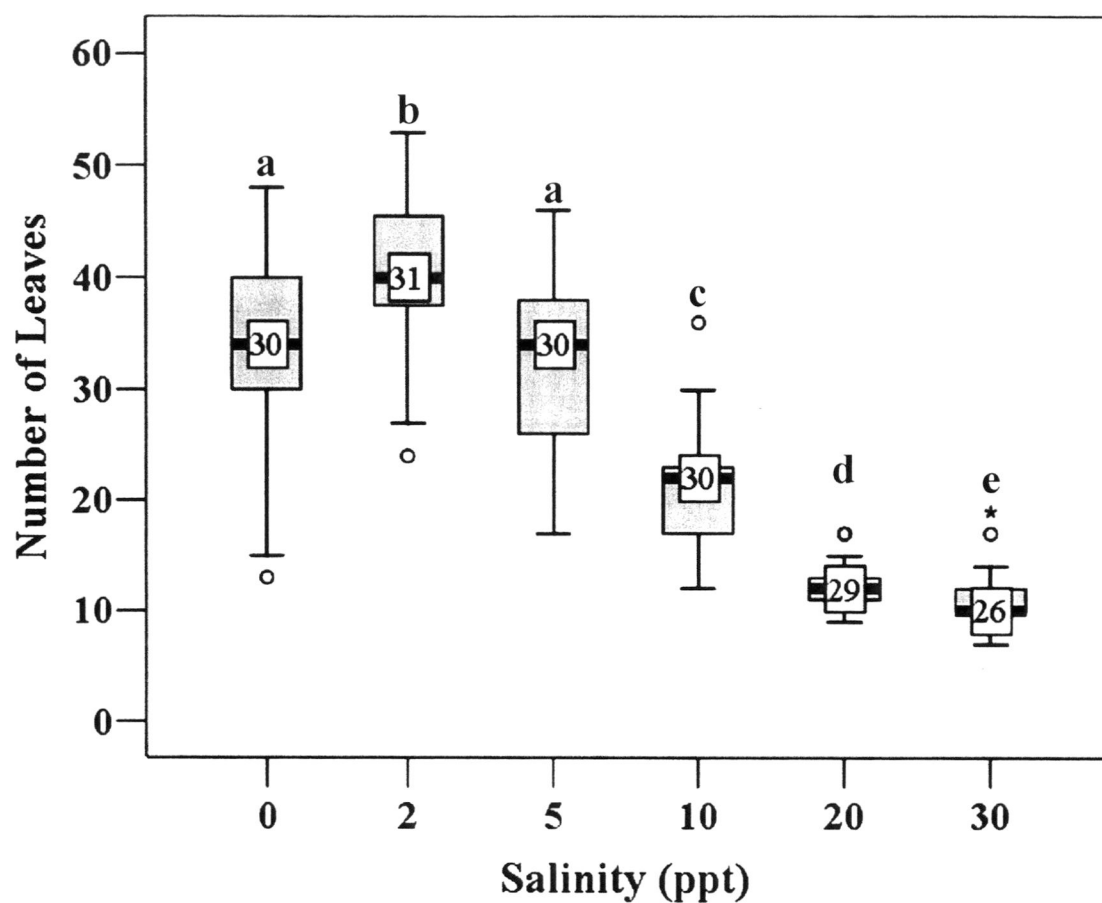


Figure 10. Mean leaf number of *Amaranthus pumilus* plants grown at six salinities. Box plots depict the median, quartiles, maximum, minimum, outliers, and sample sizes.

Homogenous superscripts denote equal means (Tukey's post hoc test, $P \leq 0.05$).

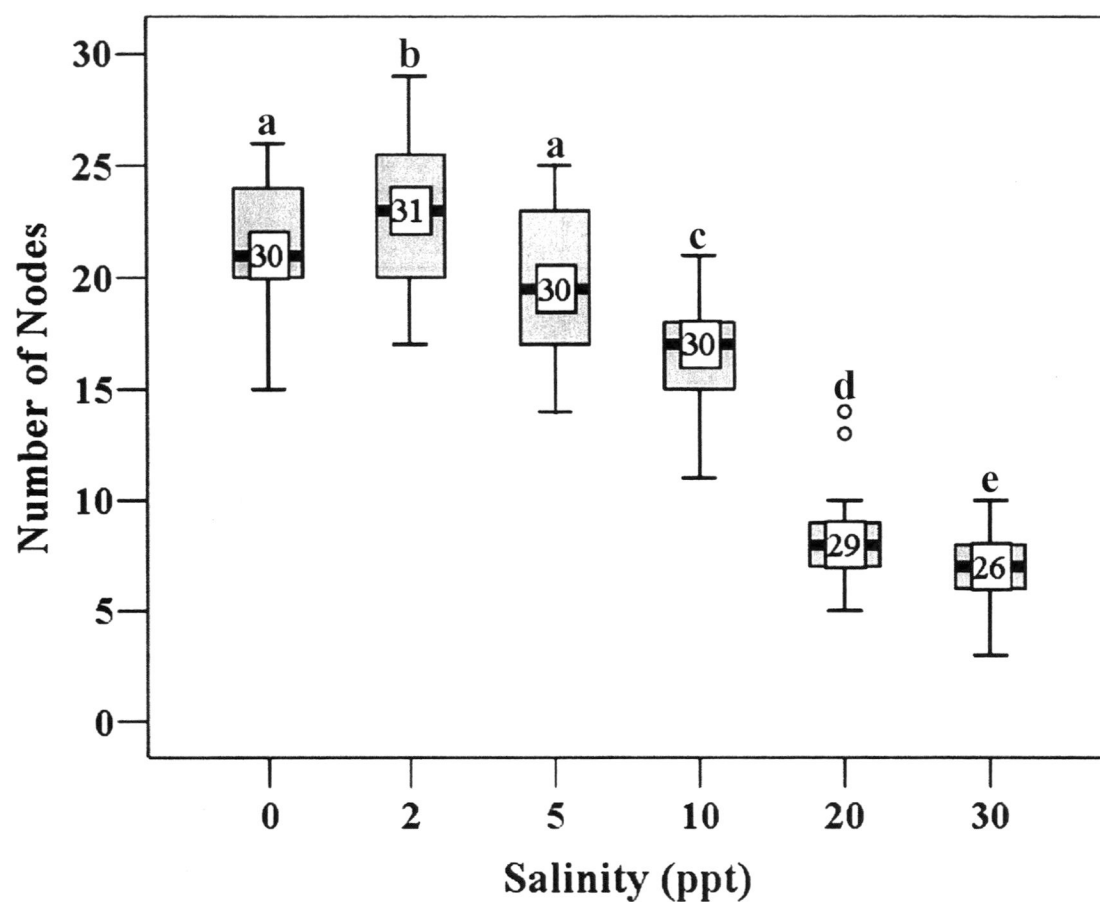


Figure 11. Mean number of nodes in *Amaranthus pumilus* plants grown at six salinities.

Box plots depict the median, quartiles, maximum, minimum, outliers, and sample sizes.

Homogenous superscripts denote equal means (Tukey's post hoc test, $P \leq 0.05$).

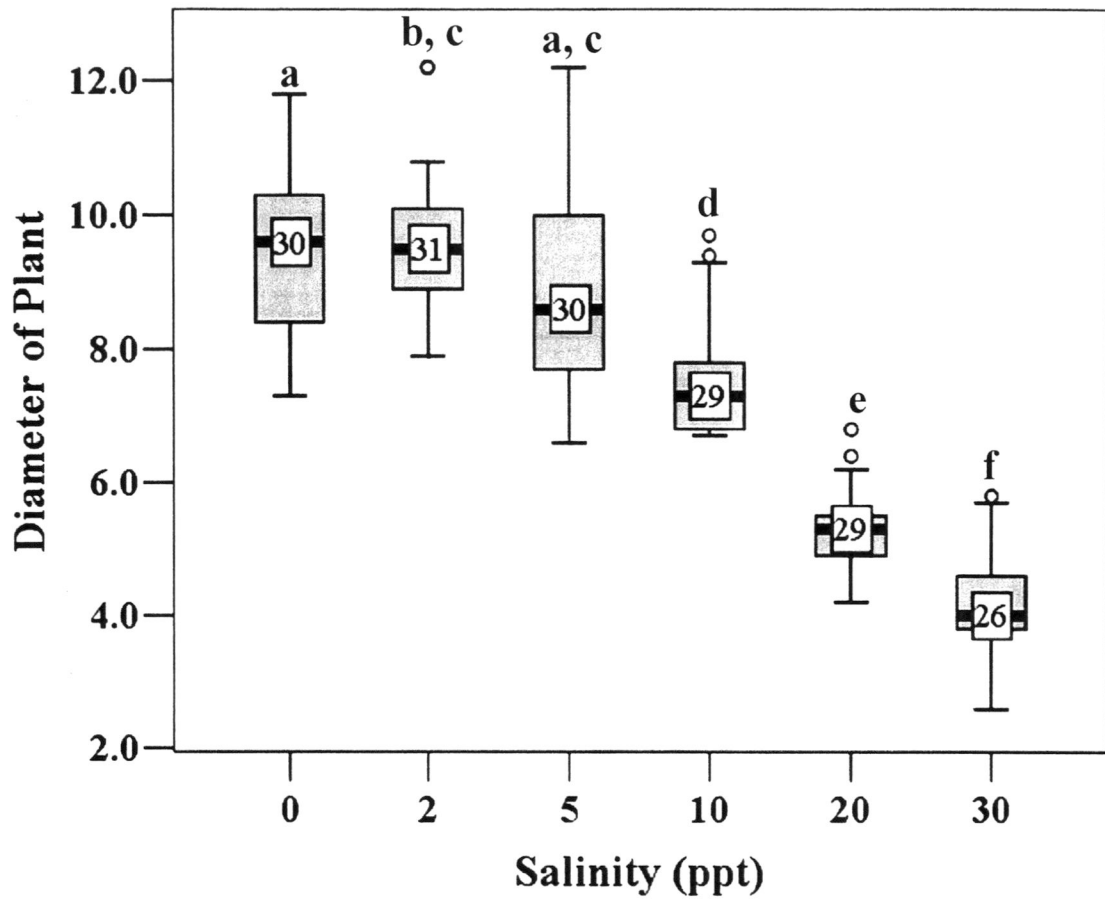


Figure 12. Mean crown diameters of *Amaranthus pumilus* plants grown at six salinities.

Box plots depict the median, quartiles, maximum, minimum, outliers, and sample sizes.

Homogenous superscripts denote equal means (Tukey's post hoc test, $P \leq 0.05$).

Survival and Growth Responses to Water Availability. Statistically significant differences were detected in the number of plants surviving among groups receiving 1, 2, 3, and 4 DWW ($X^2 = 7.9462$, $df = 3$, $P < 0.05$, Figure 13). Significant differences in survival were also detected when examining only among the three most extreme drought treatments, 2, 3, and 4 DWW (Chi-square = 6.7122, $df = 2$, $P < 0.05$). Survival was highest in groups receiving ≤ 2 DWW ($\geq 97\%$), lower after 3 DWW (68%), and lowest after 4 DWW (52%).

Analysis of variance detected significant differences among water treatments, in mean number of leaves ($F = 37.117$, $df = 4, 126$, $P < 0.001$, Figure 14), mean number of nodes ($F = 38.470$, $df = 4, 122$, $P < 0.001$, Figure 15), and mean plant diameter ($F = 19.633$, $df = 4, 126$, $P < 0.001$, Figure 16). Mean leaf number, node number, and diameter decreased with increased drought (DWW). Plants in the 0 DWW treatment group had the highest mean number of leaves, 32.65 ± 2.34 ($n = 31$), the highest mean number of nodes, 33.90 ± 1.91 ($n = 31$), and the highest mean crown diameter, 10.06 ± 0.48 ($n = 31$). Plants treated with 4 DWW had the lowest mean number of leaves, 12.86 ± 0.82 ($n = 14$), number of nodes, 13.64 ± 0.75 (mean $\pm$ SE, $n = 14$), and smallest crown diameter, 5.72 ± 0.31 (mean $\pm$ SE, $n = 14$). Tukey's post hoc tests showed no significant differences for any plant size metric between plants receiving 0 DWW and 1 DWW ($P \geq 0.1$). Mean number of leaves, number of nodes, and plant diameters were significantly higher in the 0 DWW watering regime than in the 2 DWW ($P < 0.05$), 3 DWW ($p < 0.001$), and 4 DWW ($P < 0.001$) regimes. Mean leaf and node numbers were significantly higher in the 2 DWW watering regime than in the 3 DWW regime

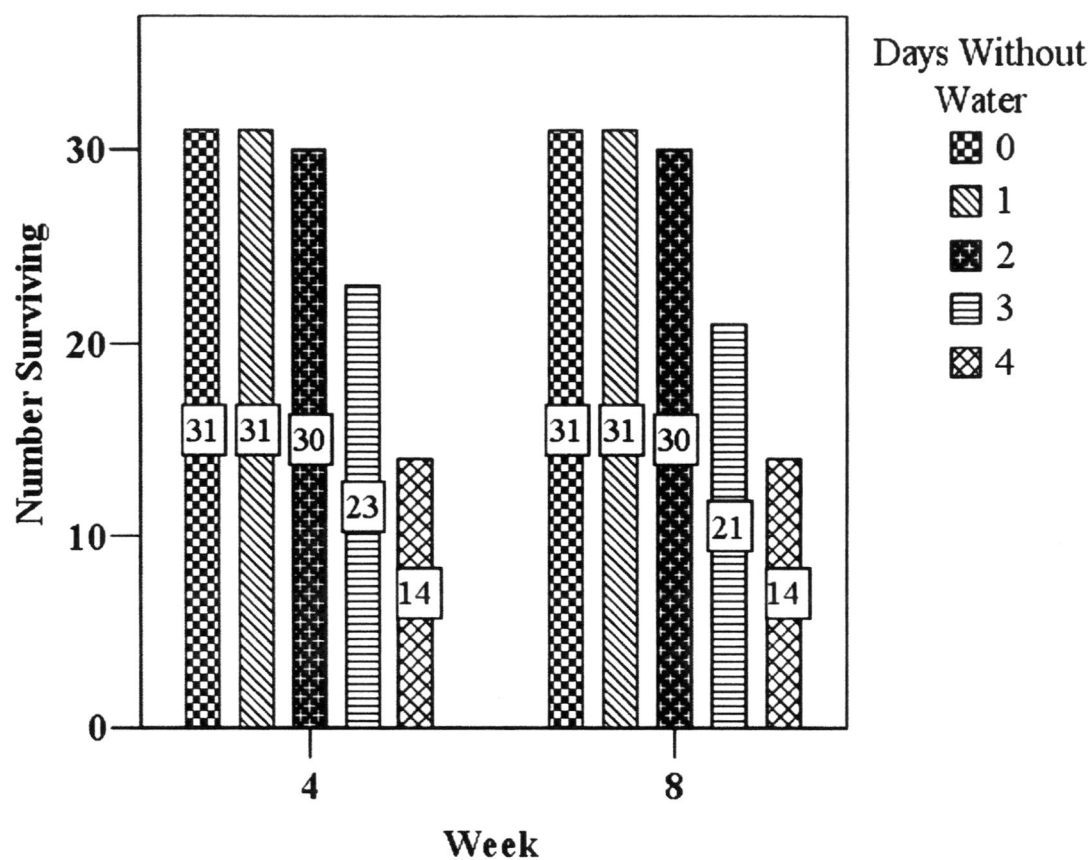


Figure 13. Survival of *Amaranth pumilus* plants grown at five watering regimes. Plants were subjected to regimes of 0, 1, 2, 3 and 4 DWW; 31 plants were grown in each regime for 8 wk. All plants receiving 0 and 1 DWW survived for the duration of the experiment.

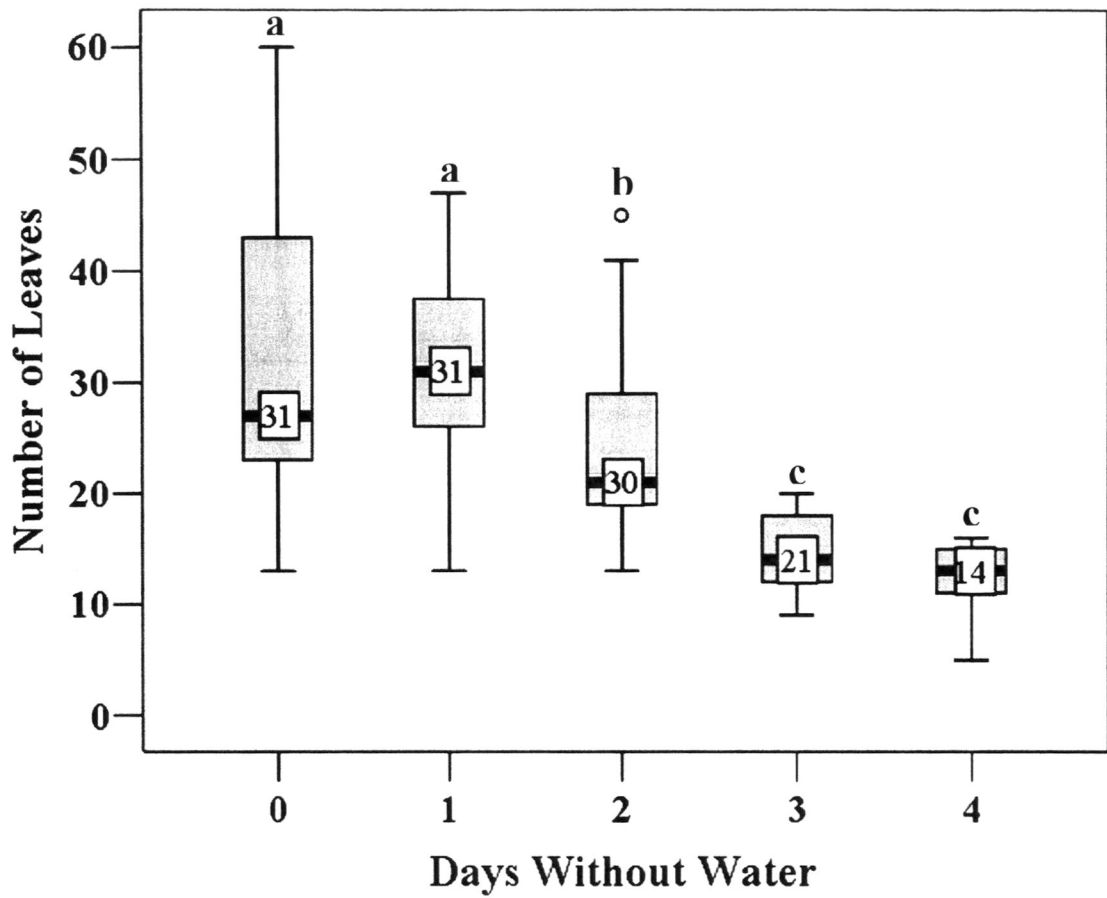


Figure 14. Mean leaf numbers of *Amaranthus pumilus* grown at five watering regimes. Box plots depict the median, quartiles, maximum, minimum, outliers, and sample sizes. Homogenous superscripts denote equal means (Tukey's post hoc test, $P \geq 0.05$).

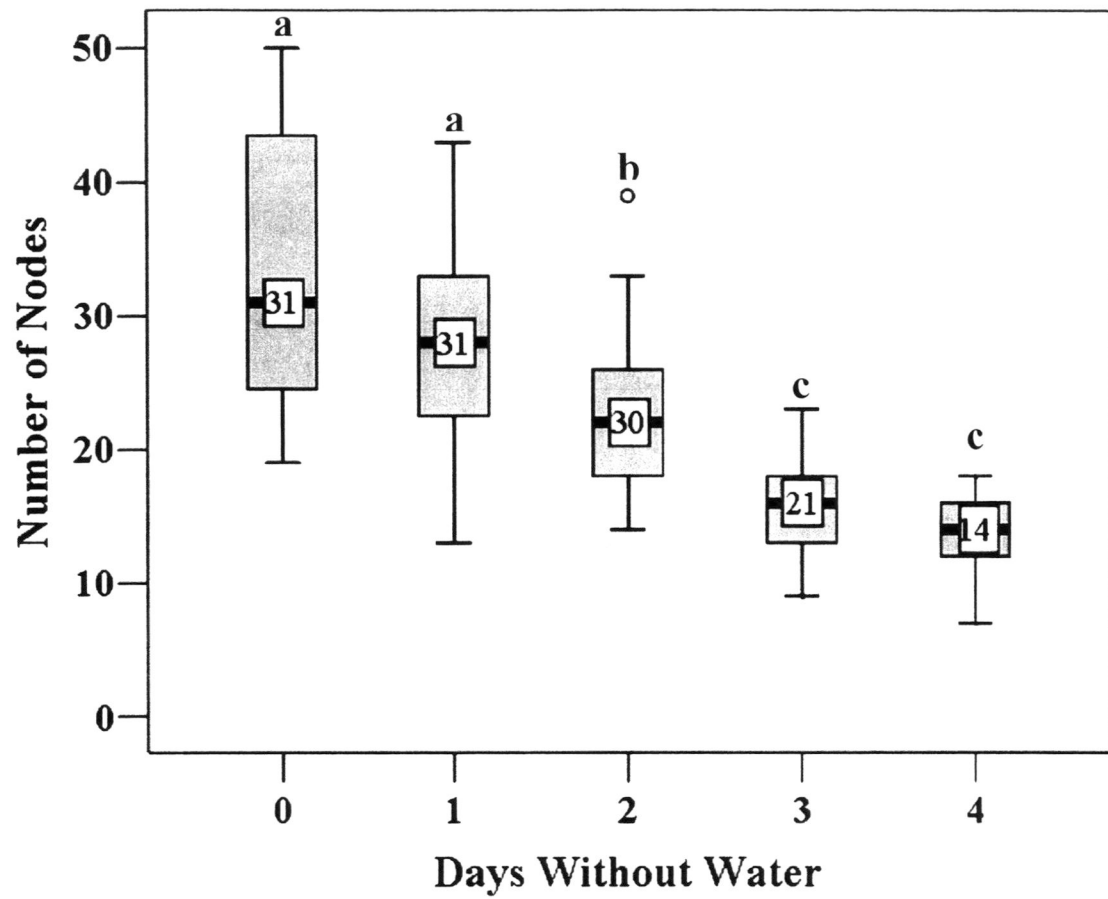


Figure 15. Mean number of nodes of *Amaranthus pumilus* grown at five watering regimes. Box plots depict the median, quartiles, maximum, minimum, outliers, and sample sizes. Homogenous superscripts denote equal means (Tukey's post hoc test, $P \geq 0.05$).

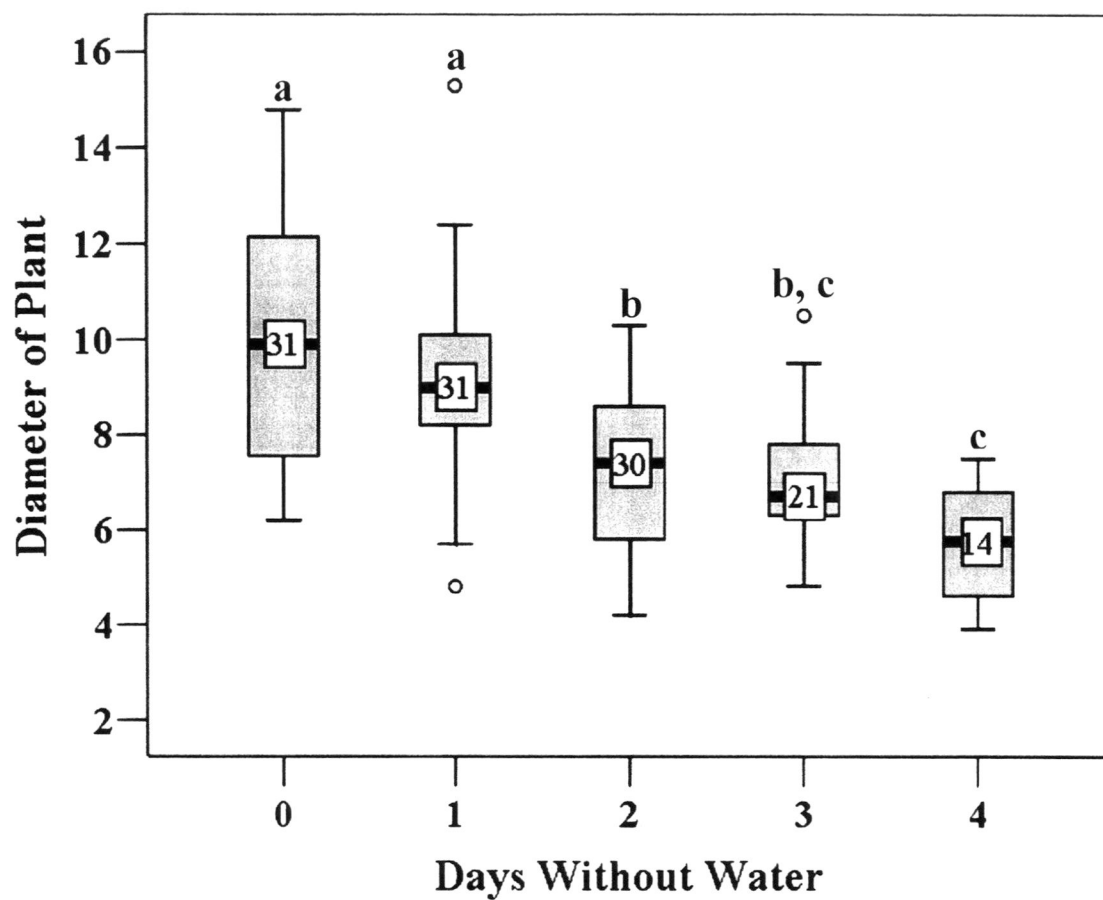


Figure 16. Mean crown diameters of *Amaranthus pumilus* grown at five watering regimes. Box plots depict the median, quartiles, maximum, minimum, outliers, and sample sizes. Homogenous superscripts denote equal means (Tukey's post hoc test, $P \geq 0.05$).

($P < 0.05$); mean diameter, however was not significantly different ($P < 0.05$). No significant differences were observed for any metric between plants in the 3 DWW compared to the 4 DWW regimes.

Discussion

This study demonstrates that, in controlled environments, although seabeach amaranth can tolerate high salinities, it only grows well in soils with moderate to low salinities. The observed decreases in germination, growth, and survival at higher salinities, suggest that, in continuous exposure, seabeach amaranth is only tolerant of soil salinities below 10 ppt and that plants grow best in salinities below 5 ppt. On the short term, plants can tolerate salinity as high as seawater (30 ppt). These results agree with other research showing strand plants to be intolerant halophytes or true glycophytes (Oosting 1945, Barbour 1970, Barbour *et al.* 1985, Christensen 1988).

A limited tolerance to salinity in seabeach amaranth is not surprising when the low field salinities reported in other studies are considered. Salinities in maritime dune and foredune soils are reported to be less than 2 ppt normally (Martin 1959, Mariko *et al.* 1992, Erickson and Young 1995), or between 2 and 6 ppt (Ishikawa *et al.* 1995). Maritime dunes are close to the ocean, however, and it is not surprising that salinities are also spatially variable (Oosting and Billings 1942, Mariko 1992). Salinity stress influences population distributions (Larcher 1995, Lambers *et al.* 1998) and my experiment suggests limited salinity tolerance in seabeach amaranth. Therefore, salinity may be among factors having a strong influence on the distribution of seabeach amaranth especially at the lower limits of its elevation range.

Results from the germination experiment provide additional strong evidence for limited salinity tolerance in seabeach amaranth. Germination greater than 20% occurred only in salinities at or below 5 ppt, and germination was nearly or completely inhibited in salinity at or above 10 ppt. These results suggest that seeds of seabeach amaranth may remain dormant until substrate salinity levels are reduced to tolerable levels, potentially by dilution and rinsing of salinity in the soil by rainwater or by storm swash removing the seeds to a lower salinity site. Dormancy, induced by soil salinity, may suggest temporal or spatial fluctuations in soil salinity. Horizontally-oriented leaves like those of seabeach amaranth receive ten times less salt-spray than vertically oriented leaves of grasses, (Barbour 1978) potentially allowing for a reduced salinity exposure. The phenology of seabeach amaranth may also allow for a reduced exposure to salinity as it does in some other salt tolerant species (Zedler *et al.* 2003). The April through June growing season of seabeach amaranth (Bucher and Weakley 1990) occurs between spring and fall equinoctial high tides, a period of relatively reduced risk of overwash (Ignaciuk and Lee 1980). Weather patterns common to southeastern shores may result in periods of varying soil salinity. Overwash from nor'easter storms usually occurs in the spring before seabeach amaranth germination, and hurricanes normally occur during or after seed set. Also, the equinoctial high tides occur before and after the growing season of seabeach amaranth, resulting in reduced risk of inundation during the summer months. Seed dormancy studies are greatly needed in this species and may expose salinity-induced dormancy as an adaptation to longer term temporal fluctuations in soil salinity.

Tolerances to salinity in germination were similar to tolerances in growth. This

matches results Woodell (1985) and Mariko *et al.* (1992) found in studies of salinity tolerances in other coastal plants. In a study of the North Carolina maritime strand annual *Ammophila breviligulata*, only 33 % of seeds of germinated and plants grew very little after exposure to 10 ppt salinities (Seneca and Cooper 1971). Tests showing low salt tolerance in a species suggest low salinity in that species' habitat (Pearch and Ustin 1984, Schat and Scholten 1986, Earle and Kershaw 1989, Zedler 1990, Ishikawa *et al.* 1991). Therefore, these data suggest that soil salinities in natural seabeach amaranth habitat also may be low, although, much needed field measurements of soil salinity are the most accurate indicator of the soil salinities experienced by plants.

Plants were significantly larger in 2 ppt than in 0 ppt soil salinities. This was unexpected because increases in salinity generally increase stress by reducing water availability (through reduced water potential), and increase Na ion toxicity (Bernstein and Hayward 1958). Salt tolerance, however, may increase water use efficiency (Glenn and Brown 1998) and seabeach amaranth plants are known to tolerate several hours of inundation with seawater in the field (Sellars, pers. com.). Also, soil salinity is known to increase growth rates and water use efficiency in some annuals, particularly under drought conditions (Richards 1992). Furthermore, members of the family Amaranthaceae are known to use the C4 photosynthetic pathway (Stowe and Teeri 1978); C4 plants have been shown to reach higher growth rates with trace amounts of Na than without (Subbarao *et al.* 2003). It is also possible that the observed responses to salinity were influenced by variations in growing conditions inherent in the experimental design. Increased growth in the low salinity treatments may have been influenced by small

differences in pH detected between the salt free control solution and the salt-containing watering solutions. The watering solution for the control group (0 ppt) did not receive any salt and had a pH of 7.08. The saline solutions 2 – 30 ppt had pH values of 6.70, 6.70, 6.68, 6.64, and 6.62, respectively. It is possible that lower pH resulted in the observed increases in growth in the 2 ppt treatment rather than a preference or need for salinity.

These experiments represent the first analysis of salinity tolerance in seabeach amaranth. In general, results of these experiments show that seabeach amaranth plants are intolerant of high salinities and suggest this species requires a low saline environment to be successful. Together, observed patterns of soil salinity in beach strand habitats and this study suggest that salinity may play a role in determining both high and low elevation habitat boundaries for amaranth populations.

In contrast to a possible “preference” for slightly elevated salinities, water requirement for seabeach amaranth should be assumed to be generally high but also quite variable if based on the results in this drought experiment. Plants grew larger in the highest water availability regimes yet quite poorly in the low availability regimes. The decreases in growth and survival at lower water availabilities demonstrated in this experiment suggest that, under prolonged exposure, seabeach amaranth is only tolerant of moderate drought. The percent water capacities experienced by plants in the most extreme drought regime were above the normal wilting point for herbaceous plants. This suggests that seabeach amaranth’s most suitable habitat may only be mildly water limited most of the time.

Survival results may suggest that seabeach amaranth is adapted to endure dry soil conditions at least occasionally. Survival in the most extreme drought regime was quite high, with roughly half of the plants surviving. The physiology of close relatives of seabeach amaranth and several of its neighbors also suggests a potentially water limited habitat. Of the nine North American dicotyledonous families having members known to use the C4 photosynthetic pathway (Stowe and Teeri 1978), four, including the Amaranthaceae, have representatives in the maritime strand. C4 plants have higher water use efficiency than C3 species (Ehleringer and Monson 1993). Thus, the habitat of seabeach amaranth is likely to have limited water availability, at least occasionally.

Successful and vigorous recovery from drought must accompany survival for drought tolerance in seabeach amaranth habitat to be supported. Recovery from drought was not examined in this study; however, it is suspected based on personal observations that seabeach amaranth plants recover quite well from severe drought. Discarded and neglected plants from unrelated experiments have been observed to return to rapid growth after watering was resumed.

The percent field capacity minimums experienced by the plants likely decreased through time as the plants grew larger and transpiration increased. The percent field capacity minimums also likely decreased more for larger plants than for smaller plants and could have had an increasingly stronger affect through time on the treatment groups receiving the most water. If water treatment methods that maintained soil water content based on weight had been used, greater differences among treatments in mean plant size may have resulted. When combined with existing knowledge about vertical and

horizontal patterns of water availability in maritime strands, the results of this drought tolerance study suggest water availability may be among the key edaphic parameters shaping seabeach amaranth habitat

Hopefully, the salinity and water availability studies I present here will lead to further studies of seabeach amaranth and its habitat. Measurement of salinity and soil water content in the field at varying depths, across sites, and through time are greatly needed for defining habitat for seabeach amaranth and other strand plant species. Experimental analyses are needed of seabeach amaranth germination responses to different water availabilities, salinities, and combinations of water availability and salinity. *In situ* watering and salinity treatments would also likely provide useful information about seabeach amaranth and its habitat.

The growth chamber experiments presented in this chapter of my thesis have demonstrated that seabeach amaranth responds strongly to relatively low salinities and moderate reductions in water availability. These data suggest salinity and water availability may have the potential to influence distributions of seabeach amaranth by reducing germination, growth, and survival.

CHAPTER IV

PLANT DISPERSION AND HABITAT AREA OF SEABEACH AMARANTH AT CAPE LOOKOUT AND CAPE HATTERAS NATIONAL SEASHORES.

Introduction

Habitat loss is the most significant cause of population declines (Chapin *et al.* 1997, Meffe and Carroll 1997, Vitousek *et al.* 1997). Species with high habitat specificity such as rare coastal taxa are more likely to suffer extinction or population loss with loss of habitat (Vitousek *et al.* 1997, Zedler *et al.* 2001). Modeling suitable habitat, therefore, has become an integral part of species-based conservation (Chapin *et al.* 1996, Wiser *et al.* 1998, Matter 2003). Models are particularly useful for identifying temporal variability and overall change in habitat size through time (Crawley 1990, Velazquez 1996), narrowing searches for existing populations, and for finding restoration and reintroduction sites.

Use of geographic information systems (GIS) technology and statistical analyses has become integral in creating habitat models (Dunning *et al.* 1995, Kobler *et al.* 2000, Debljak *et al.* 2001). GIS assembles categories of information about habitat, such as elevation, soil type, or rainfall as layers. Information in each layer often is presented as a grid with each cell in the grid containing a value appropriate to its location on the grid (Dunning *et al.* 1995). For example, in an elevation layer, each cell would provide the elevation value for that location in the layer. Overlaying global positioning system (GPS) coordinates for individuals of a study species enables extraction and analysis of the elevation, or other data, from layers under each GPS position. There are many examples of GIS-based plant habitat mapping, including coastal environments. Young *et al.* (1995)

mapped *Myrica cerifera* thicket expansion through time on a Virginia barrier island using aerial false color infrared photos. Buell *et al.* (1995) used mapped invasion of *Ammophila arenaria* into central and northern California beaches based on a combination of historical records and a series of black and white photos. Underwood *et al.* (2003) mapped the distribution of invasive plants in a coastal dune scrub community in central California using the light spectrum signatures of each plant and aerial light spectrum images.

Habitat for the maritime dune fugitive seabeach amaranth has also been modeled (Sellars 2001, Jolls and Sellars, 2000). Habitat loss is the primary reason for precipitous declines in seabeach amaranth populations in North Carolina (Bücher and Weakley 1990, USFWS 1996). Sellars' (2001) model uses three data layers: 1) Light Detection and Ranging Data (LIDAR), 2) panchromatic (black and white) passive reflectance images (reflectance), and 3) GPS positions of naturally-occurring plants.

LIDAR elevation data are recorded by a laser transmitter-receiver mounted in the belly of a low flying air craft. The transmitter sends very short laser pulses toward the ground; the time it takes for each pulse to be reflected back to the sensor determines the distance to each pulse's reflection point on the dune or vegetation surface below. Distances are recorded for multiple points of reflectance from the surface. The altitude and horizontal location of the aircraft are determined using a high accuracy onboard global positioning system (GPS). Laser pulses are sent out in a circular scanning pattern so that the sensor receives data for a swath of the surface below the aircraft during each pass over the beach. Swath width varies with aircraft altitude; several passes over each

beach are made and swaths are combined to model the full beach width.

Reflectance data were used in Sellars' model to map spatial patterns of vegetation. Reflectance data are collected simultaneously with LIDAR and are considered "passive" because the sensor receives ambient sun-light reflected off of the ground surface rather than using an artificially-created light source. Each grid cell in a reflectance image has a value ranging from 0 to 255, with 0 indicating the lowest reflectance and 255 indicating the highest reflectance associated with open sand and low vegetation cover.

Sellars' model determined the range of LIDAR and reflectance values associated with GPS locations of the naturally-occurring *Amaranthus pumilus* plants in his study. He created a model of habitat that maximized the proportion of study plant locations encompassed by the model while minimizing the proportion of dune strand area included as habitat by the model. Sellars' model includes areas with an elevation range of 0.77 to 2.00 m above mean high water that also have reflectance values higher than 170.

In this chapter of my thesis, I ask: 1) what is the spatial distribution of seabeach amaranth within its habitat, and 2) what is the extent of seabeach amaranth habitat at Cape Lookout and Cape Hatteras National Seashores? I also make comparisons between sites and among years with available elevation data. In the first part of this chapter I study the dispersion of plants within areas Sellars' model defines as habitat. Mapped natural plant locations seem aggregated at smaller sites within the larger model habitat area. Information on the dispersion of *A. pumilus* may lead to improvements in the model and better understanding of seabeach amaranth and its habitat. Distribution of

plants evenly throughout habitat predicted by the model would suggest that the most important habitat variables are being used and/or that those variables are being used in a successful way. If plants are aggregated then there may be additional factors determining habitat suitability. A third possibility is that the model is successfully predicting habitat, and that other factors such as dispersal or limited seed banks are influencing dispersion of seabeach amaranth. In the second part of this chapter, I used methods outlined in Sellars' model and ArcView GIS (ESRI, Redlands, CA) to estimate change in suitable habitat based on all available LIDAR elevation and passive reflectance data.

Materials and Methods

GIS Modeling of Habitat Area. For both dispersion and habitat analyses it was first necessary to identify habitat area. I used methods outlined in Sellars' model and ArcView GIS (ESRI, Redlands, CA) identify habitat based on all available LIDAR elevation and passive reflectance data. LIDAR Data were available from aerial surveys of portions of Cape Hatteras National Seashore during 1996, 1997, 1999, and 2000, and surveys of portions of Cape Lookout National Seashore from surveys during 1997, 1998, 1999, and 2000. LIDAR and reflectance data sets were provided free of charge from the National Oceanic and Atmospheric Administration's Coastal Services Center (NOAA-CSC, Charleston, SC) using the LIDAR Data Retrieval Tool (LDART) at the following web site: http://www.csc.noaa.gov/cgi-bin/crs/tcm/ldart_start.pl. Retrieval of the data is via electronic download.

A number of data format options are available when downloading from LDART. Data sets in this study were downloaded in binary raster data format using the Universal

Transverse Mercator projection and North American Datum of 1983 (NAD83). The vertical datum used for the elevation data was the North American Vertical Datum of 1988 (NAVD88). The data formats used were chosen to provide consistency with data formats used by National Park Service personnel. Data sets were available with a minimum grid cell size of $1 \times 1 \text{ m}^2$. A resolution of $3 \times 3 \text{ m}^2$ was used for all data sets to reduce file sizes and computer processing time. Data were readily imported into ArcView GIS 3.2 (ESRI, Redlands CA) using the LIDAR Data Handler Tool provided in the software. The ArcView GRID format was used for all subsequent analyses and processes.

Data were ordered and processed in a series of small batches to reduce file sizes. The size and location of each batch was delineated by a rectangular Tile created in the GIS. Together the series of 12 contiguous rectangular Tiles encompassed the entire study area (Figure 17). ArcView GRIDS were created for each of the Tiles, one GRID for each data layer (LIDAR and reflectance) for each year's aerial survey.

Only those grid cells containing data for all years were included in analyses so that differences in habitat area within a Tile did not result from differences in the total areas compared. Flight paths were never replicated exactly among years during annual surveys; this resulted in variability in the amount and location of the land surface surveyed. A map query was performed in ArcView to determine what GRID cells were common to all potential analysis GRIDS for a particular Tile. For each Tile, ArcView output a mask GRID with two types of grid cells: 1) cells containing 1's, indicating the cells contained data in all surveys, and 2) cells containing 0's, indicating lack of data in

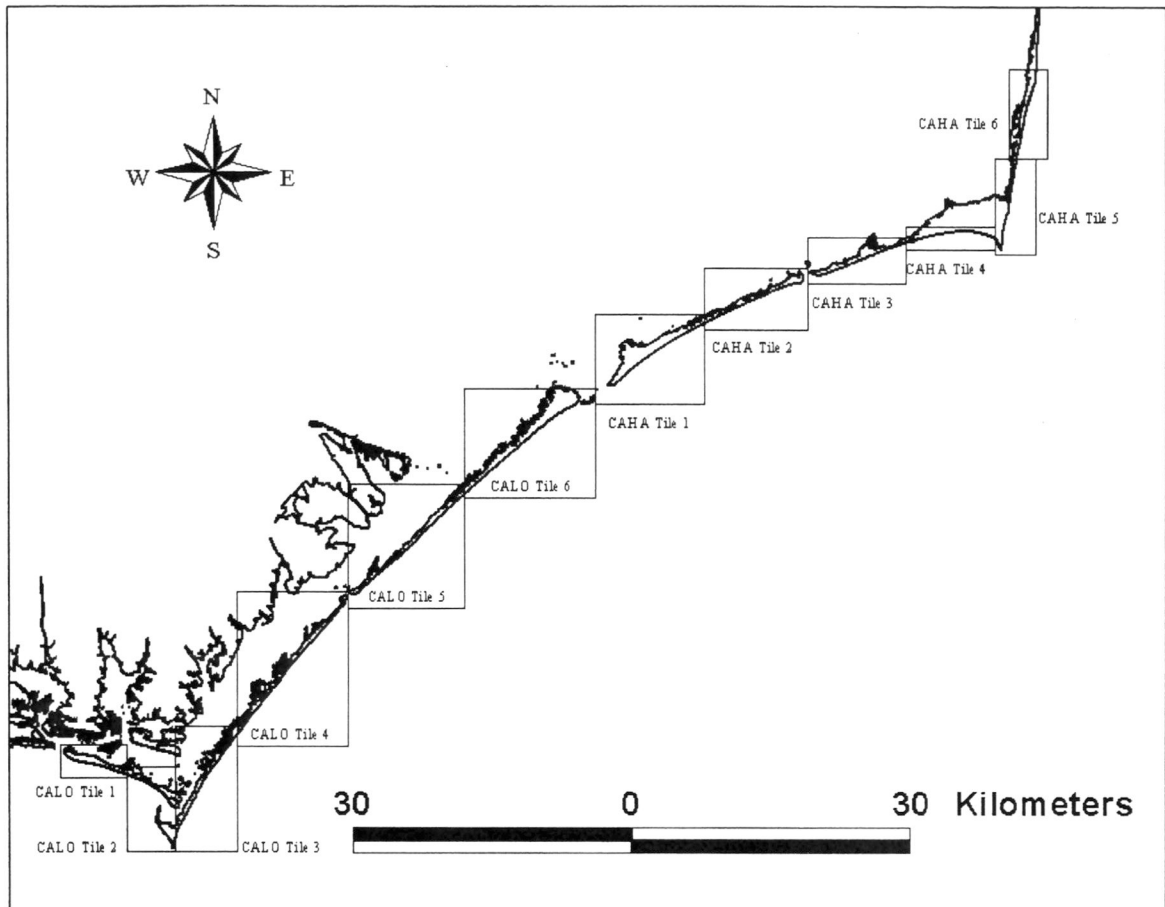


Figure 17. GIS data Tiles at two North Carolina national seashores. Remotely sensed data for Cape Hatteras (CAHA) and Cape Lookout (CALO) are separated into rectangular Tiles for ease of handling.

one or more surveys. The mask GRID was used to determine the area of analyses for each Tile. This excluded from analysis any cells that had not been surveyed in one or more surveys of a particular Tile. Therefore, analyses among years, within each Tile were conducted using the same total area.

I mapped areas of suitable habitat for each Tile following the methods of Sellars (2001) and from Jolls and Sellars (2000). Paired LIDAR and reflectance GRIDS from a given year were analyzed to determine which GRID cells contained suitable habitat. GRID cells in both GRIDS overlapped exactly because the LIDAR data and reflectance data were downloaded simultaneously using the same area coordinates. If both elevation and reflectance input GRID cell values were within the suitable parameters then the corresponding habitat GRID cell was labeled suitable. For example, for a habitat cell to be deemed suitable its corresponding LIDAR elevation input cell would have to have a value greater than 0.77 m and less than 2.00 m and the reflectance input cell would also have to have a digital number greater than 170. The elevation range and reflectance minimum values that bracket habitat in Sellars' model were determined based on the specific elevation, reflectance, and plant location data Sellars used. Therefore, applying the model "as is" to other sites assumes that the elevation range and reflectance minimum habitat brackets in the model apply equally well to the different elevation and reflectance data sets being used.

Dispersion. To assess the spatial pattern of naturally-occurring seabeach amaranth plants, I used GPS plant location data from surveys at Cape Lookout and Cape Hatteras and the Holgate (1965) Plotless Index of Dispersion. The Holgate index does

not require establishment of plots and can be easily applied to distance data calculated using GIS. ArcView GIS 3.2 (ESRI, Redlands CA) was used to establish 30 random reference points within the habitat area polygon and then calculate the distances between the random points and positions of naturally-occurring plants. Distances between each random point and the two plants nearest each point (d_1 and d_2 respectively), were employed in Holgate's Index of Dispersion $\{[(\Sigma(d_1^2/d_2^2))/n] - 0.5\}$. Values output by the index range from -0.5 to 0.5; results of < 0 , 0 , and > 0 indicate uniform, random, and contagious dispersal, respectively (Holgate 1965).

Habitat Area. I used ArcView to calculate shoreline length of the two National Seashores. Measurement of shoreline enabled comparison of habitat at the two parks adjusted for differences in shoreline. It was first necessary to create a contour of the shoreline. I defined an elevation contour within the LIDAR digital elevation model at the elevation of mean high water. The above process was repeated for all the Tiles in each year at each park. The elevations of mean high water are 0.38 m and 0.24 m at Cape Hatteras and Cape Lookout, respectively (Sellars 2001). Finally, I used a distance measurement tool to determine the total length of shoreline at each park for each year.

Total hectares of modeled habitat area was calculated by multiplying the number of suitable cells from the habitat GRID by 9 m^2 (the area of one cell), to get total m^2 , then dividing by 10,000 m^2 (the area of one hectare). Habitat area was determined for each Tile and each year and then summed across Tiles to determine total habitat for each year at each national seashore. To determine average suitable habitat area at each park, total habitat at each park was summed over all years and then divided by the number of years.

Average suitable habitat area at each park was divided by kilometers of shoreline to determine the average area of suitable habitat per kilometer of shoreline. Comparisons of total habitat area and area per kilometer of shoreline were made.

Results

Dispersion. Dispersion of naturally-occurring plants ranged from moderately to highly aggregated based on Holgate's index at both CALO and CAHA for all years (Table 4). The range of possible Holgate index values is from negative 0.5 to positive 0.5 with higher values indicating higher degrees of clumping. Holgate index values, across CAHA and CALO, through all years, ranged from 0.12 to 0.44, with a mean of 0.30 ± 0.046 (mean $\pm$ SE, $n = 7$). Mean index values were 0.29 ± 0.050 (mean $\pm$ SE, $n = 3$) at CAHA and 0.31 ± 0.097 (mean $\pm$ SE, $n = 4$) at CALO.

Habitat Area. Two- to three-fold differences in total habitat occurred between seashores (Table 5). The average area of suitable habitat based on the model for Cape Hatteras was 254 ha over the period from 1997 to 1999. In contrast, the average area of suitable habitat for Cape Lookout was 532 ha based on the model for the two year period from 1997 to 1998.

Average hectares of suitable habitat area per kilometer of shoreline were calculated to reduce the influence of the differences in overall park size and shoreline length from the habitat area comparison. Shoreline lengths at CAHA and CALO were 69.3 and 90.1 km, respectively. Similarly, there was much less suitable *Amaranthus pumilus* habitat per length of shoreline at CAHA than at CALO, 3.7 and 5.9 ha/km, respectively.

Table 4. Holgate's Index of Dispersion and the number of naturally-occurring *Amaranthus pumilus* plants used in calculation of the index (in parentheses) at Cape Hatteras and Cape Lookout National Seashores for the years 2000 – 2003. Values > 0 indicated a clumped distribution pattern.

Year	CAHA	CALO
2000	— (—)	0.24 (20)
2001	0.42 (42)	0.44 (168)
2002	0.40 (119)	0.23 (330)
2003	0.12 (56)	0.25 (526)

Table 5. Hectares of suitable seabeach amaranth habitat, kilometers of shoreline length, and the ratio of suitable habitat to shoreline length at Cape Hatteras and Cape Lookout National Seashores for the years 1997 – 1999

	CAHA			CALO		
	1997	1998	1999	1997	1998	1999
SUITABLE HABITAT (ha)	243	231	287	597	467	-
SHORE LENGTH (km)	69.0	69.3	69.5	89.5	90.6	-
HABITAT/SHORE (ha/km)	3.5	3.3	4.1	6.7	5.2	-

Discussion

Dispersion of naturally-occurring seabeach amaranth is shown in this study to be highly contagious within modeled bounds of suitable habitat. The aggregated dispersion pattern may be a result of aggregated patterns in dispersal. For example, seeds dispersed in clumps of wrack, dispersal in the locale of a previous year's population, or from contagious spatial distribution in a seed bank. Potentially, contagious dispersion could reflect a naturally low utilization of available habitat, or simply reflect low or declining population sizes. Another possible explanation for the observed contagious distribution is a similarly clumped spatial pattern of resource availability, e.g., water, nutrients, salinity or other resources limiting germination and/or survival to a few microsites. However, if seabeach amaranth habitat area is more restricted than the model predicts, as a result of environmental factors, then the model may need refinement. A refined model may define a smaller habitat area; this would bring random points in the Index of Dispersion closer to positions of naturally occurring plants and result in a more even dispersion relative to the smaller suitable habitat area. Thus, contagious dispersion may be a result of ecological factors and/or an artifact of overestimation of habitat by the model.

This preliminary evaluation of *A. pumilus* spatial pattern does not allow elimination of any of these possible explanations for the clumped distribution. Repeated calculation of the index annually at these and other sites would greatly enhance the interpretability of these data. If plant populations were to exist at different sites in subsequent annual observations there would be more support for the model being an

adequate description of habitat. Conversely, if populations occur at the same sites repeatedly but only vary in number or density, one or more additional restricting parameters may be needed in the model. My study suggests seabeach amaranth populations may have a contagious dispersion; however, with such a diversity of potential causes, the contagious dispersion primarily underscores the need for improved knowledge of seabeach amaranth seed banks and habitat parameters.

Quantification of seabeach amaranth habitat using LIDAR and the Jolls and Sellars model suggests there are differences in overall habitat between Cape Hatteras and Cape Lookout National Seashores. The differences in number of inlets and island-ends between seashores may, in part, explain the greater amount of habitat at Cape Lookout. Bücher and Weakley (1990) include island ends in a list of important habitat sites for seabeach amaranth. Cape Hatteras has four island ends compared to seven at Cape Lookout including the two point areas. Also, Cape Hatteras point is smaller in length and breadth than Cape Lookout point. The point areas and inlets are, however, only a small portion of the total seashores. Patterns of mean habitat area per kilometer of shoreline suggest that a smaller seabeach amaranth habitat area at CAHA is not simply a function of differences in island size. The average ratio of habitat to length of shoreline at Cape Hatteras was almost 66% less than at Cape Lookout (3.7 and 5.9 ha/km, respectively).

The aspect to open ocean at each national seashore may also explain some of the difference in habitat area. Bucher and Weakley (1990) report that seabeach amaranth plant populations are more likely to occur on accreting beaches and on south-facing beaches. Prevalence of populations on south-facing beaches may suggest increased

habitat area. South-facing shorelines may experience less disturbance as a result of their aspect to open ocean waves and storms. The two major storm system types along the eastern seaboard, nor'easters and hurricanes, cause waves and beach erosion that may differ in their effect on beaches that face different directions. Hurricanes also are known to deposit or remove large amounts of sand and significantly influence beach morphologies on North Carolina's barrier islands (White and Wang 2003). East and northeast winds from nor'easters can produce some of the largest waves experienced by the North American Atlantic coast (Jones and Davis 1995). Although the strongest winds hurricanes produce come out of the south-southeast (Casson and Coles 1998), hurricane winds change to east and northeasterly as storms pass leaving much of the impact on east facing beaches. In addition, many storms skirt the coast and produce waves that come from farther out at sea as the storms pass to the east. Overall, the largest erosional wave influence comes out of the northeast and north south oriented barrier islands generally have the highest rates of erosion (Dolan *et al.* 1977). Two-thirds (46 km) of Cape Hatteras' shoreline faces south/southeast with a short portion (10 km west of the point) facing south; the remaining one-third faces almost due east. Most of the shoreline (73 km) at Cape Lookout faces southeast, with a small portion (17 km) facing south-southwest. Thus, the Cape Hatteras shoreline faces roughly east-southeast while Cape Lookout has at least some shoreline facing southward. These shoreline aspect proportions roughly match the pattern of higher habitat per kilometer of shoreline at CALO. Therefore, the habitat area analysis data suggest that definition of seabeach amaranth habitat using the Jolls and Sellars habitat assessment model can, at a minimum,

bear out habitat differences on this scale.

Higher plant population sizes at Cape Lookout could support the pattern of habitat area differences seen in this study. However, population abundance records at Cape Hatteras and Cape Lookout, as summarized by Sellars (2001), show only highly variable and seemingly declining populations, and therefore, no obvious population size trends. Furthermore, the record of plant abundances in North Carolina is short, 20 yr, and began only after seabeach amaranth numbers had been declining noticeably (Bücher and Weakley 1990). The record also shows large fluctuations in plant abundance that may be more indicative of a plant in decline than of normal plant occurrence patterns (Sellars 2001). Lack of concurrence between patterns of plant abundance and habitat quantified suggests some combination of the following two conclusions: 1) Sellars' model may be improved to better reflect true suitable habitat by adding additional environmental factors such as distance from shore, and/or 2) Sellars' model may model habitat well and current *Amaranthus pumilus* abundance is influenced by additional factors such as seed source, seed dormancy, and human encroachment on habitat.

While large scale quantifications of habitat provided useful information on overall habitat availability, small scale comparisons did not. For this analysis the model was applied to available LIDAR and reflectance data "as is". The same reflectance breaking point (> 170) was used for all data sets and ideally would have been recalibrated independently for each data set. Variability in reflectance and elevation data sets resulted in a wide range in habitat areas among Tiles and years. As an example, through the 1997 to 1999 period, suitable habitat in Tile 5 at CAHA, as determined by the model, varied

from 4 to 47 ha (Table 6).

Errors in measurement of elevation and or surface reflectance can result in errors in habitat area calculation and render small spatial-scale and short temporal-scale habitat comparisons inconclusive. Detailed inspection of LIDAR and reflectance data sets suggests wide variation in elevation and reflectance values among swaths on certain days, among Tiles, and between and among years at both seashores. Differences in elevation of 40 cm or more were observed among data subsets for parking lots or other stationary surfaces where elevation could be assumed to remain constant from one year to the next. Large variation also was observed among the multiple overlapping swaths of data collected at different times during a single day. LIDAR laser-distancing sensor errors and aircraft GPS positioning errors are known to occur (Maas 2002) and may explain these data discrepancies.

Variation in reflectance data also was a significant source of error in habitat area quantification. Two factors were likely to cause variation in reflectance values, time of day and wetness of the surface. Daylight is the light source for the “passive” reflectance images; time of year, time of day, variable cloud cover or other influences on available daylight may cause variation. For example, a sunny section of sandy beach would tend to have higher reflectance than the same or a similar nearby section of beach shadowed by a cloud. Soil surface wetness after rain may also affect reflectance. In addition to reflectance variation observed among cells and between swaths, some entire data sets contained reflectance values that were generally low for all cells and swaths and thus, were visibly dark in color throughout the image. Applying the model “as is” without

Table 6. Hectares of suitable seabeach amaranth habitat, kilometers of shoreline, and habitat area adjusted to shoreline (Ratio) for each year and each Tile at Cape Hatteras and Cape Lookout National Seashore, respectively.

Tile & Year		Habitat area (ha)	Shoreline (km)	Ratio (ha/km)
CALO 1	97	50	7.5	6.7
	98	32	7.6	4.2
CALO 2	97	80	12.8	6.2
	98	83	13.4	6.2
CALO 3	97	99	14.3	6.9
	98	32	14.3	2.2
CALO 4	97	142	20.0	7.1
	98	125	20.5	6.1
CALO 5	97	105	17.6	6.0
	98	80	17.6	4.6
CALO 6	97	121	17.3	7.0
	98	114	17.2	6.7
CAHA 1	97	76	13.7	5.5
	98	67	13.8	4.9
	99	57	13.9	4.1
CAHA 2	97	50	11.9	4.2
	98	60	11.9	5.0
	99	59	11.9	5.0
CAHA 3	97	53	11.2	4.7
	98	56	11.2	5.0
	99	62	11.2	5.5
CAHA 4	97	20	10.2	2.0
	98	40	10.2	3.9
	99	39	10.2	3.9
CAHA 5	97	27	11.4	2.4
	98	4	11.6	0.3
	99	47	11.7	4.0
CAHA 6	97	16	10.6	1.5
	98	4	10.6	0.4
	99	23	10.6	2.1

calibrating each reflectance data set may also have resulted in both over and underestimation of habitat. The first LIDAR test flights were flown in 1996 (NOAA – CSC) and it is likely that data precision and accuracy improved with time.

Quantification of suitable habitat using LIDAR and Sellars' model can be useful for long-term and large-scale monitoring of seabeach amaranth habitat. Determining yearly changes in habitat area or comparisons on a site by site basis, however, requires greater consistency and accuracy in LIDAR and reflectance data sets as well as appropriate data processing and calibration. Utility of these smaller scale comparisons will likely increase with increased frequency and improved accuracy of LIDAR and reflectance surveys. Frequent habitat area assessments using these methods would increase spatial and temporal resolution in habitat monitoring and would provide much needed knowledge of the habitat of seabeach amaranth and other beach taxa. Continued efforts using these methods can provide information about the general trends in strand habitat variability through time. Habitat and vegetation patterns may be compared to the magnitude and frequency of disturbances, park management practices, coastal development (White and Wang 2003) and plant abundances.

CHAPTER V

CONCLUSIONS

Seabeach amaranth is threatened with extinction primarily as a result of habitat loss (Bücher and Weakley 1990) and its conservation will depend on preservation of its habitat. Before habitat can be preserved, habitat must be defined using specific biotic and abiotic parameters (Kruckeberg and Rabinowitz 1985, Chapin *et al.* 1996, Wiser *et al.* 1998); before parameters can be defined, they must be identified. This thesis has begun the process of defining seabeach amaranth habitat through 1) *in situ* tests of the plant's previously identified suitable habitat elevation range, 2) by identifying some abiotic parameters with potential to influence plant establishment, growth, and survival, and 3) by examining the aggregation of plants, and size of habitat.

Elevation and Success of Transplants of Amaranthus pumilus. Restriction of seabeach amaranth habitat to a narrow elevation range is further supported by the transplantation experiment data presented here. Reduced survival (in some cases 100% mortality) at elevations below the model's elevation range suggests that overwash may in large part determine the low elevation boundary of seabeach amaranth habitat. This same pattern of survival has been observed for the lakeshore dune annual *Cakile edentula* (Payne and Maun 1984). Lakeshore nesting and forage habitat of Piping Plover (*Charadrius melodus*) is also delimited by overwash at low elevations (Espie *et al.* 1997). High growth rates in transplants suggest that edaphic variables restrict success of seabeach amaranth less at low elevations. Alternatively, high survival, and very low growth at the high end of the elevation range (2.0 m) predicted by the model, further

suggest that the restriction of *A. pumilus* habitat below these high elevations results in large part from edaphic characteristics. Increased vegetation, including some potential competitors (Johnson 2005), may also restrict seabeach amaranth success at its highest elevations and further suggests the importance of overwash. Overwash disturbance causes temporal and spatial variability in dune strand habitat (Ignaciuk and Lee 1980, Ehrenfeld 1990, Hayden *et al.* 1991) in turn increasing the risk of extinction (Karr 1982, Pimm 1988, Quintana-Ascencio and Menges 1996, Turner *et al.* 1996, Fisher and Stocklin 1997). Yet, overwash disturbance is also the primary factor creating new habitat by depositing new sand and reducing the populations of potential competitors (Seneca 1969, van der Valk 1974, Bazzaz 1979, Barbour *et al.* 1985, Crawford 1989). Low within-site linear regressions of elevation with plant growth suggest that the influences of overwash disturbance, competition, and other biotic and abiotic factors are complex, and that they influence seabeach amaranth differently at different seashores.

Responses to Salinity and Water Availability. This work suggests seabeach amaranth may be sensitive to salinity during both germination and juvenile stages. Thus, salinity may have the potential to act as a strong habitat variable influencing zonation of seabeach amaranth populations. In this study, although seawater salinity is 35 ppt, *A. pumilus* did not germinate well in soil salinities greater than 5 ppt and germination was completely inhibited in 20 ppt salinities. Reduced germination at higher salinities is associated with increases in seed dormancy in some plants (Maun 1994, Walmsley and Davy 1997, Huang *et al.* 2003). Seed dormancy, when coupled with long term viability and resistance to decomposers, indicates potential to form a seed bank (Baker 1989).

Seed banks help plant populations persist when habitat availability is temporally variable (Kalisz and McPeck 1992). Seabeach amaranth may have the potential to form a seed bank as do several other dune species (Zhang and Maun 1994). Seeds of seabeach amaranth and other dune species are dormant at dispersal (Ignaciuk and Lee 1980, Baskin and Baskin 1998a), and require light to germinate (Zhang and Maun 1994, Hamzé and Jolls 2000). Long-term viability and resistance to decomposers in seabeach amaranth seeds may be suggested by prolonged storage of seeds in the lab (pers. obs.) and by survival of seeds in Sellars' (2001) field stratification experiment, respectively. If seabeach amaranth and other dune species are capable of forming a seed bank, they may be able to reduce their likelihood of germinating in higher salinity sites, i.e., salt flats, or submerged marine sites, and increase their likelihood of germinating within suitable habitat.

This work suggests that zonation of seabeach amaranth populations may be influenced through salinity's effects on survival and growth of juvenile plants. Plant survival in the salinity experiment suggested that *A. pumilus* plants may be able to tolerate high salinities (> 20 ppt). This is not surprising because storms can easily expose maritime strand habitat to seawater overwash or spray (Erickson and Young 1995, Cheplick and Demetri 1999). Differences in growth in the salinity experiment, however, suggest *A. pumilus* plants are unlikely to be successful after prolonged exposure to moderate or high soil salinities (> 5 ppt). This result was also not surprising, because high salinities fall after storms leaving low salinities as the normal condition (Boyce 1954, Martin 1959, Whittecar and Emry 1992, Erickson and Young 1995), and because

other strand species have been categorized as glycophytes (Oosting 1945, Barbour *et al.* 1985, Christensen 1988). Amaranth plants treated with 2 ppt salinity grew larger than plants treated with no salinity, suggesting very low levels of salinity may allow for increased seabeach amaranth growth. The increases in growth were small, however, and, although they were statistically detectable, the increases in growth may have been practically insignificant or a response to other factors such as pH.

Survival and growth of plants in the water treatment experiment suggest water availability may also have potential to influence growth and survival and thus zonation of seabeach amaranth habitat. Exposure to moderately low field capacities slowed growth rates and low field capacities halted growth, caused loss of leaves, and reduced survival in *Amaranthus pumilus*. Reduced water availability is known to influence distribution of other dune species. Survival, growth, and seed output of naturally occurring *Cakile lacustris* was reduced at higher elevations as a result of limited water availability in its sandy lake shore soils (Payne and Maun 1984). *In situ* measurement may reveal low water availability as a growth limiting factor, particularly at the highest elevations of *A. pumilus* habitat.

Aggregated Plant Dispersion. Naturally occurring amaranth plants were highly aggregated in their dispersion within modeled suitable habitat. Although the reasons for the observed dispersion patterns are unknown, aggregated dispersions of plants are believed to result from: 1) localized dispersal resulting in aggregations of progeny from a single parent or aggregations of parents, 2) non-random dispersal, resulting in “site preference” (for example wrack-lines) (Payne and Maun 1984), and 3) clumped habitat

patterns resulting in spatial variation in germination success, seedling survival and/or competition (Whipple 1980). Consistent patterns of dispersion may be revealed through repeated annual dispersion surveys that identify population absences and/or reoccurrences at particular sites. These data, although currently limited in their interpretability, are the first assessment of seabeach amaranth population dispersion patterns and can serve a baseline for future comparisons with dispersion patterns of seabeach amaranth and other maritime strand annuals.

Spatial Extent and Patterns of Habitat Distribution. Habitat comparisons between Cape Lookout and Cape Hatteras National Seashore, using combined habitat data from 1997 through 1999, showed a much greater area of suitable habitat per length of shore at Cape Lookout. It is suspected that an increased number of inlets may have increased modeled habitat because of the low, wide expanses of open sand associated with island ends. In addition, a more southerly aspect to the ocean of the Cape Lookout shorelines may have increased modeled habitat. Another potential explanation of these data is that a single habitat definition is not appropriate for both seashores and/or that the definition should be altered to apply to the different seashores in different ways.

Maritime strand habitat of *A. pumilus* and other shoreline dune habitats (lakeshores) have highly variable habitat availability (Ignaciuk and Lee 1980, Ehrenfeld 1990, Hayden *et al.* 1991), in large part as a result of high levels of disturbance (Ignaciuk and Lee 1980, pers. obs.). This thesis has shown that remotely sensed data and GIS techniques be employed to quantify and monitor large scale spatial and temporal patterns in *A. pumilus*' maritime strands and potentially other similar open sandy dune habitats.

Analysis of consecutive annual surveys of habitat area could also provide valuable information on the temporal variability (or consistency) of habitat availability and magnitude and extent of disturbance in sandy shoreline dune habitats in general (Dech *et al.* 2005). Detecting year to year changes in habitat area based on the Jolls and Sellars model, however, will require better consistency and accuracy in recording of future remotely sensed elevation and reflectance data sets. Data processing techniques that compensate for reduced reflectance under shadows have been developed and may improve the utility of existing and future reflectance data sets (Dech *et al.* 2005).

General Conclusions. *Amaranthus pumilus* and other maritime dune species occupy a narrow swath of habitat with borders that seem to be created by limited water availability and higher elevations on the landward side and by salinity and overwash disturbance on the seaward side. Important edaphic variables in strand habitats, i.e., water availability, salinity, and elevation, are physically and physiologically interrelated in maritime dunes. Water availability is negatively affected by salinity because salinity decreases water potential (Bernstein and Hayward 1958). Elevation is related to salinity and water availability, especially in maritime strands, because both factors can vary widely with changes in elevation (Martin 1959, Barbour 1978, Whittecar and Emry 1992, Ullman *et al.* 2003). Low levels of salinity may increase water use efficiency in salt tolerant species (Glenn and Brown 1998). Limited water availability and elevated salinity may negatively influence nutrient use (Houle 1997). Seabeach amaranth plants are shown in this study to survive prolonged exposure to salinity; they are known to tolerate several hours of inundation with seawater in the field (Sellars, pers. comm.).

Relatively nutrient-rich water can percolate through from the inland side of barrier islands and that water is more likely to be encountered at lower elevations (Windom and Niencheski 2003). Future laboratory studies should be designed to expose interactions between drought and salinity or, additionally, the range of nutrient levels suitable for growth in this species. Future field transplant studies should include *in situ* watering and salinity treatments at different elevations as well as comparisons of natural soil salinity and water availability with plant response.

Measurements of soil salinity and water availability in maritime dunes show variation with changes in elevation (Oosting 1954, Martin 1959, Barbour 1978, Whittecar and Emry 1992, Anderson *et al.* 2000, Ullman *et al.* 2003). This thesis presents the first experimental data on the ranges of soil salinities and water availabilities, tolerated and optimal, for seabeach amaranth growth, albeit in a growth chamber. Heterogeneity of subsurface soils is known to influence the depth of water tables on barrier islands (Anderson *et al.* 2000); this may result in heterogeneity of fresh water availability in seabeach amaranth habitat. Barrier island size and morphology influence capture and retention of fresh rainwater and salt water exclusion (Whittecar and Emry 1992), and therefore, may be important variables influencing fresh water availability in proximal shoreline habitat of *Amaranthus pumilus*. Anderson *et al.* (2000), citing personal communication with National Park Service (NPS) personnel, reported releases of ponded rainwater at 0 – 37,800 m³/d through an NPS gate-valve on the south side of Hatteras island. NPS at least occasionally uses earth-moving equipment to remove a section of the primary dune to allow low-saline water (< 2 ppt) to flow from the gate-valve into to the

ocean (pers. obs.), suggesting natural island morphologies would retain at least some of the water. Accelerating human consumption of island ground water and release of ponded island rainwater through man-made culverts may further reduce fresh ground water availability in *A. pumilus* habitat.

Ways of refining the elevation portion of Sellars' seabeach amaranth habitat model may become apparent when observations in this thesis, including moderate survival of plants at elevations below 0.77 m above MHW, highly aggregated plant distributions, strong responses to salinity, and differences in habitat between seashores, are considered together. Using a different higher elevation vertical reference in the model, such as mean higher high water (MHHW) may improve the model's ability to predict plant occurrences. In his *Amaranthus pumilus* habitat model, Sellars (2001) used MHW as an elevation baseline to help compensate for differences in mean sea level between sites. He could also have used other baselines, such as MHHW. MHW and MHHW depend largely on tidal amplitude (partially on wave height); for example, two beaches may have the same MSL but the beach having the higher tidal amplitude would have higher MHW and MHHW. The latitudinal range of seabeach amaranth habitat is correlated with a range of low tidal amplitudes (USFWS 2001). Just as MHW and MHHW are not a constant among seashores, they are not constant within seashores; i.e., net outflow of water from inlets requires that amplitudes are different at inlets than at the center parts of islands. Thus, the elevation range of seabeach amaranth may change across sites and/or along the shore as MSL, MHW, and MHHW change. Also, in developing his model, Sellars found that using an offset of 0.77 m above MHW as the

low elevation boundary encompassed the largest proportion of naturally-occurring plants while excluding the largest proportion of island area as habitat. MHHW occurs at a higher elevation, by definition the highest of the daily tidal amplitudes (USACE glossary, <http://chl.erdc.usace.army.mil/glossary>) and thus more closely approximates the reach of non-storm overwash. Using MHHW as the elevation baseline in the model would reduce and adjust the offset for each beach the model is applied to.

Low plant growth in transplants at high elevations and strong responses to experimental drought treatments demonstrated in this thesis may also suggest ways of redefining the upper elevation boundary for seabeach amaranth habitat and for the model. Low within-site relationships of elevation with plant growth suggest that suitability of habitat may vary substantially across sites; the complexity of habitat factors may require greater complexity in the model. In searches for transplant sites, no suitable sites that represented LOW-OUT, IN, and HIGH-OUT elevations simultaneously were found. At many sites, erosion caused the beach to grade steeply across the elevation ranges, as is described by USFWS (2001). Also, among all beaches examined with moderate grades, either the beach or dune surface did not reach the HIGH-OUT elevation or the LOW-OUT elevation appeared at the water-line. This suggests the elevation range of seabeach amaranth may not be a constant and that redefining the model's upper limit of habitat on some habitat parameter, rather than a standard vertical offset, may improve model's ability to predict *Amaranthus pumilus* plant occurrences. If soil water availability is a limiting factor at higher elevations, it may be useful to base the high elevation boundary of habitat on some standard off set from MSL, or on an island's water table.

Redefining the upper and lower habitat boundaries as described above may improve habitat modeling for seabeach amaranth and improve understanding of habitat of other maritime dune species. Beach-specific MHHW and water tables may be used to identify beach specific vertical habitat ranges. Although there may be advantages to the researcher in this potentially more accurate definition, determination of site-specific MHHW and water tables could be more time-consuming and complex for site managers.

Additional knowledge of spatial variation in soil temperatures and their influence on water availability may also help explain distribution of seabeach amaranth and other species in maritime strands. High insularity on the relatively flat maritime beaches results in soil surface temperatures as high as 53 °C (Oosting and Billings 1942). High temperatures can cause plant stress but high soil water content buffers temperatures (Nobel and Geller 1987). In environments with limited vegetation cover, such as maritime dunes, remotely sensed microwave and infrared data can be used together to identify soil moisture and temperature at the soil surface (Schmugge *et al.* 2002). Remotely sensed microwave and infrared data could be added as variables in a GIS habitat model. It is possible that soil temperatures vary among microsites. The strong heat sink characteristic of water may stabilize and lower soil surface temperatures more at lower elevations closer to the water table (Ullman *et al.* 2003) creating spatial variation in habitat suitability for seabeach amaranth and other dune species.

This work may also have broader implications for dune taxa, in general, and the dune ecosystem as a whole. Answers to many of the questions addressed in this thesis can appropriately be applied to habitat of other dune taxa. A management/conservation

focus on umbrella species can facilitate management/conservation of other co-occurring species (Walters 1991, Launers and Murphey 1995); *Amaranthus pumilus* can serve well as one of those “umbrella species” (Wilcox 1984). Several of the floral and faunal taxa that co-occur with seabeach amaranth are listed federally or by states as threatened, endangered, or rare (USFWS 2001) and may benefit from conservation of this dune ecosystem. Among these are: seabeach knotweed (*Polygonum glaucum*), seabeach morning glory (*Ipomoea stolonifera*), Piping Plover (*Charadrius melodus*), Least Tern (*Sterna antillarum*), American Oystercatchers (*Haematopus palliatus*), leatherback sea turtles (*Dermochelys coriacea*), and loggerhead turtles (*Caretta caretta*) (USFWS 2001).

Recovery of *Amaranthus pumilus* will depend on habitat preservation and restoration (Bücher and Weakley 1990); this thesis has begun some of the necessary prerequisites, defining habitat and identification of habitat parameters. Results of this thesis may assist interpretation of future studies of large temporal and spatial patterns of soil salinity and water availability. This work sheds light on the importance of a narrow elevation range that is often suitably broad and flattened only on beaches with naturally sculpted morphologies (Ignaciuk and Lee 1980). Anthropogenic effects on beach morphologies, such as dune construction (Pilkey and Neal 1992), should be considered in road, bridge, and other park construction and management plans. Actions having the potential to refresh shallow freshwater aquifers and reduce intrusion of saltwater, such as retaining (rather than draining) inland ponds (Anderson et al. 2000) and soil compaction and sand drying as a result of off road vehicles (Hosier and Eaton 1980) should be considered in management practices. Recovery efforts including repeated remotely

sensed data collection and analysis, plant population surveys and studies, and habitat preservation must out-pace encroachment, dune building, and other causes of habitat loss to halt or reverse population losses.

REFERENCES

- Anderson, W. P., D. G. Evans, and S. W. Snyder. 2000. The effects of Holocene barrier island evolution on water table elevations, Hatteras Island, North Carolina, USA. *Hydrogeology Journal* **8**:390-404.
- Baker, H. G. 1989. Some aspects of the natural history of seed banks. Pages 9–12 in M. A. Leck, V. T. Parker, and R. L. Simpson, editors. *Ecology of soil seed banks*. Academic Press, San Diego, California, USA.
- Barbour, M. G. 1970. Germination and early growth of the strand plant *Cakile maritime*. *Bulletin of the Torrey Botanical Club* **97**:13-22.
- . 1972. Seedling establishment of *Cakile maritime* at Bodega Head, California. *Bulletin of the Torrey Botanical Club* **99**:11-16.
- . 1978. Salt spray as a micro environmental factor in the distribution of beach plants at Point Reyes, California. *Oecologia* **32**:213-224.
- Barbour, M. G., and T. M. DeJong, 1977. Response of west coast beach taxa to salt spray, seawater inundation, and soil salinity. *Bulletin of the Torrey Botanical Club* **104**:29-34.
- Barbour, M. G., T. M. De Jong, and B. M. Pavlik. 1985. Marine beach and dune plant communities. Pages 296-332. in B. F. Chabot and H. A. Mooney, editors. *Physiological ecology of North American plant communities*. Chapman and Hall, New York, New York, USA.
- Baskin, C. C., and J. M. Baskin. 1998. *Seeds; ecology, biogeography, and evolution of dormancy and germination*. University of Kentucky, Lexington KY. Academic Press, San Diego, California, USA.
- . 1998b. Seed dormancy and germination in the rare plant species *Amaranthus pumilus*. *Castanea* **63**:493-494.
- Baskauf, C. J., and W. G. Eickmeier. 1994. Comparative ecophysiology of a rare and widespread species of *Echinacea* (Asteraceae). *American Journal of Botany* **81**:958-964.
- Bazzaz, F. A. 1979. The physiological ecology of plant succession. *Annual Review of Ecology and Systematics*, **10**:351-371.
- Bernstein, L., and N. E. Hayward. 1958. Physiology of salt tolerance. *Annual Review of Plant Physiology* **9**:25-46.

- Bowman, D. M., and L. Mcdonough. 1991. Tree species distribution across a seasonally flooded elevation gradient in the Australian monsoon tropics. *Journal of Biogeography*, **18**:203–212.
- Boyce, S. G. 1951. Salt hypertrophy in succulent dune plants. *Science* **114**:544-545
- Bram, M. R., and J. A. Quinn. 2000. Sex expression, sex-specific traits, and the effects of salinity on growth and reproduction of *Amaranthus cannabinus* (Amaranthaceae), a dioecious annual. *American Journal of Botany* **87**:1609-1619.
- Bücher, M. A., and A. S. Weakley. 1990. Status survey of seabeach amaranth (*Amaranthus pumilus* Rafinesque) in North Carolina and South Carolina. North Carolina Plant conservation Program, North Carolina Department of Agriculture, Raleigh, North Carolina and Endangered Species Field Office, U.S. Fish and Wildlife Service, Ashville, North Carolina, USA. unpubl. report. 86 pp.
- Casson, E., and S. Coles. 1998. Extreme hurricane wind speeds: Estimation, extrapolation and spatial smoothing. *Journal of Wind Engineering and Industrial Aerodynamics* **76**:131-140.
- Chambers, J. C., and J. A. MacMahon. 1994. A day in the life of a seed: Movements and fates of seeds and their implications for natural and managed systems. *Annual Review of Ecology and Systematics* **25**:263-292.
- Chapin III, F. S., M. S. Torn, and M. Tateno. 1996. Principles of ecosystem sustainability. *American Naturalist* **148**:1016-1037.
- Chapin III, F. S., B. H. Walker, R. J. Hobbs, D. U. Hooper, J. H. Lawton, O. E. Salsa, and D. Tilman. 1997. Biotic control over the functioning of ecosystems. *Science* **277**:500-504.
- Cheplick, G. P., and H. Demetri. 1999. impact of saltwater spray and sand deposition on the coastal annual *Triplasis purpurea* (Poaceae). *American Journal of Botany* **86**:703-710.
- Christensen, N. L. 1988. Vegetation of the southeastern coastal plain, Pages 317-363 in M. G. Barbour, and W. D. Billings, editors. *North American terrestrial vegetation*. Cambridge University Press, Cambridge, United Kingdom.
- Clevering O. A. 1994. Germination and seedling emergence of *Scirpus lacustris* L. and *Scirpus maritimus* L. with special reference to the restoration of wetlands. *Aquatic Botany* **50**:63-78.

- Clausen, J., D. D. Keck, and W. M. Heisey. 1940. Experimental studies on the nature of species. Carnegie Institution of Washington. Washington, DC, USA.
- Colosi, J. C., and J. F. McCormick. 1978. Population Structure of *Iva imbricata* in five coastal dune habitats. *Bulletin of the Torrey Botanical Club* **105**:175-186.
- Crawley, M. J. 1990. The population dynamics of plants: philosophical transactions. *Biological Sciences* **330**:125-140.
- Crawford, R. M. 1989. Studies in plant survival: survival on coastal habitats. Blackwell Scientific, Boston, Massachusetts, USA.
- Debeljak, M., S. Dzeroski, K. Jerina, A. Kobler, and M. Adamic. 2001. Habitat suitability modeling for red deer (*Cervus elaphus* L.) in South-central Slovenia with classification trees. *Ecological Modeling* **138**:321-330.
- Dolan, R., B. Hayden, J. Heywood, and L. Vincent. 1977. Shoreline forms and shoreline dynamics. *Science* **197**:49-51
- Dunning, J. B. Jr., D. J. Stewart, B. J. Danielson, B. R. Noon, T. L. Root, R. H. Lamberson, and E. E. Stevens. 1995. Spatially explicit population models: current forms and future uses. *Ecological Applications* **5**:3-11.
- Earle, J. C., and K. A. Kershaw. 1989. Vegetation patterns in James Bay coastal marshes. Salinity and elevation as factors influencing plant zonation. *Canadian Journal of Botany* **67**: 2967-2974.
- Ehrenfeld, J. 1990. Dynamics and processes of barrier island vegetation. *Reviews in Aquatic Sciences* **2**:437-480.
- Ehleringer, J. R., and R. K. Monson. 1993. Evolutionary and ecological aspects of photosynthetic pathway variation. *Annual Review of Ecology and Systematics* **24**:411-439.
- Erickson, D. L., and D. R. Young. 1995. Salinity response, distribution, and possible dispersal of a barrier island strand glycophyte, *Strophostyles umbellata* (Fabaceae). *Bulletin of the Torrey Botanical Club* **122**:95-100.
- ESRI. 1996. ArcView GIS: the geographic information system for everyone. Environmental Systems Research Institute, Inc., Redlands, California, USA.
- . 1999. ArcView GIS 3.2. Environmental Systems Research Institute, Inc., Redlands, California, USA.

- Fischer, M., and J. Stocklin. 1997. Local extinctions of plants in remnants of extensively used calcareous grasslands 1950-1985. *Conservation Biology* **11**:727-737.
- Gagne, J., and G. Houle. 2002. Factors responsible for *Honckenya peploides* (Caryophyllaceae) and *Elymus mollis* (Poaceae) spatial segregation on subarctic coastal dunes. *American Journal of Botany* **89**:479-485.
- Glenn, E. P., and J. J. Brown. 1998. Effects of soil salt levels on the growth and water use efficiency of *Atriplex canescens*. *American Journal of Botany* **85**:10-17.
- Guterman, Y. 1994. Strategies of seed dispersal and germination in plants inhabiting deserts. *The Botanical Review* **60**:373-415.
- Hapke, C., A. Gibbs, B. Richmond, M. Hampton, B. Jaffe, J. Dingler, A. Sallenger, B. Benumof, K. Brown, G. Griggs, L. Moore, D. Scholar, C. Storlazzi, W. B. Krabill, R. N. Swift, And J. Brock. 1998. A collaborative program to investigate the impacts of the 1997-98 El Nino winter along the California coast. *Shore and Beach* **66**:24-32.
- Harris, P. T., and A. D. Heap. 2003. Environmental management of elastic coastal depositional environments: inferences from an Australian geomorphic database. *Ocean & Coastal Management* **46**:457-478.
- Hayden, B. P., R. D. Dueser, J. T. Callahan, and H. H. Shugart. 1991. Long-term research at the Virginia Coast Reserve. *Bioscience* **41**:310-318.
- Holgate, P. 1965. Some new tests of randomness. *Journal of Ecology* **53**:261-266.
- Hosier, P. E., and T. E. Eaton. 1980. The impact of vehicles on dune and grassland vegetation on a south-eastern North Carolina barrier beach. *Journal of Applied Ecology* **17**:173-182.
- Houle, G. 1997. Interactions between resources and abiotic conditions control plant performance on subarctic coastal dunes. *American Journal of Botany* **84**:1729-1737.
- Houle, G., L. Morel, and C. E. Reynolds. 2001. The effect of salinity on different developmental stages of an endemic annual plant, *Aster laurentianus* (Asteraceae). *American Journal of Botany* **88**:62-67.
- Ishikawa, S. I., T. Oikawa, and A. Furukawa. 1991. Responses of photosynthesis, leaf conductance and growth to different salinities in three coastal dune plants. *Ecological Research* **6**:217-226.

- Ishikawa, S. I., A. Furukawa, and T. Oikawa. 1995. Zonal plant-distribution and edaphic and micrometeorological conditions on a coastal sand dune. *Ecological Research* **10**:259-266,
- Ignaciuk, R., and J. A. Lee. 1980. The germination of four annual strandline species. *New Phytologist* **84**:581-591.
- Johnston, M., C. P. Grof, and P. F. Brownell. 1988. The effect of sodium nutrition on the pool sizes of intermediates of the C-4 photosynthetic pathway. *Australian Journal of Plant Physiology* **15**:749-760
- Jolls, C. L., and J. D. Sellars. 2000. Germination ecology and restoration of seabeach amaranth (*Amaranthus pumilus* Raf., Amaranthaceae). Final Report, Plant Conservation Program, North Carolina Department of Agriculture and Consumer Services, Raleigh, North Carolina, USA, Contract No. C00432. 50 pp.
- Jones, G. V., and R. E. Davis. 1995. Climatology of Nor'easters and the 30 KPA jet. *Journal of Coastal Research* **11**:1210-1220.
- Karr, J. R. 1982. Population variability and extinction in the avifauna of a tropical land bridge island. *Ecology* **63**:1975-1978.
- Kobler, A., and M. Adamic. 2000. Identifying brown bear habitat by a combined GIS and machine learning method. *Ecological Modeling* **135**:291-300.
- Krabill, W. B., C. W. Wright, R. N. Swift, E. B. Frederick, S. S. Manizade, J. K. Yungel, C. F. Martin, J. G. Sonntag, M. Duffy, W. Hulslander, and J. C. Brock. 2000. Airborne laser mapping of Assateague Island National Seashore Beach. *Photogrammetric Engineering and Remote Sensing* **66**:65-71.
- Kruckberg, A. R., and D. Rabinowitz. 1985. Biological aspects of endemism in higher plants. *Annual Review of Ecology and Systematics* **16**:447-479.
- Launer, A. E., and D. D. Murphy. 1995. Umbrella species and the conservation of habitat fragments: a case of a threatened butterfly and a vanishing grassland ecosystem. *Biological Conservation* **69**:145-153.
- Lawrence, W. E. 1945. Some ecotypic relations of *Deschampsia caespitosa*. *American Journal of Botany* **32**:298-314.
- Maas, H. G. 2002. Methods for measuring height and planimetry discrepancies in airborne laserscanner data. *Photogrammetric Engineering and Remote Sensing* **68**:933-904.

- Martin, W. E. 1959. The vegetation of Island Beach State Park, New Jersey. *Ecological Monographs* **29**:1-46.
- Matter, S. F. 2003. Modeling the density-area relationship in a dynamic landscape: an examination for the beetle *Tetraopex tetraophthalmus* and a generalized model. *Ecological Modeling* **169**:103-117.
- Maun, M. A. 1994. Adaptations enhancing survival and establishment of seedlings on coastal dune systems. *Vegetatio* **111**:59-70.
- Mariko, S., N. Kachi, S. Ishidawa, and A. Furukawa. 1992. Germination ecology of coastal plants in relation to salt environment. *Ecological Restoration*. 7:225-233.
- Meffe, G. K., C. R. Carroll, and contributors. 1997. *Principles of conservation biology*, second edition. Sinauer associates, inc. Sunderland, Massachusetts, USA.
- Meredith, A. W., W. B. Krabill, J. List, T. Reiss, E. B. Frederick, C. F. Martin, J. C. Brock, R. J. Swift, R. A. Holman, K. L. Morgan, S. S. Manizade, J. G. Sonntag, A. H. Sallenger, Jr., M. G. Hearne, M. Hansen, C. W. Wright, and J. K. Yungel. 1998. An assessment of NASA's airborne topographic mapper instrument for beach topographic mapping at Duck, North Carolina. Coastal Services Center Technical Report: NOAA/CSC/9-98/001. Charleston, South Carolina, USA.
- Mitsch, W. J., and J. G. Gosselink. 1993. *Wetlands* second edition. Van Nostrand Reinhold, New York, New York, USA. 234 pp.
- Naidoo, G., and K. Naicker. 1992. Seed-germination in the coastal halophytes *Triglochin bulbosa* and *Triglochin striata*. *Aquatic Botany* **42**:217-229.
- NOAA Coastal Services Center Web Site. 2004.
<http://www.csc.noaa.gov/crs/tcm/index.html>
- Noe, G. B. 1999. Abiotic effects on the annual plant assemblage of southern California upper intertidal marsh: does experimental complexity matter? Ph.D. dissertation, San Diego State University, San Diego, California, USA.
- Noe, G. B., and J. B. Zedler. 2000. Differential effects of four abiotic factors on the germination of salt marsh annuals. *American Journal of Botany* **87**:1679-1692.
- Oosting, H. J., and W. D. Billings. 1942. Factors affecting vegetational zonation on coastal dunes. *Ecology* **23**: 131-142.
- Oosting, H. J. 1945. Tolerance to salt spray of plants of coastal dunes. *Ecology* **26**:85-89.
- . 1954. Ecological processes and vegetation of the maritime strand in the southeastern United States. *The Botanical Review* **20**: 226-262.

- Payne, A. M., and M. A. Maun. 1981. Dispersal and floating ability of dimorphic fruit segments of *Cakile edentula* var. *lacustris*. *Canadian Journal of Botany* **59**:2595-2602.
- . 1984. Reproduction and survivorship of *Cakile edentula* var. *lacustris* along the Lake Huron shoreline. *American Midland Naturalist* **111**: 86-95.
- Pearcy, R. W., and S. L. Ustin. 1984. Effects of salinity on growth and photosynthesis of three California tidal marsh species. *Oecologia* **62**:68-74.
- Pilkey, O. H., and W. J. Neal. 1992. Save beaches, not buildings. *Issues in Science and Technology* **8**:36-41.
- Pimm, S. L., H. L. Jones, and J. Diamond. 1988. On the risk of extinction. *American Naturalist* **132**:775-785.
- Quintana-Ascencio, P. F., and E. S. Menges. 1996. Inferring metapopulation dynamics from patch-level incidence of Florida scrub plants. *Conservation Biology* **10**:1210-1219.
- Raup, D. M. 1991. A kill curve for Phanerozoic marine species. *Paleobiology* **17**:37-48.
- Richards, R. A. 1992. Increasing salinity tolerance of grain crops – is it worthwhile? *Plant and Soil* **146**:89-98.
- Seneca, E. D. 1969. Germination response to temperature and salinity for four dune grasses from the outer banks of North Carolina. *Ecology* **50**:45-53.
- Seneca, E. D., and A. W. Cooper. 1971 Germination and seedling response to temperature, daylength, and salinity by *Ammophila breviligulata* from Michigan and North Carolina. *Botanical Gazette* **132**:203-215.
- Sellars, J. D. 2001. Habitat assessment and restoration methodologies for seabeach amaranth (*Amaranthus pumilus*, Amaranthaceae). M. S. in Biology thesis, Department of Biology, East Carolina University, Greenville, NC, USA.
- Subbarao, G. V., O. Ito, W. L. Berry, and R. M. Wheeler. 2003. Sodium – a functional plant nutrient. *Critical Reviews in Plant Sciences* **22**:391-416.
- Stowe, L. G., and J. A. Teeri. 1978. The geographic distribution of C₄ species of the Dicotyledonea in relation to climate. *The American Naturalist* **112**:609-623.
- Turner, I. M., and I. T. Corlett. 1996. The conservation value of small, isolated fragments of lowland tropical rain forest. *Trends in Ecology & Evolution* **11**:330-333.

- Ullman, W. J., B. Chang, D. C. Miller, and J. Madsen. 2003. Groundwater mixing, nutrient diagenesis, and discharges across a sandy beachface, Cape Henlopen, Delaware (USA). *Estuarine, Coastal and Shelf Science* **57**:539-552.
- Underwood, E., S. Ustin, and D. DiPietro. 2003. Mapping nonnative plants using hyperspectral imagery. *Remote Sensing of the Environment* **86**:150-161.
- USFWS. 1993. Endangered and threatened wildlife and plants; determination of seabeach amaranth (*Amaranthus pumilus*) to a threatened species. *Federal Register* **58**:18035-18042.
- USFWS. 1996. Recovery plan for seabeach amaranth (*Amaranthus pumilus*) Rafinesque. Atlanta, Georgia, USA.
- USFWS. 2001. Seabeach amaranth (*Amaranthus pumilus*) life history, status and threats. Newark, New Jersey, USA.
- van der Valk, A. G. 1974. Environmental factors controlling foredune plant communities in Cape Hatteras National Seashore. *Ecology* **55**:1349-1358.
- . 1974. Environmental factors controlling the distribution of forbs on coastal foredunes in Cape Hatteras National Seashore. *Canadian Journal of Botany* **52**:1057-1073.
- Velazquez, A., and G. W. Heil. 1996. Habitat suitability study for the conservation of the volcano rabbit (*Romerolagus diazi*). *Journal of Applied Ecology* **33**:543-554.
- Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of earth's ecosystems. *Science* **277**:494-499.
- Walker, P. A. 1990. Modeling wildlife distributions using a geographic information system: kangaroos in relation to climate. *Journal of Biogeography* **17**:279-289.
- Walmsley, C. A., and A. J. Davy. 1997. Germination characteristics of shingle beach species, effects of seed ageing and their implications for vegetation restoration. *Journal of Applied Ecology* **34**:131-142.
- Walters, J. 1991. Applications of ecological principles to the management of endangered species: the case of the Red-cockaded Woodpecker. *Annual Review of Ecology and Systematics* **22**:505-523.
- Watkinson, A. R. 1990. The population dynamics of *Vulpia fasciculata*: a nine year study. *Journal of Ecology* **78**:196-209.

- White, S. A., and Y. Wang. 2003. Utilizing DEMs derived from LIDAR data to analyze morphologic change in the North Carolina coastline. *Remote Sensing of Environment* **85**:39-47.
- Whittecar, G. R., and J. S. Emry. 1992. Hydrogeology of a regressive barrier island segment, Bodie Island, North Carolina. 208 Pages in C. A. Cole, and K. Turner, editors. *Barrier island ecology of the mid-atlantic coast: a symposium*. Technical Report NPS/SERCAHA/NRTR-93/04.
- Whipple, S. A. 1980. *Bulletin of the Torrey Botanical Club* **107**:71-76.
- Wigent, C. A., K. E. Trueblood, J. D. Sellars, and C. L. Jolls. 2002. Plant size, fecundity and remote sensing: implications for the recovery of seabeach amaranth (*Amaranthus pumilus*) in North Carolina. *Journal of the North Carolina Academy of Science* **118**:134-135 abstr.
- Wilcox, B. A. 1984. *In situ* conservation of genetic resources: determinants of minimum area requirements. Pages 639-647 in J. A. McNeely, and K. R. Miller, editors. *National parks, conservation, and development*. Smithsonian Institution Press, Washington, DC, USA.
- Windom, H., and F. Niencheski. 2003. Biogeochemical processes in a freshwater-seawater mixing zone in permeable sediments along the coast of southern Brazil. *Marine Chemistry* **83**:121-130.
- Woodell, S. R. 1985. Salinity and seed germination patterns in coastal plants. *Vegetatio* **61**:223-229.
- Wiser, S. K., R. K. Peet, and P. S. White. 1998. Prediction of rare-plant occurrence: a southern Appalachian example. *Ecological Applications* **8**:909-920.
- Zedler, J. B., E. Paling, and A. McComb. 1990. Differential responses to salinity help explain the replacement of native *Juncus kraussii* by *Typha orientalis* in western Australian salt marshes. *Australian Journal of Ecology* **15**:57-72.
- Zedler, J. B., J. C. Callaway, and G. Sullivan. 2001. Declining biodiversity: why species matter and how their functions might be restored in Californian tidal marshes. *Bioscience* **51**:1005-1016.
- Zedler, J. B., H. Morzaria-Luna, and K. Ward. 2003. The challenge of restoring vegetation on tidal, hypersaline substrates. *Plant and Soil* **253**:259-273.
- Zhang, J., and M. A. Maun. 1994. Potential for seed bank formation in seven Great Lakes sand dune species. *American Journal of Botany* **81**:387-394.

Zhang, J. 1994. Interactive effects of soil nutrients, moisture and sand burial on the development, physiology, biomass and fitness of *Cakile edentula*. *Annals of Botany* **78**:591-598.