ECOPHYSIOLOGY OF BARRIER ISLAND BEACH PLANTS: RESPONSES IN FORM AND FUNCTION TO DAILY, SEASONAL AND EPISODIC STRESSES

By

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TABLE OF CONTENTS

ACKNOWLEDGEMENTS...................................................................................ii

LIST OF TABLES........................................................................................................v

LIST OF FIGURES.....................................................................................................vi

ABSTRACT.............................................................................................................x

Chapter

I. INTRODUCTION

Study Site..............................................................................................................2

Species.................................................................................................................3

Literature Cited....................................................................................................4

II. BARRIER ISLANDS, RELEVENT RESEARCH AND SPECIES SPECIFICS

The Dynamic Nature of Barrier Islands.........................................................13

A Review of Relevant Beach Plant Ecology Research.........................19

A Review of Relevant Physiological Plant Ecology Research...........24

Species Specifics....................................................................................................26

Literature Cited....................................................................................................34

III. LEAF FORM AND FUNCTION: TESTING A MODEL

Introduction........................................................................................................47

Materials and Methods.......................................................................................50

Results......................................................................................................................53

Discussion..............................................................................................................57

Literature Cited....................................................................................................64

IV. IMPORTANCE OF AND RESPONSE TO WATER STRESS IN BARRIER
ISLAND BEACH PLANT SPECIES

Introduction...........................................................................81
Materials and Methods..........................................................84
Results..................................................................................87
Discussion.............................................................................97
Literature Cited......................................................................106

V. USE OF PHOTOSYNTHETIC CARBON GAIN AS A COMMON
CURRENCY: MODELING RESPONSE OF FOUR PLANT SPECIES TO THE
PRESENT DAY BARRIER ISLAND BEACH ENVIRONMENT

Introduction...........................................................................123
Materials and Methods..........................................................125
Results..................................................................................129
Discussion.............................................................................134
Literature Cited......................................................................141

VI. CONCLUSIONS AND PREDICTIONS FOR THE FUTURE OF FOUR
BARRIER ISLAND BEACH PLANT SPECIES IN RESPECT TO CLIMATE
CHANGE..................................................................................163
CURRICULUM VITAE.................................................................172
LIST OF TABLES

Table I-1. *Amaranthus pumilus, Cakile edentula, Hydrocotyle bonariensis* and *Iva imbricata* representing different plant functional groups………………...7

Table IV-1. Average daily distribution and total monthly rainfall (cm) on Topsail Island, NC 1 July 2002 through 30 June 2003…………………………113

Table IV-2. Soil water content (%) of 100 g substrate samples taken at different depths from Topsail Island, NC in the spring and summer of 2004……………………………………………………………………..114

Table V-1. Total assimilation (mol CO$_2$ m$^{-2}$ day$^{-1}$) for *Amaranthus pumilus*, *Cakile edentula*, *Hydrocotyle bonariensis* and *Iva imbricata* during representative days from June 2002 until May 2003…………………………..148

Table V-2. Total monthly assimilation (mol CO$_2$ m$^{-2}$ month$^{-1}$) for *Amaranthus pumilus*, *Cakile edentula*, *Hydrocotyle bonariensis* and *Iva imbricata* From June 2002 until May 2003.................................................................149

Table V-3. Best-fit equations for the photosynthetic light response of *Amaranthus pumilus, Cakile edentula, Hydrocotyle bonariensis* and *Iva imbricata*……………………………………………………………………...150
LIST OF FIGURES

Figure I-1. Global distribution of major coastal barrier island ecosystems…………………8

Figure I-2. Formerly 3rd row home now within the intertidal zone of North Topsail Beach, North Carolina…………………………………………………………9

Figure I-3. Specific study site located on the southwestern end of Topsail Island, North Carolina……………………………………………………………………………………………………10

Figure I-4. Habitats located within the barrier island beach environment on the southwestern end of Topsail Island, North Carolina………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………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المتو
Figure III-9. Photosynthetic light response of *Cakile edentula* leaves illuminated on the adaxial and abaxial leaf surfaces.................................77

Figure III-10. Photosynthetic light response of *Hydrocotyle bonariensis* leaves illuminated on the adaxial and abaxial leaf surfaces.........................79

Figure III-11. Photosynthetic light response of *Iva imbricata* leaves illuminated on the adaxial and abaxial leaf surfaces...............................80

Figure IV-1. Daily rainfall totals on Topsail Island, NC from 1 July 2002 until 30 June 2003..............................................................................115

Figure IV-2. Photosynthetically Active Radiation (PAR) measurements taken on representative days during 2002 and 2003....................................116

Figure IV-3. Diagramatic representation of *Amaranthus pumilus, Cakile edentula, Iva imbricata, and Hydrocotyle bonariensis* life-history traits on Topsail Island, NC.................................................................117

Figure IV-4. Diurnal xylem water potential (Ψ) measurements taken on representative days during 2002-2003..............................................118

Figure IV-5. Diurnal assimilation rates (A) taken on representative days during 2002-2003........................................................................119

Figure IV-6. Diurnal stomatal conductance rates (g) taken on representative days during 2002-2003...............................................................120

Figure IV-7. Diurnal transpiration rates (E) taken on representative days During 2002-2003........................................................................121

Figure IV-8. Diurnal xylem water potential measurements (Ψ), assimilation
rates (A), conductance rates (g) and transpiration rates (E) taken on
21 Jun 2002…………………………………………………………………..…122

Figure V-1. PAR measurements taken on representative days during 2002 and 2003…………………………………………………………………..…151

Figure V-2a. Diurnal assimilation rates (A) taken once per month from June 2002 until September 2002……………………………………………..…152

Figure V-2b. Diurnal assimilation rates (A) taken once per month from October 2002 until January 2003……………………………………………..…153

Figure V-2c. Diurnal assimilation rates (A) taken once per month from February 2003 until May 2003……………………………………………..…154

Figure V-3. Photosynthetic light response of *Amaranthus pumilus*, *Cakile edentula*, *Hydrocotyle bonariensis* and *Iva imbricata* measured on 7 July 2002…………………………………………………………………..…155

Figure V-4. Predicted (A) and actual (B) photosynthetic carbon gain (PCG) for *Amaranthus pumilus*, *Cakile edentula*, *Hydrocotyle bonariensis* and *Iva imbricata*……………………………………………………….………156

Figure V-5. Schematic diagram of the three *Amaranthus pumilus*
transplantation sites on Topsail Island, NC………………………………….…..157

Figure V-6. Diurnal photosynthesis for representative *Amaranthus pumilus*
Plants at each of the transplantation sites as well as individuals found naturally growing in the driftline and foredune habitats………………………..158

Figure V-7. Conceptual model of how photosynthetic carbon gain (PCG) Thresholds could relate to life-history stages in *Amaranthus pumilus*..............159
Figure V-8. Photosynthetic light response of *Amaranthus pumilus* plants

Both inundated and non-inundated with saltwater during a 9 July 2004 overwash event on Topsail Island, NC (A.G. Snow, unpublished data)...........160

Figure V-9. Conceptual model of barrier island beach abiotic stresses, species response and resultant photosynthetic carbon gain (PCG)..............161

Figure V-10. Idealized relationship between abiotic stresses, plant response, photosynthetic carbon gain (PCG), allocation patterns and fitness in the barrier island beach environment..............................................162

Figure VI-1. Southwestern end of Topsail Island before (6 August 2001) and after (6 October 2001) a storm overwash event.................................171
ABSTRACT

Hancock, Thomas, E.

ECOPHYSIOLOGY OF BARRIER ISLAND BEACH PLANTS: RESPONSES IN FORM AND FUNCTION TO DAILY, SEASONAL AND EPISODIC STRESSES

Dissertation under the direction of William K. Smith, Ph.D., Charles H. Babcock
Professor of Botany

Barrier islands (BIs) are transient, highly dynamic geological structures of fairly recent origin found along most continental shorelines. In particular, eighty-five percent of the East and Gulf Coasts of the United States are fronted by BIs. Within this environment, the BI beach is considered physically controlled due to the harsh abiotic factors that predominate. The small suite of plant species that survive in this habitat have been the subject of numerous ecological studies for greater than one-hundred years. This research has provided a general understanding of how BI beach plants and their environment interact and affect one another. Unfortunately, research on the physiological ecology of BI beach plants is essentially nonexistent, with the exception of several West Coast (USA) studies, and therefore a detailed understanding of the physiological processes involved in plant response to stress is lacking. The most general objective of this dissertation is to incorporate the tools of physiological ecology into an ecological study that investigates the response of four plant species representing different functional groups to daily, seasonal and episodic stresses present on Topsail Island, North Carolina (USA).
Leaf stomatal frequency measurements, microscopic examination of internal leaf anatomy and photosynthetic light response measurements of *Amaranthus pumilus*, *Cakile edentula*, *Hydrocotyle bonariensis* and *Iva imbricata* were made in an effort to test predictions of a leaf form and function model proposed by Smith et al. (1997).

*Amaranthus pumilus*, a C₄ summer annual, had more stomata on the adaxial than abaxial leaf surface, typical Kranz anatomy, and higher adaxial photosynthetic light response. *Cakile edentula*, a C₃ cool weather annual, had slightly more stomata on the adaxial leaf surface, unifacial leaf anatomy and equal adaxial and abaxial photosynthetic light response. *Hydrocotyle bonariensis*, a C₃ perennial that grows by asexual rhizomes, had equal numbers of stomata on both leaf surfaces, bifacial leaf anatomy and equal adaxial and abaxial photosynthetic light response. *Iva imbricata*, a C₃ woody perennial, had equal numbers of stomata on both leaf surfaces, unifacial leaf anatomy and equal adaxial and abaxial photosynthetic light response. These results generally fit model predictions for a stressful environment.

In a second study, micrometeorological measurements were taken and soil water content determined in an effort to assess water availability in the BI beach environment. Additionally, plant strategies for mediating water stress were addressed via life-history trait determination, xylem water potential and gas exchange measurements. Moderate to high levels of rainfall occurred February through September, with forty percent of the yearly total associated with three storm systems (March, May and August). Soil water content was approximately three percent which is similar to values reported for several previous BI studies. *Amaranthus pumilus* had the shortest growing season (seven months), some of the highest assimilation rates and appeared to mediate transpiration and
xylem water potential via stomatal control. *Cakile edentula* was absent during the hottest months of the year when vapor pressure deficits would have been greatest (late July through late October). *Cakile edentula* had moderate to high assimilation rates, some of the highest stomatal conductance rates and lowest xylem water potential measurements. *Hydrocotyle bonariensis* exhibited the longest growing season (ten months), lowest assimilation rates and maintained an almost constant, high xylem water potential due to rhizomes that accessed water from slacks located inland of the foredunes. *Iva imbricata* had a nine month growing season, moderate assimilation and transpiration rates as well as moderate xylem water potential values. Based on these findings, *A. pumilus, H. bonariensis* and *I. imbricata* could be considered to employ tolerance strategies with *C. edentula* employing an avoidance strategy.

The importance of photosynthetic carbon gain (PCG) as a common currency was addressed in a third study by modeling the response of *A. pumilus, C. edentula, H. bonariensis* and *I. imbricata* to the present day BI beach environment. Micrometeorological, gas exchange and photosynthetic light response measurements as well as a transplantation experiment were conducted to estimate potential and realized PCG for each species. The realized yearly PCG was 63.14 mol CO$_2$ m$^{-2}$, 69.91 mol CO$_2$ m$^{-2}$, 59.10 mol CO$_2$ m$^{-2}$ and 80.16 mol CO$_2$ m$^{-2}$ for *A. pumilus, C. edentula, H. bonariensis* and *I. imbricata*, respectively. A PCG model based upon PAR measurements and the photosynthetic light response of each species suggested that there were several environmental factors responsible for the difference in realized and potential PCG. The response of each species to environmental stresses (including the genetic potential to respond to these stresses) can account for species differences in both potential
and realized PCG. A yearly PCG threshold may exist, as well as numerous life-stage PCG thresholds, that must be met in order for plants to survive and produce viable offspring. Each species in this study can acquire these thresholds via a unique combination of life-history, anatomical and physiological attributes.

The final chapter of this dissertation explored predictions for the future of *A. pumilus*, *C. edentula*, *H. bonariensis* and *I. imbricata* in the face of climate change. Many studies have indicated that in addition to a continuing (and possibly accelerated) rise in sea level, the intensity and frequency of extreme episodic storm events are likely to increase. These pressures when added to current and future habitat loss due to development and hardening of the shoreline will certainly result in a very different BI beach landscape than is seen today. Shorelines are predicted to retreat a few kilometers to tens of kilometers inland depending upon geographic location. How humans respond to these changes will determine the future of many BI beach plant species. Of the four species addressed in this study, *A. pumilus* is likely to be most negatively affected. *Amaranthus pumilus* was listed as federally threatened in 1993 due to habitat loss. Studies have shown that *A. pumilus* requires areas of suitable habitat that include accreting ends of BIs that do not contain hardened structures. These habitats are likely to become less common except in areas that are preserved or properly managed as dynamic landscapes. The Coastal Barrier Island Network is a recently funded (National Science Foundation) diverse group of biologists, geologists, engineers, economists and sociologists that have begun to work toward a national policy that promotes sustainable preservation, conservation and development of BI ecosystems within the natural limits imposed by this highly dynamic environment.
CHAPTER I

INTRODUCTION

Barrier islands are relatively young, dynamic, and transient geological features found along most continental shorelines (Figure I-1). The barrier island (BI) beach environment is physically controlled by daily, seasonal and episodic stresses whose intensities vary widely. These stresses are thought to have important implications for plant physiology, growth, reproduction and survival, ultimately dictating plant distribution patterns. The most general objective of this dissertation is to incorporate the tools of physiological ecology into an ecological study that investigates the response of four plant species representing different functional groups (as defined by Shao et al. 1996, Crawford 2008) to daily, seasonal and episodic stresses present on a North Carolina BI beach.

Chapter I provides an introduction to the study site, study species and dissertation objective. Chapter II reviews the dynamic nature of BIs, relevant ecological and ecophysiological studies and specifics of the study species. Leaf form and function in respect to a model proposed by Smith et al. (1997) is examined in Chapter III. Chapter IV investigates water availability and adaptations to plant water stress in the BI beach environment. Photosynthetic carbon gain (PCG) as a common currency is explored in Chapter V along with qualitative modeling of abiotic stressors, plant response and species fitness in the BI beach environment. Chapter VI focuses on predictions for the future of these plants in respect to global climate change.
Study Site

Topsail Island, North Carolina (USA) served as the study location for all investigations in the following chapters. Topsail Island is a low topographic relief, 42 km long barrier island that varies in width from 150 to 500 m located approximately 40 km northeast of Wilmington, North Carolina (Stallman 2004). The island is bounded on its northeastern end by New River Inlet and by New Topsail Inlet on its southwestern end. It is extensively developed with single family homes and cottages along its length (Frankenberg 1997). North Topsail Island has been designated as one of the highest risk real estate development zones in the United States due to erosion caused by the southwestern migration of New River Inlet as well as overwash from extreme episodic storm events (Pilkey et al. 1998, Pilkey and Pilkey-Javis 2007). Many formerly 2nd and 3rd row homes are now within the intertidal zone (Figure I-2).

Since 1900, North Carolina has averaged one hurricane strike every four years, including two exceptionally intense periods of activity during 1953-1960 and 1993-1999 (Barnes 2001). Topsail Island experienced four devastating hurricanes during the mid to late 1990’s with Hurricane Bertha (1996) flooding over 1/3 of the island land area and destroying most of the structures on the northeast end of the island, Hurricane Fran (1996) destroying nearly all 1st row homes along the entire length of the island and Hurricane Bonnie (1998) and Tropical Storm Dennis (1999) damaging many newly repaired structures (Barnes 2001).

The specific study site was located on the southwestern end of the island (34° 20’ 50” N, 77° 39’ 5” W) adjacent to New Topsail Inlet (Figure I-3). Due to migration of the inlet to the southwest at an average rate of 35 m per year, an extensive beach
environment extends approximately 1-2 km from the last beach home to the inlet. Within this beach environment a number of habitats can be defined and within each habitat a number of species can be found (Figure I-4).

Species

*Amarnathus pumilus* Rafinesque, *Cakile edentula* (Bigelow) Hooker, *Hydrocotyle bonariensis* Lamarck and *Iva imbricata* Lamarck were chosen for the current study as representative of different functional plant groups (Table I-1, Figure I-5) that occupy the same BI beach environment. The following chapters will detail investigations that compare and contrast the structural, physiological, and ecological aspects of each species in an attempt to evaluate mechanisms enabling their growth, reproduction, and survival within their respective microhabitats in the BI beach community. Speculation about future impacts of current scenarios for global climate change is also presented in Chapter VI.

*Amaranthus pumilus*

*Amaranthus pumilus* is a pioneer C₄ annual species that inhabits the driftline and foredune area of the BI beach (Weakley and Bucher 1992). Thus, this species has a distinct photosynthetic physiology that differs from the other three study species (all C₃ plants). The whole-plant architecture consists of a prostrate growth form, succulent leaves and pink to reddish stems. Acting as a low-lying sand collector, *A. pumilus* creates microtopographic mounds as the growing season progresses. These plants often become 30 cm in diameter, occasionally producing crowns with nearly 100 cm diameter ground cover (Weakley and Bucher 1992). As a result of population decline due to habitat loss,
A. pumilus was listed as federally threatened in 1993 (United States Fish and Wildlife Service 1993).

Cakile edentula

_Cakile edentula_ is a pioneer C₃ annual species that has an upright growth form and succulent leaves (Radford et al. 1968). The plant is common within its range (Barbour and Rodman 1970) and unlike _A. pumilus, C. edentula_ can persist into a second growing season in moderate climates (Barbour and Rodman 1970, Boyd and Barbour 1993, Cody and Cody 2004).

Hydrocotyle bonariensis

_Hydrocotyle bonariensis_ is a C₃ perennial species whose range includes the Gulf and East Coasts of the United States as well as locations in South America (Radford et al. 1968, Evans 1992). Seeds only germinate in swales located landward of the primary dune on BI beaches. Plants can grow seaward into the foredune via rhizomes (Evans 1992). Leaves are peltate, vary in width from 4 to 12 cm and senesce in winter with the rhizomes persisting underground until the next growing season (Radford et al. 1968).

Iva imbricata

_Iva imbricata_ is a woody C₃ shrub with succulent leaves found along the coasts of southern Virginia to the Florida Keys, Gulf Coast of the United States and on beaches of Caribbean islands (Jackson 1960). The plant can grow to heights of 1 m and widths of 3 m (Radford et al. 1968). As a seedling, _I. imbricata_ coinhabits the driftline with _A. pumilus_ and _C. edentula_.

Literature Cited


Table I-1. *Amaranthus pumilus*, *Cakile edentula*, *Hydrocotyle bonariensis* and *Iva imbricata* representing different plant functional groups.

<table>
<thead>
<tr>
<th>Species</th>
<th>Growth Form</th>
<th>Leaf Orientation</th>
<th>Leaf Form and thickness</th>
<th>Photosynthetic Pathway</th>
<th>Reproduction</th>
<th>Length of Growing Season</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Amaranthus pumilus</em></td>
<td>herbaceous, prostrate</td>
<td>90° angle from incident sunlight</td>
<td>spatulate, 3 mm</td>
<td>C₄</td>
<td>seeds ~ 3 mm long</td>
<td>6-7 months</td>
</tr>
<tr>
<td><em>Cakile edentula</em></td>
<td>herbaceous, erect</td>
<td>45° angle from incident sunlight</td>
<td>sinuately lobed, often crenate, 4 mm</td>
<td>C₃</td>
<td>seeds ~ 4-6 mm long</td>
<td>9 months</td>
</tr>
<tr>
<td><em>Hydrocotyle bonariensis</em></td>
<td>herbaceous, clonal</td>
<td>leaf angle and azimuth can change daily and seasonally</td>
<td>elliptate, 2 mm</td>
<td>C₃</td>
<td>seeds ~ 1-2 mm long, clonal growth</td>
<td>10 months</td>
</tr>
<tr>
<td><em>Iva imbricata</em></td>
<td>deciduous, shrub</td>
<td>varies from 45° to 90° angle from incident sunlight</td>
<td>peltate, 4 mm</td>
<td>C₃</td>
<td>seeds ~ 4-5 mm long</td>
<td>9 months</td>
</tr>
</tbody>
</table>
Figure I-1. Global distribution of major coastal barrier island ecosystems (indicated by dots). Arrows call attention to delta barrier islands. Taken from Pilkey (2003).
Figure I-2. Formerly 3rd row home now within the intertidal zone of North Topsail Beach, North Carolina. (Photographed by William K. Smith)
Figure I-3. Specific study site located on the southwestern end of Topsail Island, North Carolina.
Figure I-4. Habitats located within the barrier island beach environment on the southwestern end of Topsail Island, North Carolina. The general positions of *Amaranthus pumilus*, *Cakile edentula*, *Hydrocotyle bonariensis* and *Iva imbricata* are indicated.
Figure I-5. *Amaranthus pumilus*, *Cakile edentula*, *Hydrocotyle bonariensis* and *Iva imbricata* representing different plant functional groups living in the barrier island beach environment on the southwestern end of Topsail Island, North Carolina.
The Dynamic Nature of Barrier Islands

Barrier islands are found on approximately 15% of the world’s shorelines with some of the most extensive chains located along the Atlantic and Gulf Coasts of North America (Ehrenfeld 1990, Figure I-1). In particular, 85% of the East and Gulf Coasts of the United States contain BIs (Snyder and Boss 2002, Stive and Hammer-Klose 2004, Adger et al. 2005). Barrier islands occur in greatest abundance along microtidal and mesotidal coasts that exhibit low-relief coastal plains and wide continental shelves that are comprised of abundant sediments readily reworked by wave action (Glaeser 1978, Ehrenfeld 1990, Hayden et al. 1991, Pilkey et al. 1998). In general, BI formation is dependent upon a dynamic equilibrium encompassing sea level rise, wave energy and sediment supply (Dolan et al. 1980, Hayden et al. 1991).

Paleogeology

During the Wisconsinan glaciation maximum which occurred around 18,000 years before present (ybp), sea level was approximately 300 feet lower than today (Frankenburg 1997). As climate warmed and glaciers melted, a period called the Holocene Transgression, sea level rose at a rate of 10 mm/year (Frankenburg 1995, Pikley et al. 1998). This rate is thought to have been too rapid for BI formation (Dolan et al. 1980, Alexander and Lazell 2000, NOAA Coastal Services Center). When sea level rise slowed to about 2-3 mm/year, a relative equilibrium with sediment accumulation was
reached (Dolan et al. 1980, Hayden et al. 1991). It was during this time, approximately 5,000 – 7,000 ybp, that East Coast (USA) BIs began to form (Dolan et al. 1980, Ehrenfeld 1990, Frankenberg 1995, Pilkey et al. 1998, NOAA Coastal Services Center).

**Hydrogeological Theories of Barrier Island Geomorphology**

Three principle theories of BI formation have been proposed (Schwartz 1971). DeBeaumont (1845) suggested that near-shore ocean floor sediment is displaced by an approaching wave. The sediment is then picked-up and transported until the wave breaks, losing much of its energy. Subsequently, the sediment settles forming an offshore bar. Over time, this offshore bar can build to such an extent that it emerges above the water’s surface and forms a barrier island. Johnson, in his 1919 classic text on BIs, supported DeBeaumont’s *emergent bar theory* of BI formation. More recently, Otvos (1970) embraced the same theory citing the United States’ Gulf Coast BIs as examples.

Hoyt (1967) developed the *dune ridge submergence theory* suggesting that BIs are formed when sea level rise causes the formation of a lagoon between coastal dune ridges and the remaining mainland. The width of the island depends upon sand accretion prior to or during submergence. The length of the island depends upon the continuity of the dune ridge. Inlets are formed in areas of low elevation. The sea islands of South Carolina and Georgia have been suggested as examples of BIs formed via this mechanism (Schwartz 1971, NOAA Coastal Services Center).

Working along lake shores, Gilbert (1885) first proposed the *breached spit theory* that supposes BIs are created from sediment transported by longshore currents. Spits that form from the accretion of this sediment can be breached during storms, thus forming BIs. Fisher (1968) was the first to apply this idea to marine coastlines. As explained by
Pilkey et al. (1998), when sea level began to rise, water flooded river valleys changing a formerly straight shoreline into a sinuous one. The formation of BIs is a mechanism that attempts to straighten the shoreline. Waves attack protruding headlands forming spits, these spits are later breached by storms and form inlets, thus defining the island. Most of the BIs found in Virginia and North Carolina are thought to have formed in this manner (Pilkey et al. 1998). In a review of the evidence for all three principle theories of BI formation, Schwartz (1971) concluded that each was viable and applicable in different geographic locations.

Depending upon sediment supply, rate of sea level rise and hydrodynamic factors, BIs accrete and advance seaward, erode and retreat landward, or stabilize (Hoyt 1967). Due to the repeated forming and melting of continental ice sheets, there have been at least six discernable sequences of BI formation within the geologic past (Hoyt and Hails 1967). Sea level, however, has been rising at a moderate rate for the past 5,000 – 7,000 years resulting in landward migration and erosion of approximately 85% of the shoreline of the United States (Pilkey et al. 1998, Pilkey and Pilkey-Javis 2007). According to the 4th Assessment Report of the Intergovernmental Panel on Climate Change (IPCC), global average sea level is currently rising 3.1 mm/year (IPCC 2007). Storms that result in landward transportation of sand via overwash are the main mechanism of BI migration (Godfrey 1976, Frankenberg 1997). For example, a 1971 storm that occurred at Cape Hatteras, North Carolina removed a large portion of the beach overnight, depositing the majority of sand in overwash fans that extended into the marsh behind the island (Pilkey et al. 1998 and Pilkey-Javis 2007).

Inlets
Inlets spatially define the boundaries of most BIs and are notoriously unstable, resulting in BI migration up or down a coastline depending upon local conditions (Pilkey et al. 1998). For example, twenty-four inlets have existed at one time or another along the North Carolina Outer Banks since 1585. Five of these inlets are currently open (Frankenberg 1995). The instability of these BIs has resulted in the region being aptly named “The Graveyard of the Atlantic” due to the hundreds of ships that have run aground and sunk (Stick 1952, Stick 1958). New Topsail Inlet, North Carolina has been migrating 30 – 40 m to the southwest per year since at least the early 1930’s (Pilkey et al. 1998, Stallman 2004). Two recent examples of inlet closure include Mad Inlet between Bird Island and Sunset Beach, North Carolina and Old Topsail Inlet between Lea and Hutaff Islands, North Carolina (personal observation). New inlets can also form during storms. Three inlets, for example, were opened on Topsail Island during hurricane Fran in 1996 (Barnes 2001).

**Beach stress**

Historically, ecologists have recognized the dynamic nature of the BI beach environment, describing it as being physically controlled (Oosting 1954, van der Valk 1974a, Godfrey 1976). Abiotic factors such as high substrate surface temperatures, low water-holding capacity, sand movement, salt aerosols, high irradiance levels and storms that result in overwash have been implicated in controlling plant distribution patterns (see Ehrenfeld 1990 for review). These factors occur over a continuous timeframe, but for ease of discussion can be categorized into daily, seasonal and episodic stresses.

*Daily and seasonal stresses*
Daily stresses present on a North Carolina BI beach include substrate surface temperatures as high as 52°C (Oosting and Billings 1942), rapid vertical movement of rainfall through the substrate resulting in low moisture levels (Au 1974), burial by sand (Martinez and Moreno-Casasola 1993), salt deposition on leaves (Boyce 1954) and irradiance values of 2000 μmol of photons m⁻² s⁻¹ for extended periods of time (personal observation). An important seasonal stress is late fall to early spring storms that move large quantities of sand to the offshore sandbar, essentially defining the line of vegetation for the following growing season (Rogers and Nash 2003, Miyanishi and Johnson 2007). In addition to the mechanical destruction caused by these seasonal overwash events, salt-water inundation has been found to have many deleterious effects on plants often resulting in death of annuals and reduction of perennial biomass (DeJong 1978b, Schat and Scholten 1986, Guy et al. 1989, Ungar 1991, Alpha et al. 1996, Martinez et al. 2002).

In contrast to these traditional studies, however, Greaver and Sternberg (2006) found that foredune plants living on their Floridian and Bahamian study sites were able to utilized ocean water as a water source.

**Episodic stress**

Episodic stresses such as hurricanes, which have been termed Extreme Episodic Storm Events (EESE) by Feagin et al. (2009), are considered the dominant force influencing species composition in some coastal systems (Turner et al. 1997, Miyanishi and Johnson 2007, CBIN). Gutshick and BassiriRad (2003) expanded this idea stating that extreme events are the driving force in trait selection of most plants. Although EESE, and to some extend seasonal stresses, have a disproportionate affect on the BI
environment (Pilkey and Pilkey-Javis 2007), their impact is influenced by daily abiotic environmental gradients (Synder and Boss 2002, Stallings and Parker 2003).

Climate change impacts

All of the stresses mentioned previously, but especially those that are seasonal and episodic, could be exacerbated by future climate change in which storm intensity and frequency are predicted to increase (Goldenberg et al. 2001, Thompson et al. 2001, Hayden and Hayden 2003, Holgate and Woodworth 2004, Pilkey and Cooper 2004, Zhang et al. 2004, IPCC 2007, Elsner et al. 2008, Schlacher et al. 2008, Mann et al. 2009). Sea-level rise will most likely intensify the effect of storms on the BI beach environment (Pilkey and Pilkey-Javis 2007), with particularly dire implications for the North Carolina coast due to the large area of land that is within one meter of current mean sea-level (Nash 2008). In a long-term study conducted on Core Banks North Carolina, Riggs and Ames (2006) found that although there was only small-scale shoreline recession over the forty-one year data set, storm events produced extremely large-scale changes. The authors stated that if given enough time, barrier islands tend to recover and approach their pre-storm location but this rarely occurs before another storm makes landfall.

Climate change could affect organisms world-wide, indeed in a review by Cleland et al. (2007) numerous plant studies were cited that found correlations between earlier spring flowering and rising temperatures. Pike and Stiner (2007) discovered that rising global temperatures were correlated with earlier nesting dates for loggerhead turtles along Cape Canaveral National Seashore. Additional studies have revealed climate change effects on the ecology of many different species (reviewed in Parmesan 2006). Ongoing
climate change is considered to be a driving factor for ecosystems in the 21st century (Jentsch et al. 2007), with loss of habitat and associated biota the most immediate threat to beaches (Schlacher et al. 2008). Crawford (2008) extends this sentiment by stating that an especially important danger to maritime vegetation will be the actions humans take to save their property from sea inundations.

**A Review of Relevant Beach Plant Ecology Research**

The study of dune plants has a long history dating back to the ecological work of Cowles (1899) and Kearney (1900) and the anatomical/morphological studies of Chrysler (1904), Kearney (1904) and Starr (1912), all undertaken within the United States. Early work conducted on European dunes has been amply reviewed in the influential publications of Salisbury (1952) and later Ranwell (1972). More recent studies of European dune plants accessed germination requirements (Pemadasa and Lovell 1975, Ignaciuk and Lee 1980), mineral requirements (Pemadasa and Lovell 1974), plant distribution in relation to abiotic factors (Pemadasa et al. 1974) and demography (Watkinson 1978, Watkinson and Harper 1978). In an attempt to remain as relevant as possible, given that Topsail Island, North Carolina (USA) is the study site for this dissertation, the following discussion will focus on historical studies conducted within the United States and in particular along the East Coast. The term “beach” includes all habitats between the spring high tide line and the back of the primary dune.

**East Coast (USA)**

Cowles, in his 1899 study located along the dunes of Lake Michigan, emphasized the dynamic nature of vegetation in relation to local geology. Studies on the importance of physical factors as major controls in the dune environment were greatly expanded by
Oosting in a series of experiments undertaken on several barrier islands (BIs) located near Beaufort, North Carolina (Oosting 1945, 1954, Oosting and Billings 1942). After careful documentation and experimentation with many aspects of the physical environment, Oosting concluded that salt spray was the main factor determining the distribution of perennials on the BI beach. Wells (1939) came to a similar conclusion in that salt spray was the limiting factor allowing *Quercus virginiana* Miller to become the dominant species in the maritime forest found on Smith Island located at the mouth of the Cape Fear River, North Carolina. Alternatively, van der Valk (1974a, 1975) stated that sand movement was the main limiting factor to the distribution of annuals on the dunes in Cape Hatteras National Seashore, North Carolina. He additionally documented macro and microclimate aspects of the BI beach environment and developed a model of nutrient cycling involving salt spray (1974b, 1977).

Boyce (1954) undertook an exhaustive study of the salt spray community found on Smith Island. This research still serves as the basis for our understanding of salt spray effects on plant morphology, physiology and ecology. In a later study, Art et al. (1974) determined that the major nutrient input into the maritime forest of Fire Island, New York was via salt spray. Au (1974) published a monograph of the ecological processes on Shackleford Bank, North Carolina in which he reported that substrate moisture levels were low (3 – 4%), but remarkably consistent – a finding echoed by van der Valk (1974b). In the same studies, Au made some of the earliest water potential measurements for East Coast BI beach plants and concluded that water availability was not a limiting factor for growth.
While studying the dune system on Cape Lookout National Seashore, Godfrey (1976) concluded that the North Carolina Outer Banks were migrating landward, that storms play a critical role in this migration and that overwash was the major mechanism of movement. Hosier and Cleary have come to similar conclusions about BIs along North Carolina’s southern coast (Hosier and Cleary 1977, Cleary and Hosier 1979).

The majority of BI plant ecology research has found that physical factors determine plant distribution patterns (see Ehrenfeld 1990 for review). There are, however, a handful of studies that indicate biological interactions are influential and therefore must be considered. Silander and Antonovics (1982) employed a perturbation approach on Core Banks, North Carolina, in which they removed dominant and subdominant species either singly or within groups and documented response of the remaining species. They were able to detect significant species interactions, concluding that these interactions are important in structuring the dune community. In a series of studies conducted on BIs in Georgia and Florida, Franks (2003a, 2003b, Franks and Peterson 2003) documented significant nurse plant effects especially with increasing disturbance severity, concluding that facilitation is important in coastal dune succession.

In a number of studies conducted by North Carolina State University researchers, much of the growing knowledge about dune plant ecology was applied to dune stabilization (Woodhouse and Hanes 1966, Woodhouse et al. 1968, Woodhouse et al. 1976, Woodhouse 1978). The general findings of these studies were that perennial plants such as Ammophila breviligulata Fernald, Uniola paniculata Linnaeus and Panicum amarum Elliot could be successfully grown in greenhouses, transplanted into the dune environment and act as sand traps that build dunes. Watering during the first few weeks
after transplantation and fertilization four times per year were critical determinates of seedling and plant survival. Recently, there has been renewed interest in using native vegetation (Rogers and Nash 2003) and especially *Quercus virginiana*, to help stabilize BIs (Feagin et al. 2009, CBIN).

Great Lakes (USA) and Canada

Keddy (1981, 1982) conducted a series of experiments on a beach in Nova Scotia using *Cakile edentula* (Bigelow) Hooker, a common C$_3$ winter annual. In these experiments, he was able to develop a model for *C. edentula* incorporating density-dependent and density-independent environmental factors that accurately predicted survivorship and reproduction along an environmental gradient. Working on the dune system of Lake Huron, Zhang and Maun (1992) determined that sand burial increased plant growth and reproductive output. Growth was the greatest in unwashed sand which may suggest possible beneficial mycorrhizal interactions. Using similar study sites, Payne and Maun (1984) determined that desiccation, insect damage, disease infection and human trampling were major causes of *C. edentula* seedling death. Maun and Lapierre (1986) reported a positive relationship between seed weight and depth of emergence for several dune species.

Zhang and colleagues focused on the dimorphic nature of *C. edentula* seeds in another set of studies also undertaken along the Lake Huron dunes. The authors found that upper seeds were selected for dispersal while lower seeds remained on the parent plant (Zhang 1994), seed mass and morphology could indirectly affect life history traits (Zhang 1993) and several dune species including *C. edentula* have the ability to form a persistent seed bank (Zhang and Maun 1994). Zhang (1996) expressed the need for
coastal dune studies to include experimental designs that test the importance of multiple environmental factors on plant growth and survival.

West Coast (USA)

Barbour and Rodman (1970) chronicled the introduction and subsequent spread of *Cakile edentula* and *Cakile maritima* Scopoli along the West Coast of the United States in a descriptive study that included details of the plants’ life-history traits. Barbour (1970) added to this descriptive knowledge in a series of experiments that included both laboratory and field manipulations involving germination and growth response of *C. maritima* to temperature, light and salt spray. In an attempt to determine causative factors for zonation patterns, Barbour and DeJong (1977) discovered that, when tested separately, tolerance to salt spray and salt water inundation of nine California dune plants were strongly correlated with their distance from mean high tide. Three plants, however, did not fit predictions leading the authors to conclude that single-factor experimental designs were not sufficient to account for the distribution of all dune plants.

Improved salt trap designs based upon the earlier work of East Coast researchers (Oosting 1945, 1954, Oosting and Billings 1942) allowed Barbour (1978) to develop comprehensive salt deposition maps that accurately accounted for the distribution of some dune plants. Building upon these studies, Boyd and Barbour (1986) determined that *C. edentula* var. *lacustris* (found along the Great Lakes) and *C. edentula* var. *edentula* (found along the East and West Coasts) had diverged physiologically over the past 9,000 years in part due to differences in salt tolerance. In several studies which focused on the historical and current distribution of *C. edentula* var. *edentula* and *C. maritima* in the dune habitat of California, Boyd and Barbour (1993) determined that the
ability of *C. maritima* to survive into a second and even third growing season may be the main reason it replaced *C. edentula var. edentula* over a forty year period. Preferential seed predation by *Peromyscus maniculatus*, the common deer mouse, probably increased the replacement rate (Boyd 1988, Boyd 1991).

**A Review of Relevant Physiological Plant Ecology Research**

The discipline of physiological plant ecology combines ecological and physiological measurements in an attempt to explain plant distribution and abundance (Billings 1985; Barbour et al. 1985; Lambers et al. 1998). According to Billings (1985), physiological ecology shared beginnings with the field of ecology and it was not until the development of transportable technologies allowing measurement of gas exchange and water balance that physiological ecology became distinct. Although the techniques of physiological plant ecology have often been employed in many extreme environments such as the desert and alpine timberline (Billings 1985), Barbour et al. (1985) found few instances in which “modern approaches to gas exchange, water balance and plant demography have been applied to beach taxa”. There has been little additional research since the publication of that finding. The following paragraphs provide a short review of the physiological plant ecology studies undertaken on coastal dunes.

DeJong completed a number of basic physiological ecology studies on the northern California dunes in which he determined the photosynthetic maximum of several species of plants in relation to light, temperature and CO$_2$ concentrations inside the leaf (DeJong 1978a), compared photosynthetic response while growing in media of different salinities (DeJong 1978b) and characterized water balance in relation to the microclimate in which the plants grew (DeJong 1979). Taking measurements from sites
in both northern and southern California, Pearcy (1976) addressed the photosynthetic plasticity of *Atriplex lentiformis* in relation to thermal regimes, identifying ecotypic differences in the subpopulations found in each region. Mooney (1980) also found ecotypic variations when he conducted a similar study using *Heliotropium curassavicum*. In another investigation, Mooney et al. (1983) characterized the physiological ecology of five herbaceous plants inhabiting the dunes of Point Reyes National Seashore in California. Working at the same location, Pavlik (1983) not only documented the photosynthetic trends of *Ammophila arenaria* and *Elymus mollis*, but brought nitrogen use efficiency (NUE) and morphological traits into his discussion.

Using gas exchange and xylem water potential measurements, Ishikawa et al. (1990) categorized plants living on Japanese dunes as heat-resistant, heat-enduring or heat-evading based upon their ecophysiological characteristics. The researchers continued their studies by examining plant distribution patterns in relation to plant soil water salinity tolerance (Ishikawa et al. 1991), site micrometeorological characteristics (Ishikawa et al. 1995) and plant resistance to drought (Ishikawa et al. 1996). In a more recent study involving ten plant species inhabiting the Lake Erie sand dunes, Perumal and Maun (2006) discovered that biomass, photosynthetic efficiency and chlorophyll-α fluorescence all increased in response to burial by sand.

In the only relevant physiological ecology study conducted on the East Coast (USA), Dubois (1977) completed a very ambitious project in which she documented water use efficiency (WUE), NUE and photosynthetic rate in relation to temperature and xylem water potential of three C₃ and five C₄ species living on the Georgia dunes. She determined that C₃ and C₄ species had similar photosynthetic temperature response
curves, but that the C₄ species had higher NUE and WUE which may be an important adaptive advantage.

**Species Specifics**

*Amaranthus pumilus*

*Amaranthus pumilus* is a pioneering C₄ annual species that inhabits the driftline and foredune area of the BI beach (Weakley and Bucher 1992). The plant has a prostrate growth form, succulent leaves and pink to reddish stems. Acting as a sand binder, *A. pumilus* creates mounds as the growing season progresses. These plants often become 30 cm in diameter, occasionally producing growths 90 cm in diameter (Weakley and Bucher 1992).

Historically, *A. pumilus* was found from Nantucket, Massachusetts to Folly Beach, South Carolina. By 1987, however, the plant was extirpated from nearly 75% of its earlier range (Weaker and Bucher 1992). Due to population decline and continued habitat loss from development, *A. pumilus* was listed as federally threatened in 1993 (United States Fish and Wildlife Service 1993). The current distribution of *A. pumilus* is limited to North and South Carolina (United States Army Corps of Engineers 1992-1995, Hancock and Hosier 2003) although several populations have reappeared in New York (Clements and Mangels 1990, van Schoik and Antenen 1993) and Maryland (Ramsey et al. 2000). *Amaranthus pumilus* population numbers have been documented to fluctuate tremendously from year to year (Weakley and Bucher 1992, United States Corps of Engineers 1992-1995, Strand 2002, Hancock and Hosier 2003).

Research involving *Amaranthus pumilus* is quite limited. The status survey conducted by Weakley and Bucher (1992) has served as the foundation for all subsequent
Baskin and Baskin (1998) conducted an investigation to determine the germination requirements of *A. pumilus*. They found that fresh seeds were physiologically dormant, cold stratification broke this dormancy and light and high temperatures (30°C) were required for germination. Norden et al. (2007) determined that treatment of nonstratified *A. pumilus* seeds with solutions of potassium salt of gibberellin A₃ (K-GA₃) removed physiological dormancy, reduced seed sensitivity to light and broadened the temperature range for germination. Hamilton (2000) conducted a series of propagation experiments which involved collecting *A. pumilus* plants growing at Huntington Beach State Park, South Carolina and transplanting them to a greenhouse. Plants were grown to reproductive maturity and seed was subsequently collected. The seeds were germinated, allowed to grow for 4-6 weeks in the greenhouse and transplanted to experimental test sites located adjacent to the original collection sites. Eighteen percent of the transplanted plants produced seed the following fall.

Strand (2002) characterized the genetic structure of *A. pumilus* populations by analyzing the amount and location of genetic variation at a variety of loci including chloroplast DNA, introic regions of nuclear DNA and anonymous PCR-based markers (RAPDS). He found no observable differences among individuals when comparing the chloroplast DNA and introic regions of nuclear DNA data. The RAPDS data, however, did reveal a pattern in which northern populations of *A. pumilus* were genetically distinct from southern populations. Strand stated that it is possible that the Chesapeake Bay provides a natural barrier to seed migration between these populations.

Other works of interest include a study in which Light Detection and Ranging (LIDAR) and Geographic Information Systems (GIS) were used to determine and model
suitable habitat for *A. pumilus* (Sellars and Jolls 2007), an investigation of the chemical components and composition of *A. pumilus* seed in respect to food value (Marcone 2000) and a short note about *Albugo bliti* fungal infection on plants used in a restoration effort in South Carolina after Hurricane Hugo (Keinath et al. 2003). Hancock and Hosier (2003) completed an ecological study of *A. pumilus* in which they found no evidence for biological control of population dynamics but determined that storm overwash was the main factor limiting seedling survival and subsequent seed set for adult plants. Additionally, they mentioned that the inability to emerge from depths greater than 1 cm as well as a short growing season may be adaptive disadvantages when compared to BI beach associates. Finally, Rosenfeld (2004) determined that distance from the ocean had a significant effect on *A. pumilus* survivorship, size and reproduction. She attributed this to gradients of physical factors such as soil salinity, salt spray and overwash rather than biological interactions.

*Cakile edentula*

*Cakile edentula* is a pioneering C₃ annual species that has an upright growth form and succulent leaves (Radford et al. 1968). The plant can reach heights of 60 cm with widths of 70 cm (personal observation). *Cakile edentula* is common within its range from southern Florida into Canada, along the West Coast of the United States and the shores of the Great Lakes (Barbour and Rodman 1970). Unlike *A. pumilus*, *Cakile edentula* can persist into a second growing season in moderate climates such as the coasts of California (Barbour and Rodman 1970, Boyd and Barbour 1993) and Australia (Cody and Cody 2004). On the East Coast of the United States, *C. edentula* is often found in association with *A. pumilus* and *Iva imbricata* growing just above the spring high tide.
(driftline) where it accumulates sand and begins the process of dune formation (Colosi and McCormick 1978, Hancock and Hosier 2003, Rogers and Nash 2003).

*Cakile edentula* has been the subject of numerous ecological and ecophysiological studies (see Maun et al. 1990) as have been reviewed in Chapter I. In fact, the majority of experiments conducted on the dunes of the Great Lakes and West Coast of the United States using ecophysiological techniques have involved *C. edentula*. There are, however, a few studies that have focused on other aspects of the biology of *C. edentula* or were undertaken in different locations.

Tyndall et al. (1986a) conducted an experiment at Currituck Beach, North Carolina to ascertain why *C. edentula* was the dominant species in the beach habitat. They discovered that *C. edentula* seeds were buoyant and that seedlings could emerge from greater depths than other beach or foredune associates; important factors given the high sand burial rate of the site. In a follow-up study meant to determine why *C. edentula* was preferentially found on beach versus foredune habitats, Tyndall et al. (1986b) concluded that low soil water potential resulted in lower leaf water potentials and stomatal conductance values of *C. edentula* living in the foredune when compared with plants living on the beach.

In a laboratory germination study designed to mimic different microenvironmental conditions, Adair et al. (1990) found that increased soil moisture provided by wrack material (detritus) and deeper seed burial were responsible for increased germination rates of *C. edentula*. Gedge and Maun (1992) experimented with different levels of herbivory on *C. edentula* and discovered that plants were able to compensate for low to medium damage but that high levels of damage reduced growth
and reproductive output. The authors suggested that natural populations are able to avoid high rates of destruction because herbivores have a difficult time locating plants.

Donohue conducted a series of studies focusing on dispersal, fitness, relatedness and selection in *Cakile edentula* growing along the shores of the Great Lakes. In one study, she determined that selection on dispersion patterns occurred through density effects rather than dispersal distance (Donohue 1997). Using the characteristic that fruits of *C. edentula* are divided into proximal segments that remain on the parent plant and distal segments that disperse (Maun et al. 1990), Donohue confirmed intuition by finding that proximal seeds had a greater probability of reproduction near the mother plant while distal seeds had a greater probability of reproduction at more distant sites. In a second study, she found that environmental factors strongly influenced the expression of plant traits which in turn influenced dispersal (Donohue 1998). In a third study, Donohue (2003) investigated the influence of relatedness on *C. edentula* plants growing close to one another along the shores of Lake Michigan. She observed significant group selection on plant size when neighbors were siblings but not when they were unrelated and that individual and group selection operated in the same direction. In a final study, she noted that individual selection was detected at low density while group selection was detected at higher densities for *C. edentula* growing on the dunes of the Great Lakes (Donohue 2004).

Dudley (1996a) conducted a study in which she raised *C. edentula* plants from a wet-site and a dry-site population in a common greenhouse environment. The dry-site population had significantly smaller leaf size and greater WUE than the wet-site. In a follow-on study, Dudley (1996b) used phenotypic selection analysis to test whether
smaller leaves and greater WUE were adaptive in drier environments. She found that in her experimental set-up, smaller leaves and greater WUE were selected for in the dry environment while neither were selected for in the wet environment. Additionally, WUE primarily affected plant fitness by increasing vegetative biomass. In a more recent experiment investigating kin recognition in plants, Dudley and File (2007) reported that allocation to the roots of *C. edentula* increased when groups of strangers shared a common pot but not when siblings shared a pot. They concluded that root interactions may provide cues for kin recognition.

*Hydrocotyle bonariensis*

*Hydrocotyle bonariensis* is a C$_3$ perennial species whose seeds germinate in swales located landward of the primary dune on BI beaches (Evans 1992a). The plants can grow seaward into the foredune via rhizomes (Evans 1992a). Leaves are peltate, vary in width from 4 to 12 cm and senesce in winter with the rhizomes persisting underground until the next growing season (Radford et al. 1968). *Hydrocotyle bonariensis* is common on the barrier islands of the southeastern United States and has been known to form extensive populations where individual clones may cover 100 m$^2$ and consist of greater than 1500 ramets (Evans 1988).

Evans conducted a series of experiments in which he investigated the ability of *H. bonariensis* to translocate nutrients and water, evaluating possible ecological and evolutionary consequences of these abilities. He discovered that *H. bonariensis* can translocate nitrogen acquired by ramets growing in areas of high concentration to ramets growing in areas of low concentration, thus allowing expansion into environments where resources are patchy or nonexistent (Evans 1988). In another study, Evans (1991) was
able to quantitatively access the fitness related benefits of nutrient and water translocation by measuring increases in total biomass, ramet proliferation and seed production. Evans (1992b) also documented that \textit{H. bonariensis} clones exhibit an integrated morphological response to a resource environment (the dune) which is variable in space and time.

\textit{Hydrocotyle bonariensis} has been observed to expand into salt marsh communities from surrounding dune systems with no apparent ill effects due to contact with saline water (Evans and Whitney 1992). In an attempt to explain this observation, the authors conducted a field experiment in which they severed some rhizomes of \textit{H. bonariensis} and did not sever others. They found that ramets attached to severed rhizomes exhibited high mortality while ramets attached to non-severed rhizomes were not affected by saline conditions. The authors concluded that translocation of water from ramets growing in dune systems allowed ramets of \textit{H. bonariensis} to grow into the salt marsh. Finally, Evans and Cain (1995) demonstrated that \textit{H. bonariensis} can respond to the environment by altering branching patterns, internodal distance and direction of rhizome growth; essentially the plant can “forage” for resources.

In other studies, Overdieck and Strain (1981) discovered that \textit{H. bonariensis} growing at three distinct sites on Shackleford Banks, North Carolina were essentially ecotypes adapted to their local environment. Longstreth et al. (1981) found that leaves of \textit{H. bonariensis} grown under high irradiances were smaller, thicker, reached maximum size more quickly and had higher photosynthetic rates than did leaves grown under low irradiances. Haddad and Mazzafera (1999) conducted an investigation in which they grew cuttings of \textit{H. bonariensis} in different concentrations of sodium chloride. They observed that regardless of the concentration, all sodium chloride solutions induced a
decrease in fresh and dry weights and chlorophyll content of leaves. Finally, Knight and Miller (2004) used reciprocal transplants to address the existence and possible causes of local adaptation in *H. bonariensis* plants growing on Saint George Island, Florida. They reported evidence for local adaptation and concluded that this adaptation was related to interactions with other dune plants.

*Iva imbricata*

*Iva imbricata* is a woody C$_3$ shrub with succulent leaves found along the coasts of southern Virginia to the Florida Keys, Gulf Coast of the United States and on beaches of Caribbean islands (Jackson 1960). The plant can grow to heights of 1 m and widths of 3 m (Radford et al. 1968). As a seedling, *I. imbricata* coinhabits the driftline with *A. pumilus* and *C. edentula*. Winter storms usually remove all vegetation from this habitat including *I. imbricata* seedlings. Seedlings that are landward (higher elevation) of winter storm overwash can survive into multiple growing seasons trapping sand and acting as dune builders (Rogers and Nash 2003). Thus on Topsail Island, *I. imbricata* essentially defines the beginning of permanent vegetation known as the foredune and/or primary dune (Frankenberg 1997).

There are only four studies that have been conducted with *I. imbricata*. Colosi and McCormick (1978) extensively documented the population structure of *I. imbricata* in five different habitats on Smith Island, North Carolina. They found that seed production and seedling emergence were greatest in the foredune habitat, but that harsh physical factors resulted in a high mortality rate so much so that populations were maintained via asexual reproduction. In habitats where environmental conditions were
In a series of studies, Franks investigated inter and intraspecific facultative interactions of *I. imbricata* on the sand dunes of Georgia and Florida. In one study, he found that interactions were facultative for survival but competitive for biomass production and that the presence or absence of neighbors was more important than whether the neighbors were conspecifics or not (Franks 2003a). In a second study, Franks and Peterson (2003) determined that facilitation increased with increasing disturbance severity but that species richness had little effect. In a third study, Franks (2003b) found support for the nucleation hypothesis in that nurse plants provided microsites for the accumulation and germination of seeds and subsequent seedling growth of *I. imbricata*.

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CHAPTER III

LEAF FORM AND FUNCTION: TESTING A MODEL

Introduction


More recently, questions concerning leaf orientation impacts on anatomy, physiology and resultant photosynthetic rates have been posed (DeLucia et al. 1991, Poulson and DeLucia 1993, Smith el al. 1998, Evans and Vogelmann 2006, Soares et al. 2007). The importance of direct versus diffuse light has also begun to be addressed (Johnson and Smith 2006, Brodersen and Vogelmann 2007, Brodersen et al. 2008). New
techniques employing fibre optic, chlorophyll fluorescence, and photo-acoustic technologies have given researchers the ability to observe leaf anatomy at the cell and chloroplast level providing the opportunity for detailed experiments addressing the relationship of leaf form to function (Evans 1999, Han et al. 1999, Yano and Terashima 2001, Yano and Terashima 2004, Evans and Vogelmann 2003, Evans and Vogelmann 2006, Wang et al. 2008 – and references therein).

Regardless of the approach employed or technologies utilized, the goal of leaf form and function research is to understand how plants maximize photosynthesis given developmental, structural and energy constraints. To this end, Smith et al. (1997) proposed a model that describes how plants maximize photosynthesis per unit leaf biomass by regulating light and CO₂ gradients inside the leaf. The model predicts leaf form and orientation in relation to a gradient of environmental stresses. According to the model, as environmental stresses increase (including sunlight), leaf anatomy changes from monotypic layers consisting of spongy mesophyll (i.e. a unifacial leaf) to differentiated layers with development of adaxial palisade mesophyll and abaxial spongy mesophyll (i.e. a bifacial leaf). As stresses continue to increase, an abaxial palisade layer begins to develop making the leaf more symmetrical. At the highest levels of stress, leaves become cylindrical with the internal anatomy reverting back to a monotypic layer of spongy mesophyll cells. The cylindrical shape of the leaf provides for a large overlap between the internal light and CO₂ diffusion gradients resulting in increased photosynthesis per unit leaf biomass. The cylindrical leaf shape (versus a planar leaf) reduces the stressful effects of sunlight due to the cosine effect (Nobel 1999). The model also predicts that leaf form will proceed from a horizontal to a vertical orientation as
environmental stresses increase. In lower stress environments, leaves are predicted to be hypostomatous (i.e. stomata only present on the abaxial surface) becoming amphistomatous (i.e. stomata present on both abaxial and adaxial surfaces) as environmental stresses increase. Importantly, this conceptual model of leaf form includes the idea that leaf morphology and anatomy is dictated by leaf orientation and the resulting sunlight exposure on both leaf sides, including the total amounts on each side, as well as the ratio of adaxial/abaxial incidence (Smith et al. 1997, 1998).

A number of studies provide support for the model’s predictions in relation to leaf anatomy (Nobel et al. 1975, Day et al. 1990, Evans 1995, Rocas and Scarano 2001, Oguchi et al. 2003), leaf orientation (DeLucia et al. 1991, Poulson and DeLucia 1993, Evans and Vogelmann 2003, Greaver and Herbert 2004), and stomatal frequency and position (Mott et al. 1982, Boardman et al. 1991, Woodward et al. 2002, Wang et al. 2008). However, the majority of these studies were conducted on agricultural species or on natural species grown in the greenhouse and artificially manipulated (with two notable exceptions – Nobel et al. 1975, Greaver and Herbert 2004). Smith et al. (1998) is the only study that has directly tested the model’s prediction and these tests were limited to species living in two stressful habitats (the United States Rocky Mountain subalpine and five Australian communities).

The leaf form versus environmental stress model awaits further validation with species from a variety of habitats with different stress levels according to quality and quantity. An excellent test of the model can be made with barrier island (BI) beach species of the east coast of the United States. Plants growing on BI beaches face numerous abiotic stresses that limit growth. Stresses such as high solar radiation, salt
spray, sand abrasion, low nutrient substrates, and salt water overwash have been documented to affect leaf form (see Erhenfeld 1990 for a review) and assumedly leaf function. Due to the characteristics of this harsh and highly transient environment, BI beach species should provide a robust test of the model’s breadth and applicability.

In the present study, four species representing distinct functional plant groups (as defined by Shao et al. 1996, Crawford 2008) were chosen to test the predictions of the leaf form/function model proposed by Smith et al. (1997).

**Materials and Methods**

**Study Site**

Topsail Island is a low topographic relief, 42 km long BI that varies in width from 150 to 500 m located approximately 40 km northeast of Wilmington, North Carolina (Stallman 2004). The island is extensively developed with single family homes along almost its entire length (Frankenburg 1997). The study site was located on the southwestern end of the island (34° 20’ 50” N, 77° 39’ 5” W) adjacent to New Topsail Inlet. Due to migration of the inlet to the southwest at an average rate of 35 m per year, an extensive beach and dune environment extends approximately 1-2 km from the inlet to the first beach home.

**Species**

*Amaranthus pumilus* (Rafinesque) is a pioneering C₄ annual species that inhabits the driftline and foredune area of the BI beach (Weakley and Bucher 1992). The plant has a prostrate growth form, succulent leaves and pink to reddish stems. As a result of population decline due to habitat loss, *A. pumilus* was listed as federally threatened in 1993 (Weakley and Bucher 1992, United States Fish and Wildlife Service 1993). *Cakile*
edentula (Bigelow) Hooker is a pioneering C₃ annual species that has an upright growth form and succulent leaves (Radford et al. 1968). The plant is common within its range (Barbour and Rodman 1970) and unlike A. pumilus, C. edentula can persist into a second growing season in moderate climates (Barbour and Rodman 1970, Boyd and Barbour 1993, Cody and Cody 2004). Hydrocotyle bonariensis is a C₃ perennial species whose seeds germinate in swales located landward of the primary dune on BI beaches (Evans 1992). The plants can grow seaward into the foredune via rhizomes (Evans 1992). Leaves are peltate, vary in width from 4 to 12 cm and senesce in winter with the rhizomes persisting underground until the next growing season (Radford et al. 1968). Iva imbricata is a succulent leaved, woody C₃ shrub that can grow to heights of 1 m and widths of 3 m (Radford et al. 1968). As a seedling, I. imbricata coinhabits the driftline with A. pumilus and C. edentula.

The Sunlight Environment

Continuous measurements of Photosynthetically Active Radiation (PAR) were taken from June 2002 until June 2004 using a LI-190 Quantum Sensor (Li-Cor, Lincoln Nebraska) mounted on a 1.5 m wooden pole (10 cm X 10 cm) interfaced with a HOBO® data logger via a Universal Transconductance Amplifier (EME Systems, Berkley CA). Individual measurements of PAR where taken every 2-3 hours from dawn until dusk approximately one day per month from June 2002 until June 2004. For individual PPF measurements, a LI-190 Quantum Sensor (Li-Cor, Lincoln, Nebraska) interfaced with a Li-250A hand-held light meter (Li-Cor, Lincoln, Nebraska) was used. The PAR sensor was oriented toward the sky approximately 2 cm above a representative leaf from each
species (PARsky). The measurement was then repeated with the PAR sensor oriented downward and approximately 5 cm above the sand substrate (PARsand).

Stomatal Frequency and Distribution

One fully expanded leaf located on the third to fifth branch of six representative individuals of each species was collected on 18 June 2003, 20 July 2003, 19 May 2004, 18 June 2004 and 18 June 2008, stored in a cooler and transported to the laboratory for determination of adaxial and abaxial stomatal frequencies. An epidermal peel of both the adaxial and abaxial surface was made following the protocol of Brewer and Smith (1994). Stomatal counts were conducted on three distinct areas of the six different leaves per side per species per sample date. A single factor ANOVA was used to test for within species stomatal frequency differences due to sampling date. A Paired Student’s t-test was used to determine significant differences between the adaxial and abaxial stomatal means.

Internal Leaf Anatomy

One fully expanded leaf located on the third to fifth branch of five representative individuals of each species was collected on 18 June 2008, stored in a cooler and transported to the laboratory. Leaves were sectioned perpendicular to the midvein with a vibratome (Smith et al. 1998, Ruzin 1999) and observed using a Zeiss Axioplan upright light microscope (Carl Zeiss Incorporated, Germany) with a 4X objective (1:1 ratio). Images were captured with a microscope mounted Hamamatsu color chilled 3CCD camera (Hamamatsu Global, Japan) and analyzed using Image Pro-Plus 6.2 software (Media Cybernetics, Bethesda, Maryland).

Photosynthetic Light Response
Photosynthetic light response of both the adaxial and abaxial leaf surface of each species was measured using the Transportable Photosynthesis System (PP Systems, Amesbury Massachusetts). The first fully expanded leaf of nine to twelve individuals of each species was chosen for measurement. Neutral density filters were used to attenuate natural light resulting in PAR values ranging from 2000 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) (full sun) to 100 \( \mu \text{mol m}^{-2} \text{s}^{-1} \). Leaves were allowed to acclimate to new light intensities for two minutes between readings. Previous measurements have shown that leaves return to a maximum photosynthetic rate for a given PAR value within two minutes and that order of light attenuation (high to low, low to high, or random) does not affect readings. Measurements were taken on June 18, 2008 between 1245 and 1445 hours (solar time). Best-fit linear and quadratic regression equations were used to describe the relationship between PAR and photosynthesis (i.e. assimilation rate, A). Due to the quadratic relationship between A and PAR for \( H. \) bonariensis, assimilation rates were log10 transformed (Norman and Streiner 2000). The relationship between A and PAR for all other species was linear. The A:PAR ratio for each leaf surface (per species) was then determined and tested for significant differences using a single-factor ANOVA (MacDonald 2008).

Results

The Sunlight Environment

Figure III-1 shows PAR measurements of four representative sunny to partly cloudy days dispersed throughout one year. PAR values ranged from a minimum of 0 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) to a maximum of 2200 \( \mu \text{m} \text{m}^{-2} \text{s}^{-1} \) for 12 August 2002, 23 March 2003 and 29 June 2003. Maximum PAR values for 26 November 2002 were 1450 \( \mu \text{m} \text{m}^{-2} \text{s}^{-1} \). Passing clouds reduced instantaneous PAR by 9-72%. Measurements taken when the LI-
Quantum Sensor was oriented toward the sky (PAR$_{sky}$) and interfaced with the LI-250A hand-held light meter were in general agreement with the continuous PAR readings. Measurements taken when the LI-190 Quantum Sensor was oriented toward the substrate (PAR$_{sand}$) were on average 27% of the PAR$_{sky}$ measurements, indicating that the albedo of the study site substrate was 0.27 (n=112, S.E. = 0.007).

Stomatal Frequency and Distribution

Adaxial stomatal frequency differences due to sampling date were not discernable among the four species (F = 0.337, p = 0.800 for *A. pumilus*; F = 3.290, p = 0.073 for *C. edentula*; F = 3.14, p = 0.053 for *H. bonariensis* and F = 1.420, p = 0.279 for *I. imbricata*) therefore data were pooled and averaged to give the following results (Figure III-2). Average adaxial and abaxial stomatal frequencies for *A. pumilus* were significantly different (t = 9.290, p < 0.001) with 69 adaxial stomata mm$^{-2}$ (S.E. = 3.54) and 41 abaxial stomata mm$^{-2}$ (S.E. = 5.42). This resulted in an adaxial to abaxial stomatal frequency ratio of 1.67. Average adaxial and abaxial stomatal frequencies for *C. edentula* were significantly different (t = 2.502, p = 0.028) with 130 adaxial stomata mm$^{-2}$ (S.E. = 7.94) and 110 abaxial stomata mm$^{-2}$ (S.E. = 8.14). This resulted in an adaxial to abaxial stomatal frequency ratio of 1.18. Average adaxial and abaxial stomatal frequencies for *H. bonariensis* were not significantly different (t = 1.782, p = 0.087) with 130 adaxial stomata mm$^{-2}$ (S.E. = 11.15) and 120 abaxial stomata mm$^{-2}$ (S.E. = 7.15). This resulted in an adaxial to abaxial stomatal frequency ratio of 1.09. Average adaxial and abaxial stomatal frequencies for *I. imbricata* were not significantly different (t = 1.222, p = 0.239) with 98 adaxial stomata mm$^{-2}$ (S.E. = 9.87) and 90 abaxial stomata mm$^{-2}$ (S.E. = 11.74). This resulted in an adaxial to abaxial stomatal frequency ratio of 1.09.
Internal Leaf Anatomy

Micrographs of *A. pumilus*, *C. edentula*, *H. bonariensis* and *I. imbricata* are presented in Figure III-3. *Amaranthus pumilus* leaves were bifacial with an average thickness of 511 μm (SE = 34 μm). Tissues layers included the upper epidermis (comprising 6% of leaf thickness on average), upper mesophyll (13%), vascular tissue/bundle sheath cells (35%), lower mesophyll (37%) and lower epidermis (9%). *Amaranthus pumilus* leaves oriented at a 90° angle from incident sunlight (Figure III-4).

*Cakile edentula* leaves were unifacial with an average thickness of 1020 μm (SE = 71 μm). Tissue layers included the upper epidermis (4%), upper mesophyll (37%), vascular tissue/central parenchymal cells (18%), lower mesophyll (37%) and lower epidermis (4%). *Cakile edentula* leaves oriented at a 45° angle from incident sunlight (Figure III-5).

*Hydrocotyle bonariensis* leaves were bifacial with an average thickness of 570 μm (SE = 15 μm). Tissue layers included the upper epidermis (10%), upper mesophyll (39%), vascular tissue/lower mesophyll (38%) and lower epidermis (13%). *Hydrocotyle bonariensis* leaf angle and azimuth changed daily and seasonally (Figure III-6).

*Iva imbricata* leaves were unifacial with an average leaf thickness of 1699 μm (SE = 39 μm). Tissue layers included the upper epidermis (4%), upper mesophyll (31%), vascular tissue/central parenchyma (30%), lower mesophyll (31%) and lower epidermis (4%). *Iva imbricata* leaves oriented at a 45° to 90° angle from incident sunlight (Figure III-7).

Photosynthetic Light Response
Adaxial and abaxial photosynthetic light response of *A. pumilus* leaves were significantly different (*F* = 6.70, *p* = 0.021, Figure III-8). Although assimilation rates (A) were similar at low light intensities (0 to approximately 600 μmol m$^{-2}$ s$^{-1}$), rates began to diverge as light intensities increased. According to the equations for the best-fit line (y = 0.013x + 0.372x, $r^2 = 0.93$ for adaxial and y = 0.008x + 0.239, $r^2 = 0.84$ for abaxial), adaxial assimilation rates were approximately 7 μmol m$^{-2}$ s$^{-1}$ higher than abaxial rates at the highest light intensities (1750 μmol m$^{-2}$ s$^{-1}$).

Adaxial and abaxial photosynthetic light response of *C. edentula* leaves were not significantly different (*F* = 0.988, *p* = 0.336, Figure III-9). According to the equations for the best-fit line (y = 0.006x + 0.562, $r^2 = 0.88$ for adaxial and y = 0.006x – 0.004, $r^2 = 0.88$ for abaxial), adaxial assimilation rates were less than 1 μmol m$^{-2}$ s$^{-1}$ higher than abaxial rates across the entire range of light intensities.

Adaxial and abaxial photosynthetic light response of *H. bonariensis* leaves were not quite significantly different (*F* = 0.467, *p* = 0.502, Figure III-10). According to the equations for the best-fit curve (y = - 5.90 x 10$^{-6}$x$^2$ + 0.015x + 0.394, $r^2 = 0.70$ for adaxial and y = - 5.22 x 10$^{-6}$x$^2$ + 0.014x – 0.023, $r^2 = 0.81$ for abaxial), adaxial assimilation rates were less than 1 μmol m$^{-2}$ s$^{-1}$ higher than abaxial rates at low light intensities (0 to approximately 600 μmol m$^{-2}$ s$^{-1}$) and 2 μmol m$^{-2}$ s$^{-1}$ higher at light intensities between 600 and 1900 μmol m$^{-2}$ s$^{-1}$.

Adaxial and abaxial photosynthetic light response of *I. imbricata* leaves were not significantly different (*F* = 0.147, *p* = 0.705, Figure III-11). According to the equations for the best-fit line (y = 0.008x + 0.077, $r^2 = 0.84$ for adaxial and y = 0.006x + 1.37, $r^2 = 0.76$ for abaxial), assimilation rates were equal at low to medium light intensities (0 to
approximately 1000 \( \mu \text{mol m}^{-2} \text{s}^{-1} \)). Adaxial rates were approximately 4 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) greater than abaxial rates at the highest light intensities (1700 \( \mu \text{mol m}^{-2} \text{s}^{-1} \)).

**Discussion**

*The Sunlight Environment*

Sunlight environment measurements presented here are in general agreement with data reported from other studies of sandy beach sites (Ehrenfeld 1990 and references therein, Greaver and Herbert 2004). While many authors have focused on measurements of \( \text{PAR}_{\text{sky}} \), reporting values ranging from 200 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) to 2000 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) depending upon cloud cover (DeJong 1978, Barbour et al. 1985, Ishikawa et al. 1995), only Greaver and Herbert (2004) have specifically recorded \( \text{PAR}_{\text{sand}} \) values. Their study site was located on the sand dunes of Key Biscayne, FL. They reported albedo values of 0.20 to 0.30 depending upon microsite differences within the dunes. These values are in close agreement with the average albedo of 0.27 for Topsail Island. In the study by Greaver and Herbert (2004), vegetational cover greatly affected the amount of reflected light. The authors stated that light was a spatially heterogenous resource on sand dunes.

*Amaranthus pumilus*

Both stomatal frequency and leaf anatomy measurements confirm that *A. pumilus* leaves sampled from Topsail Island were bifacial (Figures III-2 and III-4). The adaxial:abaxial stomatal frequency ratio was 1.67 (Figure III-2) with the upper epidermal and upper mesophyll layers comprising 19% of total leaf thickness (Figure III-4). Lower epidermal and mesophyll layers comprised 46% of total leaf thickness (Figure III-4). Additionally, Kranz anatomy (bundle sheath cells) was very apparent providing evidence that *A. pumilus* is a C\textsubscript{4} plant (Larcher 1995, Lambers et al. 1998). Chlorophyll containing
cells were only present in the bundle sheath and adjacent layers. Adaxial photosynthetic light response of *A. pumilus* leaves was significantly higher than abaxial photosynthetic light response with values similar at low PAR levels but divergent at higher levels (Figure III-8).

These data taken together demonstrate that *A. pumilus* leaves sampled from Topsail Island process adaxial and abaxial light differently. This difference makes intuitive sense because light experienced by the abaxial surface is at least reduced by 73% from that experienced by the adaxial surface. Light may be further reduced on the abaxial surface due to the prostrate growth form of *A. pumilus* with leaves oriented at a 90° angle from incident sunlight. Greaver and Herbert (2004) reached similar conclusions while studying *Ipomoea pes-caprae* on the sand dunes of Florida. They reported that adaxial and abaxial differences in stomatal frequency, leaf anatomy and photosynthetic light response were a direct result of differences in PARsky versus PARsand. Additionally, whether *I. pes-caprae* grows over an open sand dune environment or one with significant vegetative cover can influence abaxial leaf anatomy and physiology due to differences in light attenuation (albedo).

*Cakile edentula*

Stomatal frequency data would seem to indicate that *C. edentula* leaves sampled from Topsail Island are bifacial (Figure III-2). The adaxial:abaxial stomatal frequency ratio was 1.18 which is much lower than the ratio for *A. pumilus* but still indicate a significant adaxial:abaxial difference. Leaf anatomy, however, provides evidence that *C. edentula* leaves are unifacial (Figure III-5). The upper epidermal and upper mesophyll layers comprised 41% of total leaf thickness with the lower epidermal and lower
mesophyll layers also comprising 41% of total leaf thickness (Figure III-5). Vascular tissue was surrounded by parenchymal cells and taken together composed 18% of total leaf thickness (Figure III-5). Chlorophyll containing cells were present in the upper and lower mesophyll layers. These measurements provide evidence that \textit{C. edentula} is a C$_3$ plant as previously documented (Radford et al. 1968). Adaxial and abaxial photosynthetic light response of \textit{C. edentula} leaves were very similar at all light intensities (Figure III-9).

Overall these data support the idea that \textit{C. edentula} leaves sampled from Topsail Island process adaxial and abaxial light in a similar fashion. Unlike \textit{A. pumilus}, \textit{C. edentula} displays an upright growth form with leaves oriented at a 45° from incident sunlight. DeLucia et al. (1991) determined that photosynthetic symmetry was related to leaf orientation for several species found in both open and closed (understory) habitats of the mid-western United States. Vertically oriented leaves maintained equal photosynthetic rates when illuminated on the adaxial and abaxial surfaces while adaxial photosynthetic rates were significantly higher than abaxial rates for horizontally oriented leaves. DeLucia et al (1991) continue by stating that vertical leaf orientation may be adaptive in that it can increase daily photosynthetic carbon gain for the whole leaf and hence the plant.

\textit{Hydrocotyle bonariensis}

An adaxial:abaxial stomatal frequency ratio of 1.09 suggests that \textit{H. bonarensis} leaves sampled from Topsail Island are unifacial (Figure III-2). Leaf anatomy measurements, however, depict some asymmetry (Figure III-6). The upper epidermis consisted of a single cell layer and accounted for 10% of total leaf thickness while the
lower epidermis consisted of two cell layers and accounted for 13% of total leaf thickness. The upper mesophyll contained oval shaped cells and contributed 39% of total leaf thickness while the lower mesophyll contained spherical cells and contributed 38% of total leaf thickness. Chloroplast containing cells were located in the upper and lower mesophyll. These measurements provide evidence that *H. bonariensis* is a C₃ plant as previously documented (Radford et al. 1968). Adaxial and abaxial photosynthetic light response of *H. bonariensis* leaves were similar at all light intensities (Figure III-10).

These data support the conclusion that *H. bonariensis* leaves sampled from Topsail Island process adaxial and abaxial light in a similar fashion, but perhaps not identical fashion. Within the setting of this study, *H. bonariensis* is unique in that it grows via rhizomes with only the leaf and petiole emerging above ground. Joesting et al. (2009) have documented that *H. bonariensis* leaves demonstrate a complex pattern of leaf orientation to incident sunlight that is regulated on a daily and/or seasonal timeframe. Additionally, *H. bonariensis* exhibits an enormous amount of phenotypic plasticity in shoot, root and leaf structure as well as physiology (Longstreth et al. 1981, Evans and Whitney 1992, Evans and Cain 1995). The average leaf area and petiole length of *H. bonariensis* leaves growing on the foredune of Topsail Island were 10.80 cm² (S.E. = 0.63 cm², n = 17) and 1.86 cm (S.E. = 0.16 cm, n = 17) as compared with 33.97 cm² (S.E. = 2.06 cm², n = 17) and 19.18 cm (S.E. = 1.92 cm, n = 17) for leaves growing in swales behind the primary dune (personal observation). Longstreth et al. (1981) found that plants grown under low PAR conditions had maximal photosynthetic rates of 20 μmol m⁻² s⁻¹ while plants grown under high PAR conditions had maximal photosynthetic rates of 30 μmol m⁻² s⁻¹. The present study is the first to combine observations of stomatal
frequency, internal leaf anatomy and photosynthetic light response of *H. bonariensis* leaves. It appears that *H. bonariensis* has the ability to utilize light efficiently on either leaf surface. Stomatal frequency data support this idea. Although there are slight internal anatomy asymmetries within the leaf, they apparently are so small as to not differentially affect function.

*Iva imbricata*

Both stomatal frequency and leaf anatomy measurements confirm that *I.* *imbricata* leaves sampled from Topsail Island were unifacial (Figures III-2 and III-7). The adaxial:abaxial stomatal frequency ratio was 1.09 (Figure III-2) suggesting an essentially equal distribution of stomata on the upper and lower leaf surfaces. *Iva imbricata* leaf anatomy was very unique and somewhat unusual (Figure III-7). The upper epidermis and upper mesophyll comprised 35% of total leaf thickness with the lower epidermis and lower mesophyll also comprising 35% of leaf thickness. Chlorophyll containing cells were found in alternating bands (three cells thick) with non-chlorophyll containing bands (one cell thick). The vascular tissue was surrounded by parenchymal cells that were present in the center of each cross section. These measurements demonstrate that *I. imbricata* leaves are very symmetrical (Figure III-7). As would be predicted from the stomatal frequency and leaf anatomy data, adaxial and abaxial photosynthetic light response of *I. imbricata* leaves were similar (Figure III-11).

These data suggest that *I. imbricata* leaves sampled from Topsail Island process adaxial and abaxial light in a similar manner. *Iva imbricata* displays an upright growth form with leaves orienting at a 45° to 90° angle from incident sunlight. Within the setting of this study, *I. imbricata* is unique in that it is capable of becoming a woody perennial if
individuals survive into successive years. First year plants growing in the foredune habitat were used in this study but even at an early age these plants displayed a growth habit and leaf orientation that provided substantial illumination to both leaf surfaces. Day et al. (1990) reported a similar relationship between growth form, leaf orientation and irradiance levels when studying three subalpine species found in the Rocky Mountains (USA). Much like the results presented here for *I. imbricata*, Poulson and DeLucia (1993) determined that species with vertically oriented leaves have similar adaxial and abaxial photosynthetic light responses while Boardman et al. (1991) concluded that a tendency toward amphistomaty occurs in response to increased irradiance.

**Applicability of leaf form/function model to BI beach plants**

*Amaranthus pumilus*, *C. edentula*, *H. bonariensis* and *I. imbricata* fit the leaf form and function model proposed by Smith et al. (1997) in some respects but not in others. As predicted for a high light environment, stomata were present on both adaxial and abaxial surfaces. The number of stomata mm$^{-2}$ for *H. bonariensis* and *I. imbricata* were statistically the same while the number of adaxial stomata mm$^{-2}$ were slightly higher than the number of abaxial stomata mm$^{-2}$ for *C. edentula* (Figure III-2). The number of adaxial stomata mm$^{-2}$ were higher than the number of abaxial stomata mm$^{-2}$ for *A. pumilus* (Figure III-2). This is somewhat surprising given that most amphisomatous species have lower numbers of adaxial stomata than abaxial stomata (Larcher 1995).

Internal leaf anatomy of *C. edentula* and *I. imbricata* fit well with the proposed model in that leaves of both species were symmetrical with multiple layers of cells producing adaxial and abaxial palisade mesophyll (Figures III-5 and III-7). Additionally, *C. edentula* leaves oriented at a 45° angle from incident sunlight while *I. imbricata* leaves
oriented at a 45° to 90° angle from incident sunlight. According to the model, the leaf anatomy and orientation displayed by _C. edentula_ and _I. imbricata_ predict that these plants should be found in a stressful environment although not the most stressful environment. Smith et al. (1997) state that such an environment may be very stressful when considering some abiotic factors (e.g. sunlight), but not as stressful when considering others (e.g. water limitations). Chapter IV of this dissertation examines the dynamic relationship between water availability and BI beach plant physiology and life history traits.

Leaf anatomy and orientation of _A. pumilus_ does not completely fit the model in that the leaf is bifacial (Figure III-4) and oriented at a 90° angle from incident sunlight. Perhaps the prostrate growth form of _A. pumilus_ provides substantial abaxial shading thereby affecting leaf anatomy. Additionally, _A. pumilus_ is somewhat succulent (as are _C. edentula, H. bonariensis_ and _I. imbricata_) which is considered to be an adaptation to high light environments (Nobel 1999). _Hydrocotyle bonariensis_ is enigmatic in that leaf anatomy is slightly asymmetrical (Figure III-6) and leaf orientation can change daily and seasonally (Joesting et al. 2009). Preliminary data from H.M. Joesting suggest that _H. bonariensis_ leaf anatomy, adaxial and abaxial stomatal frequency and leaf orientation change in response to microenvironmental gradients found across BI beach habitats (from foredune to swale).

Plant characteristics (i.e. leaf anatomy and orientation) are under selective pressure to maximize photosynthesis given developmental, structural and energy constraints (Smith and Hughes 2009). In the desert environment of the southwestern United States, Nobel et al. (1975) discovered that high photosynthetic rates of
*Plectranthus parviflorus* were the direct result of thicker leaves. The increased thickness of these leaves increased mesophyll surface area and hence CO$_2$ absorption leading to greater rates of assimilation (A). This study was one of the first to find a direct relationship between leaf structure and photosynthesis.


In conclusion, the leaf form of *A. pumilus, C. edentula, H. bonariensis* and *I. imbricata* generally fit model predictions for a stressful environment (Smith et al. 1997). Other studies have suggested similar leaf form for similar environmental conditions (Mott et al. 1982, Poulson and DeLucia 1993, Smith et al. 1998).

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Figure III-1. Photosynthetically Active Radiation (PAR) measurements taken on representative days during 2002 and 2003.
Figure III-2. Average adaxial and abaxial stomatal frequencies of four species of North Carolina (USA) barrier island beach plants. Stomatal counts were made on three distinct areas of six different leaves per side per species per sample date. Sample dates were 28 June 2003, 20 July 2003, 19 May 2004, 18 June 2004 and 18 June 2008. Bars represent standard error. The number above each histogram is the adaxial:abaxial stomatal ratio. Asterisks denote significant differences between adaxial and abaxial frequencies.
Figure III-3. Transverse leaf cross sections of (A) *Amaranthus pumilus*, (B) *Cakile edentula*, (C) *Hydrocotyle bonariensis* and (D) *Iva imbricata*. Leaves were sectioned perpendicular to the midvein with a vibratome and observed using a Zeiss Axioplan upright light microscope (Carl Zeiss Incorporated, Germany). Images were captured with a microscope mounted Hamamatsu color chilled 3CCD camera (Hamamatsu Global, Japan).
Figure III-4. Schematic cross section of an *Amaranthus pumilus* leaf. Chloroplast containing cells are indicated by shading. Five representative sections from five leaves were taken to obtain measurements. Leaves orient at a 90° angle from incident sunlight.
Figure III-5. Schematic cross section of a *Cakile edentula* leaf. Chlorophyll containing cells are indicated by shading. Five representative sections from five leaves were taken to obtain measurements. Leaves orient at a 45° angle from incident sunlight.
Figure III-6. Schematic cross section of a *Hydrocotyle bonariensis* leaf. Chlorophyll containing cells are indicated by shading. Five representative sections from five leaves were taken to obtain measurements. Leaf angle and azimuth can change daily and seasonally. In this representation, the leaf is oriented at a 90° angle from incident sunlight.
Figure III-7. Schematic cross section of an *Iva imbricata* leaf. Chlorophyll containing cells are indicated by shading. Five representative sections from five leaves were taken to obtain measurements. Leaves orient at a 45° to 90° angle from incident sunlight. In this representation, the leaf is oriented at a 90° from incident sunlight.
Figure III-8. Photosynthetic light response of *Amaranthus pumilus* leaves (n = 9) illuminated on the adaxial and abaxial leaf surfaces were significantly different (F = 6.70, p = 0.021). Equations located in the figure legend describe the best-fit line for each data set (adaxial and abaxial). Measurements were taken on 18 June 2008 between 1245 and 1445 hours, solar time.
Figure III-9. Photosynthetic light response of *Cakile edentula* leaves (n = 11) illuminated on the adaxial and abaxial leaf surfaces were not significantly different (F = 0.988, p = 0.336). Equations located in the figure legend describe the best-fit line for each data set (adaxial and abaxial). Measurements were taken on 18 June 2008 between 1245 and 1445 hours, solar time.
Figure III-10. Photosynthetic light response of *Hydrocotyle bonariensis* leaves (n = 12) illuminated on the adaxial and abaxial leaf surfaces were not significantly different (F = 0.467, p = 0.502, assimilation data were log$_{10}$ transformed prior to analysis). Equations located in the figure legend describe the best-fit curve for each data set (adaxial and abaxial). Measurements were taken on 18 June 2008 between 1245 and 1445 hours, solar time.
Figure III-11. Photosynthetic light response of *Iva imbricata* leaves (n = 11) illuminated on the adaxial and abaxial leaf surfaces were not significantly different (F = 0.147, p = 0.705). Equations located in the figure legend describe the best-fit line for each data set (adaxial and abaxial). Measurements were taken on 18 June 2008 between 1245 and 1445 hours, solar time.
CHAPTER IV

IMPORTANCE OF AND RESPONSE TO WATER STRESS IN BARRIER ISLAND BEACH PLANT SPECIES

Introduction

The barrier beach has been described as an abiotically challenging and physically controlled environment (as defined by Sanders 1968). Plant physical stressors include high levels of irradiation, high substrate surface temperatures, sand movement, salt aerosols, overwash due to storm surges, nutrient limitations, and low water holding capacity of the substrate (Au 1974, Barbour et. al. 1985, Ehrenfeld 1990, Hesp 1991). Several studies have proposed that low water availability can act as a limiting factor by affecting distribution, growth and reproduction in barrier beach plant species (Huiskes 1977, Ashenden 1978, Payne and Maun 1984, Maun 1994, Zhang 1996). For example, Ashenden (1978) found that drought greatly reduced the transpiration rate and growth rate of *Dactylis glomerata*, a European sand dune associate. Artificial watering treatments reversed these trends. Other studies have determined that water stress was not a limiting factor in the barrier beach environment (Au 1974, van der Valk 1974, Tyndall et. al. 1986, Ripley and Pammenter 2004). For example, Ripley and Pammenter (2004) discovered that water stored in sand dunes was sufficient to meet the growth requirements of *Arctotheca populifola*, *Ipomoea pes-caprae* and *Scaevola plumieri*, three South African barrier beach plant associates. Apparently a contradiction concerning the importance of water availability as a limiting factor exists in the literature.
Differences in microenvironment between study sites could explain some of the conflicting results found in the literature. For example, Tyndall et al. (1986) stated that water stress was not a limiting factor for *Cakile edentula* living in the driftline, but that water stress was a limiting factor for *C. edentula* living on the foredunes (see Figure I-4 for a description of BI beach habitats). Keddy (1981) and Payne and Maun (1984) found that small variations in location along transects was correlated with differential survival of *Cakile maritima*. This was partially attributable to moisture differences in relation to horizontal microsite. Any study addressing water limitations in the barrier island (BI) beach environment needs to take microenvironmental gradients into account.

Traditionally research has focused on the total amount of rain that falls in a given environment in relation to plant survival and reproduction (Ehrenfeld 1990, Salisbury and Ross 1992). More recently there has been interest in the timing and pattern of rainfall and its corresponding effects on plants as well as plant response (Cheng et al. 2006, Loik 2007, Resco et al. 2008). In a review of the literature, Schwinning et al. (2004) concluded that timing of rainfall events, threshold values and even plant “memory” of such events may be as or more important than total yearly rainfall in given ecosystems. Although coastal rainfall data is plentiful in the literature and some seasonal patterns are apparent for given locations, few studies have documented intra-month or especially intra-day rainfall patterns or relate this data to the ecophysiology of BI beach plants (Barbour et al. 1999).

Much attention has been given to the physiological response of plants to water stress (Schulze et al. 1987, Osmond et al. 1987, Ackerly 2004). Plants can conserve water by regulating stomatal opening (Nobel 1999), leaf orientation to incident sunlight
(Ehleringer and Werk 1986, Smith et al. 1997), internal and external leaf anatomy (Ehleringer and Mooney 1978, Smith and Hughes 2009) and biochemical processes (McDowell et al. 2008 and references therein). Ishikawa et al. (1990) measured the net photosynthetic and transpiration rates of three Japanese coastal dune plants and developed a conceptual framework for how they mediate water stress. The authors described each species as employing either an evading, enduring or resisting strategy. These can be combined to fit the desiccation avoidance and tolerance categories put forth by both Larcher (1995) and Lambers et al. (1998).

Few specific investigations relating the life-history traits of barrier beach plants to mediation of water stress are available in the literature (Barbour et al. 1985, Ehrenfeld 1990) although studies do exist for other environments (Salisbury and Ross 1992, Nobel 2002, Griffith and Watson 2005). For example, desert ephemerals are a well-documented group of plants that complete their life-cycle within a very short period of time when rainfall is plentiful (Barbour et al. 1999). Similarly, in one of the few studies involving life-history traits of sand dune plants, DeJong and Klinkhamer (1988) reported that germination of *Cirsium vulgare* and *Cynoglossum officinale* was strongly correlated with rainfall events. Studies in some environments have addressed modifications in plant life-history strategies with respect to global climate change (Cleland et al. 2007, Freville et al. 2007, Franks and Weis 2008).

The purposes of the following study were to:

1. Categorize water availability in the barrier island (BI) beach environment of Topsail Island, North Carolina (USA).

Materials and Methods

Study Site

Topsail Island is a low topographic relief, 42 km long BI that varies in width from 150 to 500 m located approximately 40 km northeast of Wilmington, North Carolina (Stallman 2004). The island is extensively developed with single family homes along almost its entire length (Frankenburg 1997). The study site was located on the southwestern end of the island (34° 20’ 50” N, 77° 39’ 5” W) adjacent to New Topsail Inlet. Due to migration of the inlet to the southwest at an average rate of 35 m per year, an extensive beach and dune environment extends approximately 1-2 km from the inlet to the first beach home.

Species

*Amaranthus pumilus* (Rafinesque) is a pioneering C₄ annual species that inhabits the driftline and foredune area of the BI beach (Weakley and Bucher 1992). The plant has a prostrate growth form, succulent leaves and pink to reddish stems. As a result of population decline due to habitat loss, *A. pumilus* was listed as federally threatened in 1993 (Weakley and Bucher 1992, United States Fish and Wildlife Service 1993). *Cakile edentula* (Bigelow) Hooker is a pioneering C₃ annual species that has an upright growth form and succulent leaves (Radford et al. 1968). The plant is common within its range (Barbour and Rodman 1970) and unlike *A. pumilus*, *C. edentula* can persist into a second growing season in moderate climates (Barbour and Rodman 1970, Boyd and Barbour 1993, Cody and Cody 2004). *Hydrocotyle bonariensis* Lamarck is a C₃ perennial species
whose seeds germinate in swales located landward of the primary dune on BI beaches (Evans 1992a). Plants often grow seaward into the foredune via rhizomes (Evans 1992a). Leaves are peltate, vary in width from 4 to 12 cm and senesce in winter with the rhizomes persisting underground until the next growing season (Radford et al. 1968). *Iva imbricata* Walter is a succulent leaved, woody C$_3$ shrub that can grow to heights of 1 m and widths of 3 m (Radford et al. 1968). As a seedling, *I. imbricata* coinhabits the driftline with *A. pumilus* and *C. edentula*.

**Micrometeorological Measurements**

All micrometeorological measurements were made continuously from June 2002 until June 2004. Rainfall measurements were conducted using a drip-tip bucket connected to a HOBO® data logger (Onset Computer Corporation, Bourne MA). To determine the distribution of rain within each twenty-four hour period, each day was equally divided into four time segments (0001-0559, 0600-1159, 1200-1759 and 1800-2359 Solar Time). The average monthly rainfall within each time segment was then determined. Subsequently, average yearly rainfall within each time segment was calculated and a Chi-square test for goodness of fit was performed to determine if rainfall was equally distributed throughout the day. Photosynthetically Active Radiation (PAR) was measured using a LI-190 Quantum Sensor (Li-Cor, Lincoln Nebraska) interfaced with a HOBO® data logger via a Universal Transconductance Amplifier (EME Systems, Berkley CA). Photosynthetically Active Radiation was plotted against solar time giving a daily PAR curve. Total daily PAR was calculated by determining the area under the curve. Air temperature measurements were made using a HOBO® H8 Pro Series data
logger in conjunction with a solar radiation shield (Onset Computer Corporation, Bourne MA).

Soil Water Content

A temporary transect positioned in the driftline and running parallel to the shoreline was established during each of four sampling periods from April to July 2004. Approximately 100 g of sand from 10 cm, 30 cm and 50 cm depth at three locations along the transect (0 m, 75 m and 150 m) was excavated, placed in a plastic bag, sealed and transported to the laboratory. The next day sand samples were weighed, oven dried at 30°C for twenty-four hours and reweighed. The difference in weights was used to determine soil water content on a percent basis.

Life-History Traits

Four permanent quadrats (3 m X 3 m) were established in representative areas of the foredune habitat and observed once per month from August 2001 until November 2004. Number of *H. bonariensis* leaves (genets) and reproductive structures were counted during each observation. Condition of leaves (e.g. green – actively photosynthesizing, brown – senescing) were noted.

One permanent belt-transect (25 m X 150 m) running parallel to the shoreline was established in a representative area of the driftline. Observations were made once per month from July 2004 until June 2008. Number of *A. pumilus, C. edentula* and *I. imbricata* individuals were counted during each observation. Number of leaves for each plant was estimated and noted. Condition of plants (e.g. flowers, fruits, green leaves, senescing) was also recorded.

Xylem Water Potential
Xylem water potential (Ψ) measurements were taken approximately every three hours from dawn until dusk on 21 June 2002, 12 August 2002, 26 November 2002, 23 March 2003 and 29 June 2003. The first fully expanded leaf of five different individuals for each species was excised and placed in a Scholander-type pressure chamber (PMS Instruments, Corvallis OR) to determine xylem water potential (Ψ) (see Scholander 1965 for details).

Gas Exchange

Gas exchange measurements were taken approximately every three hours from dawn until dusk on 21 June 2002, 12 August 2002, 26 November 2002, 23 March 2003 and 29 June 2003. The first fully expanded leaf of five different individuals for each species was measured using the TPS Portable Photosynthesis System (PP Systems, Amesbury, Massachusetts). Photosynthesis (A), stomatal conductance (g) and transpiration (E) were calculated from the CO₂ flux rate.

Results

Micrometerological Measurements

Rainfall patterns from 1 July 2002 until 30 June 2003 are depicted in Figure IV-1. Table IV-1 gives the total monthly rainfall from the same time period. October through January was the driest period of the year with each month accounting for approximately 4% of total yearly rainfall. February, April, June, July and September experienced moderate rain with each month accounting for approximately 8% of total yearly rainfall. March and May accounted for 10% and 12% of total yearly rainfall, respectively. This was due in part to storm events that occurred during both months (Figure IV-1). A tropical storm supplied the majority of rain over a four day period during the month of
August. As a result, August accounted for 22% of total yearly rainfall (Table IV-1). No clear pattern could be discerned for the distribution of average monthly rainfall within each time segment (Table IV-1). Average yearly rainfall occurring during each time segment was evenly distributed ($\chi^2 = 2.07$, df = 3, $p<0.001$).

Figure IV-2 shows PAR measurements taken on the same days as water potential and gas exchange measurements (with the exception of 21 June 2002). Total PAR measured on 12 August 2002 was 48.76 mol m$^{-2}$, total PAR measured on 26 November 2002 was 16.93 mol m$^{-2}$, total PAR measured on 23 March 2003 was 46.90 mol m$^{-2}$ and total PAR measured on 29 June 2003 was 63.53 mol m$^{-2}$.

The maximum air temperature on 21 June 2002 was 29$^\circ$C, while the minimum air temperature was 22$^\circ$C. The maximum air temperature on 12 August 2002 was 31 $^\circ$C, while the minimum air temperature was 21$^\circ$C. The maximum air temperature on 26 November 2002 was 14 $^\circ$C, while the minimum air temperature was 3 $^\circ$C. The maximum air temperature on 23 March 2003 was 23 $^\circ$C, while the minimum air temperature was 11 $^\circ$C. The maximum air temperature on 29 June 2003 was 31 $^\circ$C, while the minimum air temperature was 22 $^\circ$C.

**Soil Water Content**

Table IV-2 depicts soil water content measurements taken at different depths on 19 April, 19 May, 18 June and 12 July 2004. At 10 cm depth, soil water content ranged from 1.29% to 3.47% with an average of 2.81% for all measurement periods. At 30 cm depth, soil water content ranged from 2.72% to 3.73% with an average of 3.18% for all measurement periods. At 50 cm depth, soil water content ranged from 3.69% to 3.97% with an average of 3.83% for all measurement periods (Table IV-2). There was 0.15 to
There was 0.18 cm of precipitation one day before the 19 April, 19 May and 18 June measurements. There was 0.81 cm of precipitation one day before the 12 July measurement.

*Life History Traits*

Observations from quadrats (for *H. bonariensis*) and the belt-transect (for *A. pumilus, C. edentula* and *I. imbricata*) are summarized in Figure IV-3. On Topsail Island, *A. pumilus* germinates in late April or early May in association with subsurface sand temperatures reaching 32°C and a rain event (Hancock and Hosier 2003). *Amaranthus pumilus* begins flowering in July with fruits becoming mature in late August/early September. Senescence occurs from late September to early November depending upon fall storm surge, cold temperatures and possibly day length (Weakley and Bucher 1992, Hancock and Hosier 2003). *Cakile edentula* continuously germinates beginning in late October/early November through June, flowering and fruiting at low levels from December through June. A large reproductive burst occurs in June and July, continuing until late July/early August when the plant senesces. New leaves of *H. bonariensis* emerge from rhizomes in March. Flowering structures emerge in early June with fruits maturing by late August. Leaves senesce by late December when the rhizome becomes dormant (Evans 1988, 1991). *Iva imbricata* germinates in early April, flowers in July and fruits in early October. Senescence usually takes place in late December.

*Xylem Water Potential*

Xylem water potential (Ψ) varied with environmental conditions and species measured (Figure IV-4). On 12 August 2002 (clear day with scattered clouds, T<sub>max</sub> = 34°C, 0.46 cm of rain fell six days prior), *A. pumilus* and *I. imbricata* experienced a gradual decline in Ψ from -0.1 MPa to -0.3 and -0.5 MPa, respectively. *Hydrocotyle*
Cakile edentula demonstrated no change in $\Psi$. *Hydrocotyle bonariensis* had already senesced before these measurements were taken (see Figure IV-3). On 26 November 2002 (partly cloudy day, $T_{\text{max}} = 14^\circ \text{C}$, 0.81 cm of rain fell nine days prior), $\Psi$ of *C. edentula* increased during the day from -1.0 to -0.8 MPa. *Iva imbricata* exhibited a similar increase from -0.7 to -0.4 MPa. *Hydrocotyle bonariensis* did not experience an appreciable change in $\Psi$.

*Amaranthus pumilus* had senesced before these measurements were taken (see Figure IV-3). Measurements taken on 23 March 2003 (clear day with scattered clouds, $T_{\text{max}} = 23^\circ \text{C}$, 8.53 cm of rain fell two days prior), included only *C. edentula* and *H. bonariensis* due to the senescence of *A. pumilus* and *I. imbricata*. The $\Psi$ of *C. edentula* declined from -0.7 to -1.1 MPa just after 1200 solar time and then rebounded to -0.8 MPa by the final measurement period. The $\Psi$ of *H. bonariensis* did not change throughout the day. On 29 June 2003 (clear day, $T_{\text{max}} = 36^\circ \text{C}$, 3.35 cm of rain fell nine days prior), *A. pumilus* and *C. edentula* predawn $\Psi$ measurements were -0.2 and -0.8 MPa, respectively. As the day progressed, $\Psi$ values for *A. pumilus* declined to -1.1 MPa while $\Psi$ values for *C. edentula* declined to -1.5 MPa by 1600 solar time. *Cakile edentula* $\Psi$ values returned to predawn levels by the final measurement period, while *A. pumilus* $\Psi$ values returned to just below predawn levels. Xylem water potential of both *H. bonariensis* and *I. imbricata* declined slightly (-0.1 MPa) around 1600 solar time.

Gas Exchange

Figure IV-5 depicts diurnal assimilation rates (A) for *A. pumilus*, *C. edentula*, *H. bonariensis* and *I. imbricata* taken on four representative days during 2002-2003. On 12 August 2002, the assimilation rate of *A. pumilus* reached a maximum of 18 $\mu$mol m$^{-2}$ s$^{-1}$ around 1000 solar time then abruptly dropped to 9 $\mu$mol m$^{-2}$ s$^{-1}$ by the next measurement.
period. Assimilation rate declined gradually the remainder of the day. The assimilation rate of *H. bonariensis* peaked around 0830 with a value of 8 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) and remained essentially unchanged until 1415 after which time the rate declined to 0 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) by 1830 solar time. *Iva imbricata* experienced a maximum assimilation rate of 14 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) by 0830. The assimilation rate declined to 10 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) by the next measurement period then continued to decline gradually the remainder of the day. *Cakile edentula* was not present during the 12 August 2002 measurement period.

*Cakile edentula*, *H. bonariensis* and *I. imbricata* exhibited similar assimilation rates on 26 November 2002 (Figure IV-5). The maximum assimilation value for any species on this day was 6 \( \mu \text{mol m}^{-2} \text{s}^{-1} \). *Cakile edentula* was the only species present on 23 March 2003. On that day, assimilation rates for *C. edentula* reached a maximum value of 10 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) by 1100 solar time, remained at the same value during the next measurement period, then began a gradual decline to 0 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) by 1800 solar time.

On 29 June 2003, the assimilation rate of *A. pumilus* peaked at 15 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) by 1130 solar time, with values gradually declining thereafter. *Cakile edentula* and *I. imbricata* obtained assimilation rates of approximately 14 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) and 16 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) by 0900 solar time, respectively (Figure IV-5). Values of \( A \) for *C. edentula* increased to a maximum of 16 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) by mid-afternoon, after which time they declined gradually. The assimilation rate of *I. imbricata* declined to 8 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) by 1330 solar time then continued to decline, although more gradually, thereafter. The assimilation rate of *H. bonariensis* peaked at 7 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) by 0900 solar time, declined to 3 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) by 1330 solar time, increased slightly during the next measurement period, then declined to 0 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) during the final period.
Figure IV-6 shows stomatal conductance rates (g) for *A. pumilus*, *C. edentula*, *H. bonariensis* and *I. imbricata* taken on four representative days during 2002-2003. On 12 August 2002, stomatal conductance for *A. pumilus* increased from an initial value of 59 mmol m$^{-2}$ s$^{-1}$ to 100 mmol m$^{-2}$ s$^{-1}$ by 1030. Stomatal conductance then decreased to 58 mmol m$^{-2}$ s$^{-1}$ by the 1415 measurement period. Values of g remained relatively constant for the remainder of the day. The initial stomatal conductance value for *H. bonariensis* was 28 mmol m$^{-2}$ s$^{-1}$. Stomatal conductance increased to 66 mmol m$^{-2}$ s$^{-1}$ by the next measurement period, then continued to increase but more gradually until a maximum value of 79 mmol m$^{-2}$ s$^{-1}$ was reached by the 1415 solar time. Values of g decreased relatively rapidly through the last measurement period for the day. The initial g value of *I. imbricata* was 19 mmol m$^{-2}$ s$^{-1}$. Stomatal conductance increased to 91 mmol m$^{-2}$ s$^{-1}$ by the next measurement period. Values then began to decline gradually for the remainder of the day. *Cakile edentula* was not present during the 12 August 2002 measurement period.

*Hydrocotyle bonariensis* and *I. imbricata* exhibited similar patterns of stomatal conductance rates on 26 November 2002 (Figure IV-6), with initial values approximately 22 mmol m$^{-2}$ s$^{-1}$. Stomatal conductance rates increased to 66 mmol m$^{-2}$ s$^{-1}$ and 77 mmol m$^{-2}$ s$^{-1}$ by 1030 solar time for *H. bonariensis* and *I. imbricata*, respectively. *Hydrocotyle bonariensis* g values then decreased to 60 mmol m$^{-2}$ s$^{-1}$ by the next measurement period and 23 mmol m$^{-2}$ s$^{-1}$ by the final period. *Iva imbricata* stomatal conductance reached a maximum of 78 mmol m$^{-2}$ s$^{-1}$ at 1430 solar time decreasing to 24 mmol m$^{-2}$ s$^{-1}$ by the final measurement period. *Amaranthus pumilus* had senesced before these measurements were taken.
Cakile edentula was the only species present on 23 March 2003. The initial value of g was 34 mmol m$^{-2}$ s$^{-1}$. Cakile edentula reached a maximum stomatal conductance rate of 120 mmol m$^{-2}$ s$^{-1}$ at 1030 solar time and maintained this through the next measurement period. After 1250 solar time, g values declined rapidly to 35 mmol m$^{-2}$ s$^{-1}$.

On 29 June 2003, stomatal conductance for A. pumilus increased rapidly from an initial value of 12 mmol m$^{-2}$ s$^{-1}$ to 96 mmol m$^{-2}$ s$^{-1}$ by the second measurement period (Figure IV-6). Stomatal conductance continued to increase, but more gradually, until a maximum daily value of 114 mmol m$^{-2}$ s$^{-1}$ was reached at 1115 solar time. Afterwards, values of g declined gradually to 24 mmol m$^{-2}$ s$^{-1}$ by the final measurement period. The initial stomatal conductance for C. edentula was 49 mmol m$^{-2}$ s$^{-1}$ after which it reached a maximum value of 167 mmol m$^{-2}$ s$^{-1}$ by 1345 solar time. Values declined rapidly to 82 mmol m$^{-2}$ s$^{-1}$ by the next measurement period then declined more gradually to 67 mmol m$^{-2}$ s$^{-1}$ by the final measurement. The early morning pattern of stomatal conductance values for Iva imbricata was similar to those of A. pumilus and C. edentula with an initial value of 27 mmol m$^{-2}$ s$^{-1}$. Rates increased rapidly to 102 mmol m$^{-2}$ s$^{-1}$ by the second measurement period. Afterward, I. imbricata experienced a decline in g to 78 mmol m$^{-2}$ s$^{-1}$ with values remaining relatively unchanged over the next two measurement periods. Final g values fell to 35 mmol m$^{-2}$ s$^{-1}$. Stomatal conductance values of H. bonariensis were low compared to A. pumilus, C. edentula and I. imbricata. Initial and final g values for H. bonariensis were 17 mmol m$^{-2}$ s$^{-1}$ and 15 mmol m$^{-2}$ s$^{-1}$ respectively. The maximum daily g value was 52 mmol m$^{-2}$ s$^{-1}$ at 0915 solar time.

Figure IV-7 documents transpiration rates (E) for A. pumilus, C. edentula, H. bonariensis and I. imbricata taken on four representative days during 2002-2003.
Transpiration rate patterns for *A. pumilus*, *H. bonariensis* and *I. imbricata* were similar on 12 August 2002 with initial values ranging from 0.19 to 0.44 mmol m\(^{-2}\) s\(^{-1}\). By 1030 solar time, values of E were 3.07 mmol m\(^{-2}\) s\(^{-1}\), 2.61 mmol m\(^{-2}\) s\(^{-1}\) and 2.30 mmol m\(^{-2}\) s\(^{-1}\) for *A. pumilus*, *H. bonariensis* and *I. imbricata*, respectively. Values declined steadily to 0 mmol m\(^{-2}\) s\(^{-1}\) by the final measurement period. *Cakile edentula* was not present during the 12 August 2002 measurement period.

Patterns of E for *C. edentula*, *H. bonariensis* and *I. imbricata* were similar on 26 November 2002 with initial values of approximately 0.20 mmol m\(^{-2}\) s\(^{-1}\) (Figure IV-7). Transpiration rate gradually increased to a maximum of 1.19 mmol m\(^{-2}\) s\(^{-1}\), 0.68 mmol m\(^{-2}\) s\(^{-1}\) and 0.93 mmol m\(^{-2}\) s\(^{-1}\) for *C. edentula*, *H. bonariensis* and *I. imbricata*, respectively. Rates declined to approximately 0.20 mmol m\(^{-2}\) s\(^{-1}\) by the final measurement period.

*Cakile edentula* was the only species present on 23 March 2003. The initial value of E was 0.30 mmol m\(^{-2}\) s\(^{-1}\). *Cakile edentula* reached a maximum transpiration rate of 1.65 mmol m\(^{-2}\) s\(^{-1}\) at 1230 solar time. Values declined rapidly to 0.71 mmol m\(^{-2}\) s\(^{-1}\) by the next measurement period then continued to decline, but more slowly, reaching a final value of 0.18 mmol m\(^{-2}\) s\(^{-1}\) by 1800 solar time.

*Amaranthus pumilus* and *Cakile edentula* had similar transpiration patterns on 29 June 2003 (Figure IV-7). Initial rates were 0.15 mmol m\(^{-2}\) s\(^{-1}\) and 0.50 mmol m\(^{-2}\) s\(^{-1}\) for *A. pumilus* and *C. edentula*, respectively. Rates increased steeply to approximately 2.70 mmol m\(^{-2}\) s\(^{-1}\) by 1115 solar time and continued to increase, but more gradually, to the daily maximum of 2.90 mmol m\(^{-2}\) s\(^{-1}\) was reached by the next measurement period. *Amaranthus pumilus* values declined to 0.43 mmol m\(^{-2}\) s\(^{-1}\) while *C. edentula* values declined to 1.03 mmol m\(^{-2}\) s\(^{-1}\) by 1830 solar time. Transpiration rates for *H. bonariensis*
were low compared to *A. pumilus*, *C. edentula* and *I. imbricata*. Initial and final values of E for *H. bonariensis* were 0.19 mmol m\(^{-2}\) s\(^{-1}\) and 0.22 mmol m\(^{-2}\) s\(^{-1}\), respectively. Transpiration increased for *H. bonariensis* to a maximum value of 1.18 mmol m\(^{-2}\) s\(^{-1}\) by 1115 solar time, declining to 0.77 mmol m\(^{-2}\) s\(^{-1}\) by the next measurement period. Initial and final transpiration rates of *I. imbricata* were similar to the other three species measured. *Iva imbricata* reached a maximum transpiration rate of 2.02 mmol m\(^{-2}\) s\(^{-1}\) at 1345 solar time. This value was intermediate when compared to the other three species measured.

**Rain Event**

On 21 June 2002 (clear day with scattered clouds, \(T_{\text{max}} = 29^\circ\text{C}\)), the initial \(\Psi\) for *A. pumilus* was -0.4 MPa. *Amaranthus pumilus* xylem water potential increased slightly to -0.24 MPa by 1100 solar time. A rain event occurred from 1430 until 1500 solar time providing 0.81 cm of rainfall (Figure IV-8). Xylem water potential of *A. pumilus* declined to -1.1 MPa by the next measurement period. During the final measurement, *A. pumilus* \(\Psi\) had increased to its highest level of the day (-0.1 MPa). The \(\Psi\) for *C. edentula* declined rapidly to -1.2 MPa by 1100 solar time from an initial value of -0.5 MPa. During the final two measurement periods, \(\Psi\) of *C. edentula* steadily increased to its highest levels of the day. The initial value of \(\Psi\) for *H. bonariensis* was -0.1 MPa. Values declined to -0.3 MPa by the next measurement period. Recovery to approximately -0.1 MPa occurred after the rain event. *Iva imbricata* values of \(\Psi\) remained relatively constant at -0.2 MPa during the first two measurement periods, then declined to -0.5 MPa in the mid-afternoon. The \(\Psi\) of *I. imbricata* increased to its highest level of the day by the final measurement period.
On 21 June 2002, the initial assimilation rate of all four species ranged from 0.8 to 2.0 μmol m$^{-2}$ s$^{-1}$ (Figure IV-8). Values of A for *A. pumilus* reached a maximum of 17 μmol m$^{-2}$ s$^{-1}$ by 1300 solar time, then declined rapidly to 5.4 μmol m$^{-2}$ s$^{-1}$ by 1530 solar time. The final measurement of the day for *A. pumilus* was 2.0 μmol m$^{-2}$ s$^{-1}$. Assimilation rates for *C. edentula* peaked at 9.0 μmol m$^{-2}$ s$^{-1}$ during the third measurement period, remained relatively constant for the next measurement period and declined to 4.0 μmol m$^{-2}$ s$^{-1}$ by 1815 solar time. *Hydrocotyle bonariensis* assimilation rates reached 8.0 μmol m$^{-2}$ s$^{-1}$ during the second measurement period and declined steadily thereafter. Values of A for *I. imbricata* achieved a maximum rate of 13 μmol m$^{-2}$ s$^{-1}$ by 1115 solar time and declined steadily thereafter.

Stomatal conductance rates were similar for all four species during the first two measurement periods (Figure IV-8). *Amaranthus pumilus* stomatal conductance rates gradually declined to 53 mmol m$^{-2}$ s$^{-1}$ by 1530 solar time then stayed constant for the final measurement period. Values of g for *C. edentula* reached a maximum of 96 mmol m$^{-2}$ s$^{-1}$ by 1530 solar time, then declined rapidly to 52 mmol m$^{-2}$ s$^{-1}$ for the final measurement period. *Hydrocotyle bonariensis* stomatal conductance peaked at 70 mmol m$^{-2}$ s$^{-1}$ during the fourth measurement period while g values for *I. imbricata* peaked at 71 mmol m$^{-2}$ s$^{-1}$ during the second measurement period.

Transpiration rates of all four species were similar with the exception that *A. pumilus* peaked at 1300 solar time rather than 1530 solar time and that the maximum rates of E for *A. pumilus* were 0.4 mmol m$^{-2}$ s$^{-1}$ higher than the other species.
Discussion

Soil water content measured on Topsail Island, NC was 3.3% when averaged across the four measurement days, for the three measurement depths (Table IV-2). This is consistent with data taken by Au (1974) on Shackleford Bank, NC (3.0% average soil water content), van der Valk (1977) on Cape Hatteras National Seashore, NC (4.0% average soil water content) and Dubois (1977) on Sapelo Island, GA (3.5% average soil water content). Researchers generally agree that the first few centimeters of sand dries quickly after a rain, but that deeper layers (15 - 30 cm) are usually moist regardless of time between rainfalls (Kearny 1900, Au 1974, van der Valk 1977, Dubois 1977, Barbour et al. 1985). Data from Topsail Island support these earlier studies. This phenomenon has been attributed to the insulating effect of the upper layers of sand, low matrix potential of the substrate and a relatively shallow water table (Au 1974, Barbour et al. 1985, Barbour et al. 1999, Moreno-Casasola and Vazquez 1999).

On Topsail Island, the driest and coldest part of the year with the least Total PAR coincides with the dormant phases (or the stage just before dormancy) of *A. pumilus*, *H. bonariensis* and *I. imbricata* (Figures IV-1, IV-2, IV-3 and Table IV-1). These life-history patterns are typical of BI beach summer C₄ annuals – *A. pumilus* - (DeJong 1978, Barbour et al. 1985), warm weather BI beach C₃ clonals – *H. bonariensis* - (Evans 1988, 1991) and warm weather BI beach, woody, decidous C₃ species – *I. imbricata* - (Radford et al. 1968, Colosi and McCormick 1978, Franks 2003a and 2003b). Germination timing of *A. pumilus*, *H. bonariensis* (emergence of new leaves), *I. imbricata* and to an extent *C. edentula* correspond to a part of the year that can experience storms providing relatively large amounts of rainfall over short periods of time. Many coastal studies have
documented the association between germination flushes and rainfall events (DeJong 1979, Weller 1985, DeJong and Klinkhamer 1988, Ehrenfeld 1990, Hancock and Hosier 2003, Padilla and Pugnaire 2007). The life-history of *C. edentula* is unique in relation to the other three BI beach associates in that the species senesces before the hottest part of the year when total PAR levels are highest (Figure IV-1, Figure IV-2, Figure IV-3 and Table IV-1). These life-history traits may represent adaptations to the BI beach environment that correspond to tolerance (*A. pumilus*, *H. bonariensis* and *I. imbricta*) and avoidance (*C. edentula*) strategies as defined by Larcher 1995 and Lambers et al 1998.

Rainfall patterns on Topsail Island were highly variable with 40% of total yearly precipitation associated with storm systems that provided large volumes of water in a relatively small time period (Table IV-1, Figure IV-1). Smaller, more frequent systems occurred in March and May (19% of total yearly parcipitation) with one large system happening in the fall (21% of total yearly parcipitation). This seems to be a typical pattern found along the NC coast (Barnes 2001). The large amount of water input from these storm events and their random arrival during a given twenty-four hour period, obscured any underlying daily rainfall patterns when considering time segments (0001-0559, 0600-1159, 1200-1759 and 1800-2359) averaged over a given month. Average yearly rainfall occurring during each time segment was evenly distributed as stated in the Results, suggesting that rain is no more likely to occur in the afternoon than in the early morning, mid-morning or evening. It would be beneficial to take similar measurements over several years to ascertain if the patterns found in this study are the norm for Topsail Island.
Amaranthus pumilus experienced a gradual decline in $\Psi$ on 12 August 2002 due to water loss via transpiration (Figures IV-4 and IV-7), with stomatal conductance decreasing from 100 mmol m$^{-2}$ s$^{-1}$ to 58 mmol m$^{-2}$ s$^{-1}$ during the same time period (Figure IV-6). On 29 June 2003, the $\Psi$ of A. pumilus declined to -1.2 MPa during the mid-afternoon, followed by a rebound to -0.4 MPa by the next measurement period. This was most likely due to A. pumilus closing its stomata to conserve water (Figure IV-6). On the same day, transpiration rates similarly reached a maximum of 2.9 mmol m$^{-2}$ s$^{-1}$ at 1345 solar time, declining to 2.1 mmol m$^{-2}$ s$^{-1}$ by the next measurement period and continuing to decline thereafter (Figure IV-7). Amaranthus pumilus consistently had some of the highest assimilation rates of the four species measured in this study with maximum values of 18 $\mu$mol m$^{-2}$ s$^{-1}$ and 15 $\mu$mol m$^{-2}$ s$^{-1}$ measured on 12 August 2002 and 29 June 2003, respectively (Figure IV-5). As is typical for many plants during hot, dry periods (Larcher 1999, Nobel 1999), $\Psi$ of A. pumilus decreased during the day. This decrease is associated with transpiration that accompanies photosynthesis via open stomata. It is probable that A. pumilus can maintain relatively high assimilation rates while mediating transpiration by controlling stomatal aperture.

Cakile edentula was absent during the 12 August 2002 measurement period, thereby avoiding a particularly hot, dry day. During the mid-afternoon on 29 June 2003, C. edentula experienced the lowest xylem water potential recorded in this study, -1.5 MPa (Figure IV-4). Xylem water potential recovered to -0.8 MPa by the next measurement period. Similar to A. pumilus, this was most likely due to stomatal closure to conserve water. Stomatal conductance was recorded as 167 mmol m$^{-2}$ s$^{-1}$ at 1345 solar time followed by 82 mmol m$^{-2}$ s$^{-1}$ at 1600 solar time (Figure IV-6). Transpiration rates
were very similar to those experienced by *A. pumilus* (Figure IV-7). The initial xylem water potential for *C. edentula* on 26 November 2002 was -1.0 MPa. Values increased gradually to -0.8 by the end of the day (Figure IV-4). Although stomatal conductance rates were relatively high (Figure IV-6), transpiration rates remained low (Figure IV-7). This is probably due to a low vapor pressure deficit which is not uncommon in cooler months of the year (Barbour et al. 1985). During 23 March 2003, a warm and clear day, xylem water potential declined to a daily low of -1.0 MPa in the mid-afternoon, followed by recovery to -0.8 MPa during the final measurement period. As on 29 June 2003, this was most likely due to stomatal closure to conserve water. Transpiration rates peaked when $\Psi$ values were lowest, then declined (Figures IV-5 and IV-6). *Cakile edentula* assimilation rates were relatively high with maximum values of 5 μmol m$^{-2}$ s$^{-1}$, 10 μmol m$^{-2}$ s$^{-1}$ and 17 μmol m$^{-2}$ s$^{-1}$ for 26 November 2002, 23 March 2002 and 29 June 2003, respectively (Figure IV-5). Through a combination of life history traits, physiological response and tolerance, *C. edentula* is able to maintain assimilation rates that are comparable to those of *A. pumilus*.

Similar to *A. pumilus*, *I. imbricata* experienced a gradual decline in $\Psi$ on 12 August 2002 due to water loss via transpiration (Figures IV-4 and IV-7). *Iva imbricata*, however, appeared to be more sensitive to potential water deficit, reducing its maximum value of $g$ (recorded at 0830 solar time) more quickly than *A. pumilus* (Figure IV-6). Stomatal conductance continued to decline gradually throughout the remainder of the day. As would be expected given the stomatal conductance values, maximum transpiration rates of *I. imbricata* were lower than those of *A. pumilus*, although both plants did follow a similar diurnal pattern (Figure IV-7). Maximum assimilation rates of
I. imbricata on 12 August 2002 were 14 μmol m$^{-2}$ s$^{-1}$, considerably lower than those of A. pumilus (Figure IV-5). The intial xylem water potential for I. imbricata on 26 November 2002 was -0.7 MPa. Values increased gradually to -0.4 by the end of the day, following a pattern that was very similar to that of C. edentula (Figure IV-4). Stomatal conductance values for I. imbricata were similar to those recorded on 12 August 2002, but the diurnal pattern was different with maximum values being obtained at 1030 and 1430 solar time (Figure IV-6). Transpiration and assimilation rates were much lower than those measured on 12 August 2002. It is likely that I. imbricata can keep stomata open with relatively little transpiration due to the lower vapor pressure deficit present in November on Topsail Island. The xylem water potential of I. imbricata declined to -0.2 MPa during mid-morning and mid-afternoon on 29 June 2003 at the same time (mid-afternoon) that Ψ of both A. pumilus and C. edentula declined precipitously (Figure IV-4). Assimilation rates, stomatal conductance rates and transpiration rates were all lower than those of A. pumilus or C. edentula. The difference could be due to the fact that I. imbricata has a substantial tap root (Colosi and McCormick 1978, Franks and Peterson 2003) that may have access to deeper and more consistent water sources than either A. pumilus or C. edentula.

The xylem water potential of H. bonariensis remained relatively constant during each of the measurement days, never becoming more negative than -0.3 MPa (Figure IV-4). Hydrocotyle bonariensis has been shown to translocate water from slacks (low areas on the dunes were the water table is closer to the surface) to the leading edge of growth in the foredunes and primary dunes (Evans 1988, Evans 1991, Evans 1992a, Evans and Whitney 1992, Evans and Cain 1992) and is probably doing so on Topsail Island given
the consistently high $\Psi$ readings. It appears that the morphology (clonal) growth pattern of *H. bonariensis* affords it a ready supply of water throughout the growing season.

Assimilation of photosynthetic CO$_2$ (A), stomatal conductance and transpiration rates of *H. bonariensis* were lower than those of *A. pumilus*, *C. edentula* and *I. imbricata* during almost every measurement period (Figures IV-5, IV-6 and IV-7). Assimilation rates reached maximum values on 12 August 2002 (7 $\mu$mol m$^{-2}$ s$^{-1}$) and 29 June 2003 (8 $\mu$mol m$^{-2}$ s$^{-1}$), both very hot and dry days. Maximum values of A for 26 November 2002 were 4 $\mu$mol m$^{-2}$ s$^{-1}$. Stomatal conductance and transpiration rates closely mirrored assimilation rates (Figures IV-6 and IV-7), with one notable exception. Transpiration rates spiked (2.6 mmol m$^{-2}$ s$^{-1}$) at 1050 solar time on 12 August 2002 while stomatal conductance and assimilation remained steady. Other researchers have reported similar high values of E without a concomitant increase in A and g values when vapor pressure deficit is large (Nobel 1999, Barbour et al. 1999).

Measurements taken on 12 August 2002, 26 November 2002, 23 March 2003 and 29 June 2003 offer an example of *A. pumilus*, *C. edentula*, *H. bonariensis* and *I. imbricata* physiological behavior during representative rainless days throughout a typical year on Topsail Island, NC. The rain event that occurred during mid-afternoon on 21 June 2002, when plant water stress is often highest (Larcher 1995, Lambers et al. 1998), provides an opportunity to observe how BI beach plant species respond to an input of water during a critical time period (Figure IV-8).

*Amaranthus pumilus* experienced a substantial decrease in xylem water potential ($\Psi$) just after the rain event followed by an increase above predawn levels by the next measurement period. The xylem water potential of *C. edentula* reached a daily low just
before the rain event then quickly rebounded to predawn levels by the next measurement period. The diurnal pattern of *I. imbricata* Ψ was similar to that of *A. pumilus*, but the mid-afternoon decline was not as substantial. The xylem water potential pattern of *H. bonariensis* was similar to *C. edentula*, but the mid-morning decline was not nearly as substantial. These differences could be explained by differential response time between the species since stomatal conductance values were similar (with the exception of *C. edentula* just after the rain event). Transpiration rates were comparable for each species throughout the day (with the exception of *A. pumilus* just before the rain event). One difficulty with the 21 June 2002 xylem water potential data set is that only four measurements were taken throughout the day. A fairly large expanse of time (four hours) separates data taken before and after the rain event. A measurement taken closer to the start of the rain event may have more completely described the physiological behavior of each species.

*Amaranthus pumilus* had some of the highest assimilation, stomatal conductance and transpiration rates measured in this study. Given its prostrate growth form, horizontal leaf orientation and internal leaf anatomy (Chapter III), *A. pumilus* appears to maximize light interception and thereby photosynthesis. The growing season for *A. pumilus* is only six to seven months on Topsail Island and therefore the best strategy for this life history pattern may be to fix as much carbon as possible in the shortest amount of time (Chapter V). The cost of this strategy could be water loss via transpiration, but this may be mediated by stomatal control, mesophyll biochemistry (not addressed in this study) root architecture and the occurrence of rain events. According to Maun (1994), many coastal plant species undergo rapid root extension during the first few weeks of
growth. This root extension can provide the plant with a more consistent source of water (Laing 1958, DeJong 1979, Padilla and Pugnaire 2007, Saha et al. 2008). After germination (which correlates with rain fall events), roots of *A. pumilus* seedlings quickly grow to lengths of 25-30 cm (personal observation).

There is a growing body of literature addressing the importance of precipitation pulses to plant water and carbon balance (de Mattos et al. 2002, Xu and Li 2006, Xu et al. 2007) with several studies documenting rapid changes in $A$, $g$, $E$ and $\Psi$ directly after a rain event (de Mattos et al. 2002, Cheng et al. 2006). Such rain events within the growing season could provide needed moisture to maintain *A. pumilus* photosynthetic rates at high levels. In a study of the Florida scrub ecosystem where short, intense rain showers are common, Saha et al. (2008) found that eight species of co-occurring plants were “equipped to survive fluctuations in soil moisture but did not posses mechanisms to cope with persistently dry soils because persistently low soil moisture conditions rarely occur”. The environmental conditions of this system are similar to those that exist on North Carolina BI beaches.

As stated earlier, the CO$_2$ assimilation and transpirational water loss of *C. edentula* were comparable to those of *A. pumilus*, although maximum stomatal conductance values were larger and minimum $\Psi$ values more negative. It is possible that *C. edentula* is more tolerant of water stress than *A. pumilus*, which might help explain why *C. edentula* is common throughout its considerable range while *A. pumilus* is listed as threatened (Maun et al. 1990, Weakely and Bucher 1992, Hancock and Hosier 2003). The life-history pattern of *C. edentula* is most likely another important aspect of its adaptation to the BI beach environment. *Cakile edentula* is absent during some of the
hottest and driest months of the year (July, August and September), while alive and active during some of the cooler months (November through April). Although assimilation rates are not as high during the cooler months, the additive effect of photosynthesizing nine months out of the year may allow *C. edentula* to reach carbon gain thresholds that are necessary for growth and reproduction (Chapter V).

In many respects, *I. imbricata* exhibited physiological and life history traits that were intermediate when considering its BI beach associates. Values of A, g, E and $\Psi$ were never the highest or lowest of the species measured on any given day. The lowest value of $\Psi$ was -0.7 MPa recorded on 26 November 2002. This is well above -1.5 MPa given as a minimum threshold for water stress in the coastal dune environment (Au 1974, Ehrenfeld 1990, Barbour et al. 1999). Similar to *C. edentula*, *I. imbricata* has a nine month growing season although it is centered on the warmer parts of the year (April through December). Moderate assimilation rates spread over nine months may be a means to achieve required carbon gain thresholds. Perhaps *I. imbricata* is able to avoid water stress and maintain photosynthesis via a combination of stomatal control, root architecture (tap rooted, woody perennial) and life-history pattern.

*Hydrocotyle bonariensis* displays a survival strategy that is well suited to the BI beach environment. The species germinates in swales (Evans 1992b), tapping into the more plentiful water supply of that habitat and extending rhizomes into the primary dune and foredune beyond. Due to this consistent water supply, *H. bonariensis* does not appreciably experience water stress. Assimilation rates, stomatal conductance and transpiration rates are low, but steady throughout the growing season, which for *H. bonariensis* is relatively long (ten months). Leaves senesce and the species over-winters
via its rhizome, ready for the next growing season with its connection to water and nutrient supplies intact.

Conclusions

Water availability in the BI beach environment may be greater than previously thought, challenging the assumption that plants living in this environment are constantly under water stress. *Amaranthus pumilus* and *C. edentula* did experience appreciable decreases in xylem water potential on occasion but not usually to the extent that would be considered water stressed. Alternatively, *I. imbricata* and especially *H. bonariensis* maintained xylem water potentials well above values considered stressful. Each of the species involved in this study demonstrated physiological and life-history attributes that likely maximized photosynthetic carbon gain over a given year, albeit via different combinations of traits.

Literature Cited


United States Fish and Wildlife Service. 1993. Endangered and threatened wildlife and
plants; *Amaranthus pumilus* (seabeach amaranth) determined to be threatened. Federal Register 58(65): 18035-18041.


Table IV-1. Average daily distribution and total monthly rainfall (cm) on Topsail Island, NC 1 July 2002 through 30 June 2003.

<table>
<thead>
<tr>
<th>Measurement Period (Solar Time)</th>
<th>0001-0559</th>
<th>0600-1159</th>
<th>1200-1759</th>
<th>1800-2400</th>
<th>Monthly Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>July</td>
<td>3.54 cm</td>
<td>0.90 cm</td>
<td>2.35 cm</td>
<td>5.33 cm</td>
<td>12.12 cm</td>
</tr>
<tr>
<td>August</td>
<td>20.97</td>
<td>6.31</td>
<td>2.80</td>
<td>4.16</td>
<td>34.24</td>
</tr>
<tr>
<td>September</td>
<td>2.79</td>
<td>0.98</td>
<td>8.78</td>
<td>1.39</td>
<td>13.94</td>
</tr>
<tr>
<td>October</td>
<td>0.54</td>
<td>1.55</td>
<td>1.68</td>
<td>2.96</td>
<td>6.73</td>
</tr>
<tr>
<td>November</td>
<td>1.32</td>
<td>3.25</td>
<td>1.77</td>
<td>1.10</td>
<td>7.44</td>
</tr>
<tr>
<td>December</td>
<td>0.27</td>
<td>4.03</td>
<td>3.95</td>
<td>0.72</td>
<td>8.97</td>
</tr>
<tr>
<td>January</td>
<td>2.10</td>
<td>1.68</td>
<td>0.19</td>
<td>0.70</td>
<td>4.67</td>
</tr>
<tr>
<td>February</td>
<td>3.11</td>
<td>2.21</td>
<td>2.03</td>
<td>2.81</td>
<td>10.16</td>
</tr>
<tr>
<td>March</td>
<td>2.66</td>
<td>3.29</td>
<td>4.51</td>
<td>4.58</td>
<td>15.04</td>
</tr>
<tr>
<td>April</td>
<td>2.46</td>
<td>1.48</td>
<td>6.90</td>
<td>1.48</td>
<td>12.32</td>
</tr>
<tr>
<td>May</td>
<td>4.64</td>
<td>6.00</td>
<td>1.35</td>
<td>7.34</td>
<td>19.35</td>
</tr>
<tr>
<td>June</td>
<td>0.68</td>
<td>1.71</td>
<td>5.12</td>
<td>3.87</td>
<td>11.38</td>
</tr>
<tr>
<td>Yearly Total</td>
<td>45.08</td>
<td>33.39</td>
<td>41.45</td>
<td>36.44</td>
<td>156.36</td>
</tr>
</tbody>
</table>
Table IV-2. Soil water content (%) of 100 g substrate samples taken at different depths from Topsail Island, NC in the spring and summer of 2004. Standard errors are in parentheses.

<table>
<thead>
<tr>
<th>Date</th>
<th>Water Content (%)</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>10 cm</td>
<td>30 cm</td>
<td>50 cm</td>
</tr>
<tr>
<td>19 April</td>
<td>3.21 (0.40)</td>
<td>3.73 (0.24)</td>
<td>3.97 (0.36)</td>
</tr>
<tr>
<td>19 May</td>
<td>3.27 (0.40)</td>
<td>3.21 (0.09)</td>
<td>3.97 (0.79)</td>
</tr>
<tr>
<td>18 Jun</td>
<td>1.29 (0.40)</td>
<td>2.72 (0.12)</td>
<td>3.68 (0.45)</td>
</tr>
<tr>
<td>12 July</td>
<td>3.47 (0.39)</td>
<td>3.04 (0.18)</td>
<td>3.70 (0.57)</td>
</tr>
<tr>
<td>Average</td>
<td>2.81 (0.51)</td>
<td>3.18 (0.21)</td>
<td>3.83 (0.08)</td>
</tr>
</tbody>
</table>
Figure IV-1. Daily rainfall totals on Topsail Island, NC from 1 July 2002 until 30 June 2003.
Figure IV-2. Photosynthetically Active Radiation (PAR) measurements taken on representative days during 2002 and 2003.

12 August 2002
Total PAR = 48.76 mol m$^{-2}$

26 November 2002
Total PAR = 16.93 mol m$^{-2}$

23 March 2003
Total PAR = 46.90 mol m$^{-2}$

29 June 2003
Total PAR = 63.53 mol m$^{-2}$
Figure IV-3. Diagramatic representation of *Amaranthus pumilus*, *Cakile edentula*, *Iva imbricata*, and *Hydrocotyle bonariensis* life-history traits on Topsail Island, NC.
Figure IV-4. Diurnal xylem water potential ($\Psi$) measurements taken on representative days during 2002-2003. Bars represent standard error.
Figure IV-5. Diurnal assimilation rates (A) taken on representative days during 2002-2003. Bars represent standard error.
Figure IV-6. Diurnal stomatal conductance rates (g) taken on representative days during 2002-2003. Bars represent standard error.
Figure IV-7. Diurnal transpiration rates (E) taken on representative days during 2002-2003. Bars represent standard error.
Figure IV-8. Diurnal xylem water potential measurements (Ψ), assimilation rates (A), conductance rates (g) and transpiration rates (E) taken on 21 Jun 2002. A rain event totaling 0.80 cm occurred from 1430 to 1500 Solar Time.
CHAPTER V

USE OF PHOTOSYNTHETIC CARBON GAIN AS A COMMON CURRENCY: MODELING RESPONSE OF FOUR PLANT SPECIES TO THE PRESENT DAY BARRIER ISLAND BEACH ENVIRONMENT

Introduction

For many years researchers have been interested in identifying parameters that are important indicators of plant success in various environments (Salisbury and Ross 1992, Larcher 1995, Lambers et al. 1998, Barbour et al. 1999). Specific leaf area (Korner 1991), internal leaf anatomy and development (Oguch et al. 2008), carbon allocation patterns (Smith and Stitt 2007) biomass (Barbour et al. 1985), respiration rate (Nobel 1995), biochemistry (Evans et al. 1995), water relations (Schulze et al. 1987) and photosynthetic carbon gain (PCG) (Crawford 2008) are a few of the parameters that have been used. Taken alone, none of these can provide a complete picture of plant success in a given environment.

For more than two decades, researchers have been calling for studies that incorporate multiple variables and assess several factors when defining plant success (Chapin III et al. 1987, Osmond et al. 1987, Korner 1991, Ackerly et al. 2000). Such studies are ideal, but are necessarily large in scope often requiring significant resources that may call the cost to benefit ratio into question. Of all the single factors linked to plant success, PCG has enjoyed the most widespread usage (Lee and Ignaciuk 1985, Pearcy et al. 1987, Crawford 2008). As with any single parameter, there are limitations
to the applicability of PCG and results must therefore be interpreted carefully (Osmond et al. 1987, Korner 1991, Oguchi et al. 2008).

Photosynthetic carbon gain has been linked to plant fitness in a number of studies (Pearcy et al. 1987 and references therein, Oguchi et al. 2008, Nilsen et al. 2009, Russell et al. 2009), although it is necessary for researchers to clearly define what is meant by “fitness” (Barbour et al. 1999 and references therein, Arntz et al. 2000). Some authors have questioned the existence of a direct relationship between PCG and fitness stating the need to include various other variables depending upon the specific study – or specialty of the researcher (Larcher et al. 1995 and references therein, Arntz et al. 1998, Gassmann 2004). Despite all of these concerns, PCG has been shown to be a relatively efficient and effective proxy for the estimation of plant success/fitness in several environments (Solbrig 1981, Lechowicz and Blais 1988, Gerber 1990, Cheplick 1995, Lambers et al. 1998 and references therein).

Barrier island (BI) beach ecosystems have traditionally been viewed as harsh, transient and physically controlled habitats where only a small suite of plant species survive (Sanders 1968, Barbour et al. 1985, Lee and Ignaciuk 1985, Weakley and Bucher 1992, Hancock and Hosier 2003). Although general ecological and life-history models for some BI beach plant species have been proposed (Dubois 1977, Ehrenfeld 1990 and references therein, Maun et al. 1990 and references therein, Evans and McCain 1995), none have incorporated ecophysiological concepts such as PCG. Such models would provide a general understanding of how plants respond to the current daily, seasonal and episodic stresses of the BI beach environment. Baselines established from these studies could be used to predict BI beach plant response to future climate change – an especially
important topic due to the sensitivity of this habitat to sea level rise and extreme episodic storm events (Schoenbaum 1982, Feagin et al. 2009).

Quantifying limitations to PCG where possible and qualitatively describing them elsewhere (Pilkey and Pilkely-Javis 2008) would strengthen the models, making them more robust. Several barrier beach studies, both on the West Coast of the USA (DeJong 1978a, DeJong 1978b, Mooney et al. 1983) and Japan (Ishikawa et al. 1990, Ishikawa et al. 1991, Ishikawa et al. 1996), have related reductions in photosynthesis to various environmental stresses. These studies did not directly address limitations to PCG nor place findings in a larger context (e.g. ecophysiological models), although researchers in other environments have done so (Johnson et al. 2004, Quero et al. 2008).

The purposes of the present study were to:

1. Quantify PCG of four BI beach species representing distinct functional plant groups (as defined by Shao et al. 1996, Crawford 2008)
2. Quantitatively and/or qualitatively describe limitations to PCG
3. Develop conceptual models incorporating abiotic stressors, plant response and species fitness in the BI beach environment

**Materials and Methods**

**Study Site**

Topsail Island is a low topographic relief, 42 km long BI that varies in width from 150 to 500 m located approximately 40 km northeast of Wilmington, North Carolina (Stallman 2004). The island is extensively developed with single family homes along almost its entire length (Frankenburg 1997). The study site was located on the southwestern end of the island (34° 20’ 50” N, 77° 39’ 5” W) adjacent to New Topsail
Inlet. Due to migration of the inlet to the southwest at an average rate of 35 m per year, an extensive beach and dune environment extends approximately 1-2 km from the inlet to the first beach home.

**Species**

*Amaranthus pumilus* (Rafinesque) is a pioneering C₄ annual species that inhabits the driftline and foredune area of the BI beach (Weakley and Bucher 1992). The plant has a prostrate growth form, succulent leaves and pink to reddish stems. As a result of population decline due to habitat loss, *A. pumilus* was listed as federally threatened in 1993 (Weakley and Bucher 1992, United States Fish and Wildlife Service 1993). *Cakile edentula* (Bigelow) Hooker is a pioneering C₃ annual species that has an upright growth form and succulent leaves (Radford et al. 1968). The plant is common within its range (Barbour and Rodman 1970) and unlike *A. pumilus*, *C. edentula* can persist into a second growing season in moderate climates (Barbour and Rodman 1970, Boyd and Barbour 1993, Cody and Cody 2004). *Hydrocotyle bonariensis* Lamarck is a C₃ perennial species whose seeds germinate in swales located landward of the primary dune on BI beaches (Evans 1992). Plants often grow seaward into the foredune via rhizomes (Evans 1992). *Iva imbricata* Walter is a succulent leaved, woody C₃ shrub that can grow to heights of 1 m and widths of 3 m (Radford et al. 1968). As a seedling, *I. imbricata* coinhabits the driftline with *A. pumilus* and *C. edentula*.

**The Sunlight Environment**
Continuous measurements of Photosynthetically Active Radiation (PAR) were taken from June 2002 until June 2004 using a LI-190 Quantum Sensor (Li-Cor, Lincoln Nebraska) mounted on a 1.5 m wooden pole (10 cm X 10 cm) interfaced with a HOBO® data logger via a Universal Transconductance Amplifier (EME Systems, Berkley CA).

*Photosynthetic Carbon Gain (PCG)*

Gas exchange measurements were taken approximately every three hours from dawn until dusk on one representative day each month from 21 June 2002 until 20 May 2003. The first fully expanded leaf of five different individuals for each species was measured using the TPS Portable Photosynthesis System (PP Systems, Amesbury, Massachusetts). Photosynthesis (A) was calculated from the CO₂ flux rate. Total daily assimilation (mol CO₂ m⁻² day⁻¹) was quantified by determining the area under the diurnal photosynthesis curve (assimilation X solar time) for each measurement day. Total monthly assimilation (mol CO₂ m⁻² month⁻¹) was calculated by multiplying total daily assimilation times the number of days in that particular month.

*Photosynthetic Light Response*

Photosynthetic light response of the adaxial leaf surface of each species was measured using the Transportable Photosynthesis System. The first fully expanded leaf of approximately thirty individuals of each species was chosen for measurement. Neutral density filters were used to attenuate natural light resulting in PAR values ranging from 2000 μmol m⁻² s⁻¹ (full sun) to 100 μmol m⁻² s⁻¹. Leaves were allowed to acclimate to new light intensities for two minutes between readings. Previous measurements have shown that leaves return to a maximum photosynthetic rate for a given PAR value within two minutes and that order of light attenuation (high to low, low to high, or random) does
not affect readings. Measurements were taken on 7 July 2002 between 1000 and 1200 hours (solar time). Best-fit linear and quadratic regression equations were used to describe the relationship between PAR and photosynthesis (i.e. assimilation rate, A). Due to the quadratic relationship between A and PAR for *H. bonariensis*, assimilation rates were log<sub>10</sub> transformed (Norman and Streiner 2000). The relationship between A and PAR for all other species was linear. The A:PAR ratio for each species was then determined and tested for significant differences using a single-factor ANOVA (MacDonald 2008).

*Predicted versus Actual PCG*

Daily PCG was predicted for each species on 29 June 2003 by entering PAR values (see *The Sunlight Environment*) into the best-fit linear and quadratic photosynthetic light response regression equations (see *Photosynthetic Light Response*). This generated a daily photosynthesis curve whose area represented predicted PCG (see Quero et al. 2008 for a similar experimental set-up). Actual PCG was determined via the methods described in the *Photosynthetic Carbon Gain* section.

*Transplantation Experiment*

One-hundred and fifty *A. pumilus* seedlings (approximately twenty leaf-stage) were obtained from the New Hanover/Brunswick County Cooperative Extension greenhouse located on Oak Island, NC. Seedlings were grown from seeds collected on Oak Island (approximately 60 miles southwest of Topsail Island). Past studies have indicated that differences between populations of *A. pumilus* living on Oak Island and Topsail Island should be minimal (Weakley and Bucher 1992, Strand 2002). On 18 June 2004, forty-four plants were transplanted to each of three experimental sites (site 1 =
driftline, site 2 = foredune, site 3 = primary dune) on the southwestern end of Topsail Island. Eighteen of the original one-hundred and fifty plants were not used due to signs of stress/decline (yellowing leaves, stunted growth). Forty-four naturally occurring \textit{A. pumilus} plants were also observed and measured. Each plant received supplemental water (to field capacity) – once at transplantation and once later the same day at approximately 1800 solar time. Observations of the plants, including number surviving and general appearance, were made on 14 July, 11 August and 4 September 2004. Gas exchange measurements were taken on 14 July 2004 using the same protocol as depicted in the \textit{Photosynthetic Carbon Gain} section.

\textbf{Results}

\textit{The Sunlight Environment}

Figure V-1 shows PAR measurements taken on four representative days during 2002-2003. Actual PAR (PAR\textsubscript{A}) measured on 12 August 2002 was 48.76 mol m\textsuperscript{-2}, while theoretical PAR (PAR\textsubscript{T}), maximum amount of PAR given a completely clear sky throughout the day, was 57.37 mol m\textsuperscript{-2}. Passing clouds accounted for the difference between PAR\textsubscript{A} and PAR\textsubscript{T} (a 15\% reduction in total radiation for the day). PAR\textsubscript{A} for 26 November 2002 was 16.93 mol m\textsuperscript{-2} while PAR\textsubscript{T} was 28.40 mol m\textsuperscript{-2} (a 40\% reduction due to clouds). PAR\textsubscript{A} for 23 March 2003 was 46.90 mol m\textsuperscript{-2} while PAR\textsubscript{T} was 51.55 mol m\textsuperscript{-2} (a 9\% reduction due to clouds). In the final representative day, PAR\textsubscript{A} for 29 June 2003 was 63.53 mol m\textsuperscript{-2} while PAR\textsubscript{T} was 64.50 mol m\textsuperscript{-2} (a 1.5\% reduction due to clouds).

\textit{Photosynthetic Carbon Gain (PCG)}

Figures V-2a, V-2b and V-2c depict diurnal assimilation measurements (diurnal photosynthesis curves) for \textit{A. pumilus}, \textit{C. edentula}, \textit{H. bonariensis} and \textit{I. imbricata} taken
on one representative day per month from 21 June 2002 until 20 May 2003. *Amaranthus pumilus* had the highest assimilation rate (17 μmol CO$_2$ m$^{-2}$ s$^{-1}$) of any species on 21 June 2002. *Iva imbricata* had the second highest rate (14 μmol CO$_2$ m$^{-2}$ s$^{-1}$) with *C. edentula* and *H. bonariensis* assimilation rates being essentially equal (7 μmol CO$_2$ m$^{-2}$ s$^{-1}$). On 3 July 2002, maximum assimilation rates for *A. pumilus*, *C. edentula* and *I. imbricata* were 15-16 μmol CO$_2$ m$^{-2}$ s$^{-1}$, with *I. imbricata* rates declining quickly in the afternoon hours. The maximum rates of *H. bonariensis* were substantially lower (7 μmol CO$_2$ m$^{-2}$ s$^{-1}$) than the other three species. *Amaranthus pumilus* again had the highest assimilation rates on 12 August 2002 (19 μmol CO$_2$ m$^{-2}$ s$^{-1}$), followed by *I. imbricata* and *H. bonariensis* (approximately 9 μmol CO$_2$ m$^{-2}$ s$^{-1}$). *Cakile edentula* was absent during this time period.

During 17 September 2002, the maximum assimilation rate of *I. imbricata* was 15 μmol CO$_2$ m$^{-2}$ s$^{-1}$ followed by *H. bonariensis* (9 μmol CO$_2$ m$^{-2}$ s$^{-1}$) and *A. pumilus* (5 μmol CO$_2$ m$^{-2}$ s$^{-1}$). *Cakile edentula* was again absent during this time period.

On 21 October, 26 November and 17 December 2002, *C. edentula*, *H. bonariensis* and *I. imbricata* were present, but had low assimilation rates throughout the day (3 μmol CO$_2$ m$^{-2}$ s$^{-1}$, 5 μmol CO$_2$ m$^{-2}$ s$^{-1}$ and 5 μmol CO$_2$ m$^{-2}$ s$^{-1}$ maximum, respectively). *Amaranthus pumilus* was absent during both measurement periods. Only *C. edentula* was present on 15 January 2002, 4 February and 23 March 2003 when maximum assimilation rates of 5 μmol CO$_2$ m$^{-2}$ s$^{-1}$, 4 μmol CO$_2$ m$^{-2}$ s$^{-1}$ and 11 μmol CO$_2$ m$^{-2}$ s$^{-1}$ were recorded, respectively.

*Cakile edentula*, *H. bonariensis* and *I. imbricata* had very similar diurnal assimilation rates throughout the day on 17 April 2003, reaching a maximum of approximately 5 μmol CO$_2$ m$^{-2}$ s$^{-1}$ at 1200 solar time. *Amaranthus pumilus* was not
present during this measurement period. On 20 May 2003, *A. pumilus* experienced the highest assimilation rate (25 μmol CO$_2$ m$^{-2}$ s$^{-1}$) of any species. The maximum rates of *C. edentula* and *I. imbricata* were equivalent (17-18 μmol CO$_2$ m$^{-2}$ s$^{-1}$) while *H. bonariensis* had lower maximum values (13 μmol CO$_2$ m$^{-2}$ s$^{-1}$).

Total daily assimilation (area under each of the diurnal photosynthesis curves mentioned above) for *A. pumilus, C. edentula, H. bonariensis* and *I. imbricata* is shown in Table V-1. *Amaranthus pumilus* was present during five of the measurement periods, assimilating the greatest amount of CO$_2$ (0.74 mol m$^{-2}$) on 20 May 2003 and the least (0.12 mol m$^{-2}$) on 17 September 2002. *Cakile edentula* was present during ten of the measurement periods, assimilating the greatest amount of CO$_2$ (0.54 mol m$^{-2}$) on 20 May 2003 and the least (0.09 mol m$^{-2}$) on 21 October 2002. *Hydrocotyle bonariensis* was present during ten of the measurement periods, assimilating the greatest amount of CO$_2$ (0.45 mol m$^{-2}$) on 20 May 2003 and the least (0.07 mol m$^{-2}$) on 21 October 2002. *Iva imbricata* was present during nine of the measurement periods, assimilating the greatest amount of CO$_2$ (0.62 mol m$^{-2}$) on 20 May 2003 and the least (0.09 mol m$^{-2}$) on 21 October 2002.

Total monthly assimilation, computed by multiplying the total daily assimilation times the number of days in a particular month, for *A. pumilus, C. edentula, H. bonariensis* and *I. imbricata* is show in Table V-2. Obviously the yearly patterns of high and low monthly assimilation mirror those of daily assimilation for each species. Using this calculation method, *I. imbricata* had the highest total yearly assimilation (80.16 mol CO$_2$ m$^{-2}$ s$^{-1}$), *C. edentula* had the second highest (69.91 mol CO$_2$ m$^{-2}$ s$^{-1}$) with *A. pumilus*
having the third highest (63.14 mol CO$_2$ m$^{-2}$ s$^{-1}$) and \textit{H. bonariensis} the least (59.10 mol CO$_2$ m$^{-2}$ s$^{-1}$).

\textit{Photosynthetic Light Response}

The photosynthetic light response of each species is illustrated in Figure V-3. The slope of the best-fit line for \textit{A. pumilus} and \textit{I. imbricata} photosynthetic light response were the steepest of any species measured and not significantly different from one another, (F = 2.16, p = 0.15), with no evidence of light saturation. Maximum assimilation rates of \textit{A. pumilus} were approximately 24 μmol CO$_2$ m$^{-2}$ s$^{-1}$ obtained at PAR values of 1800 μmol m$^{-2}$ s$^{-1}$. Maximum assimilation rates for \textit{I. imbricata} were 22 μmol CO$_2$ m$^{-2}$ s$^{-1}$ obtained at a PAR value of 1600 μmol m$^{-2}$ s$^{-1}$. The slope of the best fit line for \textit{C. edentula} was less steep than the best-fit line for \textit{A. pumilus} (F = 48.88, p < 0.001) and \textit{I. imbricata} (F = 19.46, p < 0.001), with no evidence of light saturation. Maximum assimilation rates of \textit{C. edentula} were approximately 12 μmol CO$_2$ m$^{-2}$ s$^{-1}$ obtained at PAR values of 1600 μmol m$^{-2}$ s$^{-1}$. The relationship between assimilation and PAR for \textit{H. bonariensis} was quadratic and therefore did exhibit light saturation at PAR values greater than 900 μmol m$^{-2}$ s$^{-1}$. Maximum assimilation rates for \textit{H. bonariensis} were approximately 9 μmol CO$_2$ m$^{-2}$ s$^{-1}$. Equations for the best fit line or curve can be found in Table V-3.

\textit{Predicted versus Actual PCG}

Figure V-4 shows predicted and actual PCG for \textit{A. pumilus}, \textit{C. edentula}, \textit{H. bonariensis} and \textit{I. imbricata}. Based upon the photosynthetic light response of \textit{A. pumilus} and PAR values for 29 June 2003, predicted PCG was 1.00 mol CO$_2$ m$^{-2}$ s$^{-1}$ while actual measurements for the same day were 0.44 mol CO$_2$ m$^{-2}$ s$^{-1}$ (a negative difference of
In the same manner, the predicted PCG for *C. edentula* was 0.46 mol CO$_2$ m$^{-2}$ s$^{-1}$ while the actual PCG was 0.52 mol CO$_2$ m$^{-2}$ s$^{-1}$ (a positive difference of 21%). The predicted PCG for *H. bonariensis* was 0.36 mol CO$_2$ m$^{-2}$ s$^{-1}$ while the actual PCG was 0.19 mol CO$_2$ m$^{-2}$ s$^{-1}$ (a negative difference of 47%). Finally, the predicted PCG for *I. imbricata* was 1.00 mol CO$_2$ m$^{-2}$ s$^{-1}$ while the actual PCG was 0.40 mol CO$_2$ m$^{-2}$ s$^{-1}$ (a negative difference of 60%).

**Transplantation Experiment**

Figure V-5 is a schematic diagram of the three transplantation sites as well as a table depicting the number of plants surviving during each observation period. Of the forty-four naturally occurring *A. pumilus* plants followed through the season, thirty-four were present on 14 July, twenty-nine on 11 August and thirteen on 4 September 2004. Of the forty-four plants transplanted to site 1 (driftline), thirty-three were present on 14 July, twenty-six on 11 August and ten on 4 September 2004. Of the forty-four plants transplanted to site 2 (foredune), forty-three were present on 14 July, forty-two on 11 August and zero on 4 September 2004. Of the forty-four plants transplanted to site 3 (primary dune), forty-two were present on 14 July, forty-one on 11 August and zero on 4 September 2004.

Figure V-6 depicts diurnal photosynthesis for representative *A. pumilus* plants at each of the transplantation sites as well as individuals found naturally growing in the driftline and foredune habitats taken on 14 July 2004. The naturally occurring plants reached a maximum photosynthetic rate of 22 µmol CO$_2$ m$^{-2}$ s$^{-1}$ by 1200 solar time. The diurnal photosynthetic rates of the driftline and foredune transplants were comparable, reaching a maximum of approximately 14 µmol CO$_2$ m$^{-2}$ s$^{-1}$ at 1200 solar time, although
the photosynthetic rate of the foredune transplants did decrease more rapidly than the
driftline transplants in the afternoon/evening. The diurnal photosynthetic rate of the
primary dune transplants was substantially lower, reaching a maximum of 6 µmol CO₂ m⁻² s⁻¹ by 1200 solar time. Photosynthetic carbon gain on 14 July 2004 was 0.479 mol CO₂ m⁻² day⁻¹, 0.337 mol CO₂ m⁻² s⁻¹, 0.146 mol CO₂ m⁻² s⁻¹ and 0.579 mol CO₂ m⁻² s⁻¹ for driftline, foredune, primary dune and natural *A. pumilus* plants, respectively.

**Discussion**

*Photosynthetic Carbon Gain (PCG)*

The daily patterns of PCG for each species were influenced by both physiology
and life-history traits (Figures V-2a, b and c; Table V-1; for a full discussion of
physiology and life-history of each species see Chapter IV). For example, *A. pumilus* had
the highest assimilation rates in the months of May, June, July and August but by
September rates had noticeably declined. By October all *A. pumilus* plants were gone
from the study site. *Cakile edentula* exhibited moderate to high assimilation rates and
was absent during some of the hottest months of the year, late July, August and
September, when the vapor pressure deficit and hence transpiration would have been very
high. *Iva imbricata* also had moderate to high assimilation rates and was absent during
January, February and March. Finally, assimilation measurements for *H. bonariensis*
were the lowest recorded. *Hydrocotyle bonariensis* was present during all months except
January and February.

Table V-2 depicts the estimated yearly PCG for each plant. Although these
estimations are based on only one actual measurement day per month and these
measurement days were necessarily sunny to partly cloudy (due to the inability of taking
gas exchange measurements during a rainy day), they still offer a good starting point to discuss yearly PCG. Perhaps each of these BI beach species must reach a yearly PCG threshold that is species specific in order to complete their life cycle (or survive into a second year if they are perennials), as has been demonstrated in other plants (Pearey et al. 1987, Larcher 1995). The yearly PCG of *A. pumilus* was 63.14 mol CO$_2$ m$^{-2}$ yr$^{-1}$ while that of *C. edentula*, *H. bonariensis* and *I. imbricata* were 69.91 mol CO$_2$ m$^{-2}$ yr$^{-1}$, 59.10 mol CO$_2$ m$^{-2}$ yr$^{-1}$ and 80.16 mol CO$_2$ m$^{-2}$ yr$^{-1}$, respectively. What is interesting is how each species obtained these totals. *Amaranthus pumilus* assimilated all of its carbon via high photosynthetic rates within a five to six month time period. *Cakile edentula* had lower overall photosynthetic rates but was active during nine to ten months of the year. *Iva imbricata* exhibited relatively high photosynthetic rates and was active during nine months of the year. The photosynthetic rates of *Hydrocotyle bonariensis* were low, but the plant remained active during ten months of the year.

The yearly PCG threshold for *A. pumilus* and *C. edentula* are comparable possibly because both plants have similar life-styles and associated structural/allocation costs (both plants are annuals and are similar in size and weight at maturity). The yearly PCG threshold for *H. bonariensis* is slightly less than the other three species possibly because of reduced above ground structure and therefore lower associated costs. Finally, the yearly PCG threshold for *I. imbricata* is the highest potentially due to the high associated costs of producing and maintaining substantial perennial above-ground biomass. Several studies have linked increased PCG thresholds to increased structural costs (Lambers et al. 1998, Barbour et al. 1999, Crawford 2008). Differences in structure (annual, perennial,
herbaceous, woody, growth form) are often used to organize species into functional plant groups (Shao et al. 1996, Crawford 2008).

Perhaps there exists PCG thresholds that relate to plant life-history stages. For example, maybe *A. pumilus* seedlings must assimilate a given amount of carbon before they can move to the pre-reproductive stage which includes stem and root elongation as well as leaf development (Weakley and Bucher 1992, Hancock and Hosier 2003). Another potential stage might occur when flowers and fruits are produced. After plants become reproductive then maintenance until senescence could be an important concept to consider in relation to carbon requirements. Figure V-7 provides a conceptual model for how PCG thresholds and maintenance demands potentially relate to life-history stages in *A. pumilus*. A variety of studies have examined life-history stages in plants and found correlations between PCG and leaf age (Zhang et al. 2008, Reich et al. 2009), water status (Casper et al. 2006, Reinhardt et al. 2009) and reproduction (Arntz et al. 1998). Of course, PCG is only one part of a much larger, complete story that includes allocation patterns and metabolic costs (Korner 1991, Larcher 1995).

**Limitations to PCG**

The photosynthetic light response of each species taken on 7 July 2002 (Figure V-3) coupled with PAR measurements taken on 29 June 2003 (Figure V-1) were used to generate predicted PCG for a typical day on Topsail Island, NC (Figure V-4). Predicted PCG values deviated widely from actual values, over-estimating for three species and under-estimating for one. These results lead to the obvious conclusion that many environmental factors besides irradiance levels influence photosynthesis rates and hence PCG in these four BI beach species. *Cakile edentula* was the lone species in which actual
PCG was higher than potential PCG and this may be attributed to differences in life history patterns. *Cakile edentula* is dormant (survives only as a seed) during late July into late October whereas the other three species are active during this time period. The photosynthetic light response measurements used to calculate the predicted PCG were taken on 7 July 2002 possibly when *C. edentula* plants were beginning to senesce. This would cause the assimilation values in relation to PAR values to be lower than if measurements were taken earlier in the year, substantially reducing predicted PCG. *Amaranthus pumilus*, *H. bonariensis* and *I. imbricata* plants were actively growing during this time period therefore photosynthetic light response values were relatively high resulting in higher predicted PCG.

Between 17 June and 11 August 2004, natural *A. pumilus* plants and driftline transplants experienced similar die-offs of 34% and 41%, respectively (Figure V-5). During the same time period, foredune and primary dune transplants experienced 5% and 7% die-offs, respectively. By the final survey on 9 September 2004, however, 30% of the natural *A. pumilus* plants and 23% of the driftline transplants were present while none of the foredune or primary dune transplants were present. A potential explanation for this difference is illustrated in Figure V-6. On 14 July 2004, naturally occurring *A. pumilus* plants had the highest PCG followed by driftline, foredune and primary dune transplants. This pattern mirrors the abundance of naturally occurring *A. pumilus* plants on at least eight BI beaches located in southeastern NC, with the vast majority of plants found along the driftline, some found in the foredune and a rare few found in the primary dune (personal observation). Assuming that seed dispersal to these three habitats is relatively equal as has been suggested by several authors (Ehrenfeld 1990, Maun et al. 1990,
Weakley and Bucher 1992, Hancock and Hosier 2003), microscale differences in abiotic factors may account for differential PCG and survival. Several reviews have reached similar conclusions based on studies from a variety of environments (Pearcy et al. 1987, Baskin and Baskin 1998, Clark et al. 2007).

Factors that have been shown to limit growth of beach plants in specific situations include drought (Ishikawa et al. 1996), salinity (De Jong 1978, Ishikawa et al. 1991), salt-spray (Oosting 1945, Boyce 1954, Barbour 1978), low nutrients (Barbour et al. 1985, Barbour et al. 1999) high temperatures (Mooney et al. 1983) and salt-water overwash (Hesp 1991, Lee and Ignaciuk 1985, Hancock and Hosier 2003). Interestingly, an increase in the growth rate of some beach species has been associated with sand burial (Yuan et al. 1993, Perumal and Maun 2006, Gilbert et al. 2008, Gilbert and Ripley 2008).

Although growth rate reductions have been addressed, no studies have quantified PCG loss in relation to these abiotic factors. Indeed, the current study has in no way quantitatively assessed reduction in PCG of *A. pumilus* due to any of the above factors. However, this research has found that irradiance levels alone do not accurately predict PCG (indicating other factors are important) and that PCG (and survival) of transplants follows naturally occurring abundance patterns (driftline>foredune>primary dune). It would be advisable to pursue future research that first independently tests the effect of each factor on PCG of a selected species (e.g. *A. pumilus*) then tests the effects of multiple factors on PCG of the selected species (as recommended by Chapin et al. 1987 and Osmond et al. 1987).

In an excellent example of a one-factor test, Snow (unpublished data) measured the photosynthetic light response of both saltwater inundated and non-inundated *A.*
plants following a 9 July 2004 overwash event on Topsail Island, NC (Figure V-8). Assimilation rates of saltwater inundated plants were as much as 56% lower than non-inundated plants. Although not directly assessed, these limits to assimilation probably reduce daily PCG potentially to the point of plant death. In a 2003 study, Hancock and Hosier discovered that one of the major causes of *A. pumilus* mortality on Figure Eight Island, NC was overwash by late summer/early fall storms. The authors concluded that overwash (along with other abiotic factors) could theoretically cause up to a 98% reduction in reproductive output depending upon the timing of storms. Increases in storm intensity coupled with sea-level rise due to global climate change (IPCC 2007) is cause for concern over the future of BI beach species, especially *A. pumilus* which is currently listed as Federally Threatened (US Fish and Wildlife Service 1993).

As evidenced by the examples above, past BI studies have been able to address the effect of certain abiotic factors on assimilation, plant mortality and reproduction. What is lacking, along with data concerning multiple-factor effects on BI beach plants, is a comprehensive framework in which to integrate the ideas of potential PCG, realized PCG and species fitness. The following section introduces conceptual models intended to serve as starting points for addressing these issues.

*Modeling Abiotic Stressors, Plant Response and Species Fitness in the BI Beach Environment*

*Amarathus pumilus*, *C. edentula*, *H. bonariensis* and *I. imbricata* can be considered representatives of four distinct functional plant groups that experience harsh daily, seasonal and extreme event stresses within the highly dynamic BI beach environment. These species exhibit a variety of stress responses that include specific leaf
anatomy and orientation properties (Chapter III), physiologies (Chapter IV) and life-history patterns (Chapter IV). It can be argued that plant response to an environment should maximize PCG, or minimize loss depending upon point of view, if there are appreciable links to plant fitness/success. Indeed, there has been a recent emphasis in plant research to identify important plant ecophysiological traits, define their relationship to PCG and determine their impact on plant fitness (Arntz and Delph 2001, Gerber and Griffen 2003, Reich et al. 2003, Shipley et al. 2005, Donovan et al. 2009). The ultimate goal of such studies is to directly link functional traits to fitness and thereby begin to address the evolution of such traits (Ackeryl et al. 2000, Ackerly and Monson 2003).

Figure V-9 is a conceptual model of BI beach environmental stresses, species response and resultant PCG. The general idea of the model is that BI beach plants have a potential PCG they could attain (measured on a daily, monthly and/or yearly timeframe) if all abiotic factors were at an optimum for the particular plant species. Abiotic environmental stresses (the environmental stress “filter” or “filters”) challenge plants resulting in limited resource acquisition and increased resource expenditure. Plant response (leaf anatomy/orientation, physiology and life-history patterns) to these challenges determines realized PCG. Each response is controlled by genes and therefore a plant’s individual genetic compliment in part determines response effectiveness (Colmer and Voesenek 2009, Papdi et al. 2009, Xiao et al. 2009). At the population level selection for the “best” response (ecophysiological trait) can occur (Ackerly et al. 2000, Arntz et al. 2000, Arntz and Delph 2001, Reich et al. 2003). Figure V-10 is intended to serve as a summary diagram relating abiotic stresses, plant response, PCG, allocation patterns and fitness in the BI beach environment.
Although serving as a good beginning, there are several points that need to be resolved concerning these conceptual models. Research that directly ties PCG to species fitness is needed. Indeed, a clear definition of species fitness in the BI beach environment should be developed. Studies in other environments have used seed number (Gerber and Griffin 2003), vegetative biomass (Ackerly et al. 2000), lifetime leaf net carbon fixation (Shipley et al. 2005) and even photosynthetic rate (Arntz et al. 2000) as proxies for fitness. Path analysis has been employed in several studies and offers a detailed description of individual factors and their contribution to overall fitness (Norman and Streiner 2000, Arntz and Delph 2001).

In conclusion, PCG is potentially the most efficient single parameter in which to assess plant fitness/success in the BI beach environment. This study has provided baseline PCG estimations of four plants that represent distinct functional groups located on Topsail Island, NC, explored abiotic stress (daily, seasonal and episodic) limitations to PCG, plant response to these stresses and overall impacts on plant fitness. Conceptual models have been presented that relate abiotic stress, plant response and fitness in the BI beach environment. Although the information presented in this study is preliminary in many respects and issues/questions remain, as well as the need for more detailed research, the main ideas serve as a beginning to address the role and eventually the evolution of functional traits in BI beach plants.

Literature Cited


Cody, M.L. and T.W.D. Cody. 2004. Morphology and spatial distribution of alien...


Table V-1. Total assimilation (mol CO₂ m⁻² day⁻¹) for *Amaranthus pumilus*, *Cakile edentula*, *Hydrocotyle bonariensis* and *Iva imbricata* during representative days from June 2002 until May 2003. * denotes estimated assimilation.

<table>
<thead>
<tr>
<th>Month</th>
<th>A. pumilus</th>
<th>C. edentula</th>
<th>H. bonariensis</th>
<th>I. imbricata</th>
</tr>
</thead>
<tbody>
<tr>
<td>21 June (2002)</td>
<td>0.29</td>
<td>0.20</td>
<td>0.21</td>
<td>0.33</td>
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<tr>
<td>3 July</td>
<td>0.41</td>
<td>0.45</td>
<td>0.17</td>
<td>0.36</td>
</tr>
<tr>
<td>12 August</td>
<td>0.49</td>
<td>---</td>
<td>0.29</td>
<td>0.37</td>
</tr>
<tr>
<td>17 September</td>
<td>0.12</td>
<td>---</td>
<td>0.27</td>
<td>0.43</td>
</tr>
<tr>
<td>21 October</td>
<td>---</td>
<td>0.09</td>
<td>0.07</td>
<td>0.09</td>
</tr>
<tr>
<td>26 November</td>
<td>---</td>
<td>0.15</td>
<td>0.11</td>
<td>0.12</td>
</tr>
<tr>
<td>17 December</td>
<td>---</td>
<td>0.14</td>
<td>0.10</td>
<td>0.12</td>
</tr>
<tr>
<td>15 January (2003)</td>
<td>---</td>
<td>0.13</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>4 February</td>
<td>---</td>
<td>0.08</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>23 March</td>
<td>---</td>
<td>0.32</td>
<td>0.12*</td>
<td>---</td>
</tr>
<tr>
<td>17 April</td>
<td>---</td>
<td>0.18</td>
<td>0.14</td>
<td>0.18</td>
</tr>
<tr>
<td>20 May</td>
<td>0.74</td>
<td>0.54</td>
<td>0.45</td>
<td>0.62</td>
</tr>
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</table>
Table V-2. Total monthly assimilation (mol CO$_2$ m$^{-2}$ month$^{-1}$) for *Amaranthus pumilus*, *Cakile edentula*, *Hydrocotyle bonariensis* and *Iva imbricata* from June 2002 until May 2003. Total monthly assimilation was calculated by multiplying the total daily assimilation times the number of days in a particular month. * denotes estimated assimilation.

<table>
<thead>
<tr>
<th>Month</th>
<th><em>A. pumilus</em></th>
<th><em>C. edentula</em></th>
<th><em>H. bonariensis</em></th>
<th><em>I. imbricata</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>June (2002)</td>
<td>8.70</td>
<td>6.00</td>
<td>6.30</td>
<td>9.90</td>
</tr>
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<td>July</td>
<td>12.71</td>
<td>13.95</td>
<td>5.27</td>
<td>11.16</td>
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<td>August</td>
<td>15.19</td>
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<td>8.99</td>
<td>11.47</td>
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<tr>
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<td>8.10</td>
<td>12.90</td>
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<td>October</td>
<td>---</td>
<td>2.79</td>
<td>2.17</td>
<td>2.79</td>
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<td>November</td>
<td>---</td>
<td>4.50</td>
<td>3.30</td>
<td>3.60</td>
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<td>December</td>
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<td>4.03</td>
<td>---</td>
<td>---</td>
</tr>
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<td>February</td>
<td>---</td>
<td>2.24</td>
<td>---</td>
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</tr>
<tr>
<td>March</td>
<td>---</td>
<td>9.92</td>
<td>3.72*</td>
<td>---</td>
</tr>
<tr>
<td>April</td>
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<td>5.40</td>
<td>4.20</td>
<td>5.40</td>
</tr>
<tr>
<td>May</td>
<td>22.94</td>
<td>16.74</td>
<td>13.95</td>
<td>19.22</td>
</tr>
<tr>
<td>Yearly Total</td>
<td>63.14</td>
<td>69.91</td>
<td>59.10</td>
<td>80.16</td>
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(mol CO$_2$ m$^{-2}$ yr$^{-1}$)
Table V-3. Best-fit equations for the photosynthetic light response of *A. pumilus*, *C. edentula*, *H. bonariensis* and *I. imbricata*.

<table>
<thead>
<tr>
<th>Species</th>
<th>Best-fit Equation</th>
<th>r value</th>
<th>p value</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>A. pumilus</em></td>
<td>( y = 1.33x \times 10^{-2} + 8.66 \times 10^{-1} )</td>
<td>0.87</td>
<td>p&lt;0.001</td>
</tr>
<tr>
<td><em>C. edentula</em></td>
<td>( y = 6.13x \times 10^{-3} + 8.85 \times 10^{-1} )</td>
<td>0.68</td>
<td>p&lt;0.001</td>
</tr>
<tr>
<td><em>H. bonariensis</em></td>
<td>( y = -2.24x^2 \times 10^{-6} + 8.36x \times 10^{-3} + 6.53 \times 10^{-1} )</td>
<td>0.60</td>
<td>p&lt;0.001</td>
</tr>
<tr>
<td><em>I. imbricata</em></td>
<td>( y = 1.32x \times 10^{-2} + 1.68 )</td>
<td>0.68</td>
<td>p&lt;0.001</td>
</tr>
</tbody>
</table>
12 August 2002
PAR$_A$ = 48.76 mol m$^{-2}$
PAR$_T$ = 57.37 mol m$^{-2}$
15% reduction due to cloud cover

26 November 2002
PAR$_A$ = 16.93 mol m$^{-2}$
PAR$_T$ = 28.40 mol m$^{-2}$
40% reduction due to cloud cover

23 March 2003
PAR$_A$ = 46.90 mol m$^{-2}$
PAR$_T$ = 51.55 mol m$^{-2}$
9% reduction due to cloud cover

29 June 2003
PAR$_A$ = 63.53 mol m$^{-2}$
PAR$_T$ = 64.50 mol m$^{-2}$
1.5% reduction due to cloud cover

Figure V-1. PAR measurements taken on representative days during 2002 and 2003. PAR$_A$ = actual PAR, PAR$_T$ = theoretical PAR (red curve), % reduction due to clouds is also indicated.
Figure V-2a. Diurnal assimilation rates (A) taken once per month from June 2002 until September 2002. Bars indicate maximum standard error measured for each species.
Figure V-2b. Diurnal assimilation rates (A) taken once per month from October 2002 until January 2003. Bars indicate maximum standard error measured for each species.
Figure V-2c. Diurnal assimilation rates (A) taken once per month from February 2003 until May 2003. Bars indicate maximum standard error measured for each species.
Figure V-3. Photosynthetic light response of *Amaranthus pumilus*, *Cakile edentula*, *Hydrocotyle bonariensis* and *Iva imbricata* measured on 7 July 2002.
Figure V-4. Predicted (A) and actual (B) photosynthetic carbon gain (PCG) for *Amaranthus pumilus*, *Cakile edentula*, *Hydrocotyle bonariensis* and *Iva imbricata*.
Figure V-5. Schematic diagram of the three *Amaranthus pumilus* transplantation sites on Topsail Island, NC. The table insert depicts the number of plants surviving during each observation period.
Figure V-6. Diurnal photosynthesis for representative *Amaranthus pumilus* plants at each of the transplantation sites as well as individuals found naturally growing in the driftline and foredune habitats. Measurements were taken on 14 July 2004.
Figure V-7. Conceptual model of how photosynthetic carbon gain (PCG) thresholds could relate to life-history stages in *Amaranthus pumilus.*
Figure V-8. Photosynthetic light response of *Amaranthus pumilus* plants both inundated and non-inundated with saltwater during a 9 July 2004 overwash event on Topsail Island, NC (A.G. Snow unpublished data).
Figure V-9. Conceptual model of barrier island beach abiotic stresses, species response, and resultant PCG.
Figure V-10. Idealized relationship between abiotic stresses, plant response, PCG, allocation patterns and fitness in the barrier beach environment.
CONCLUSIONS AND PREDICTIONS FOR THE FUTURE OF FOUR BARRIER ISLAND BEACH PLANT SPECIES

This dissertation has reviewed relevant barrier beach plant ecology and physiological plant ecology research (Chapter II) identifying a rich, historical record of plant ecology studies from the West Coast (USA), East Coast (USA), Great Lakes (USA) and Canada, but revealing a lack of studies applying ecophysiological techniques to plants living in the barrier island (BI) beach environment. The objective of this dissertation was to incorporate the tools of physiological ecology into an ecological study that investigated the response of *Amaranthus pumilus*, *Cakile edentula*, *Hydrocotyle bonariensis* and *Iva imbricata*, four plant species representing different functional groups, to daily, seasonal and episodic stresses present on the coastal barrier island of Topsail Island, NC.

Chapter III examined leaf form and function in relation to the model proposed by Smith et al. (1997). Abaxial and adaxial stomatal frequencies, internal leaf anatomy and the photosynthetic response to incident sunlight on the abaxial and adaxial leaf surfaces were measured. In general, leaves of *A. pumilus*, *C. edentula*, *H. bonariensis* and *I. imbricata* fit model predictions for a stressful environment with some exceptions. Chapter IV addressed the importance of water stress and plant response in the BI beach environment. It was determined that water availability may be greater than previously thought, challenging the assumption that plants living in this environment are constantly
under water stress. None of the plants examined experienced xylem water potentials low enough to be considered very stressful. Each of the species demonstrated physiological and life-history attributes that likely maximized photosynthetic carbon gain over a given year, albeit via different combinations of traits. Chapter V explored the use of photosynthetic carbon gain (PCG) as a common currency when addressing species response to and ultimately fitness in the BI beach environment. Photosynthetic carbon gain was found to be potentially the most efficient single parameter in which to assess plant fitness/success in the BI beach environment. Total yearly PCG for A. pumilus, C. edentula, H. bonariensis and I. imbricata did vary and there appeared to be a threshold amount of carbon that each plant must assimilate in order to complete its life cycle. This carbon threshold could be related to functional group traits (structural/maintenance requirements). Conceptual models were presented that relate PCG reductions due to abiotic stresses, plant response to these stresses and overall impacts on plant fitness.

This dissertation has so far focused on historic plant ecology and ecophysiology studies relevant to East Coast (USA) BIs and response of A. pumilus, C. edentula, H. bonariensis and I. imbricata to the present BI beach environment. The remainder of this chapter will explore likely alterations to the BI beach environment due to climate change and possible ramifications for the future of these four plant species.

The Dynamic Nature of Barrier Islands section in Chapter II discussed future sea-level rise, increases in storm intensity and frequency and possible impacts upon BI beach organisms due to climate change. Because of their intimate association with the ocean, BI beaches are predicted to experience climate change impacts more quickly and intensely than almost any other environment (Gilman et al. 2008, Wu et al. 2009). This
coupled with the unprecedented population migration to coastal areas over the past three decades (Brown and McLachlan 2002) puts extreme pressure on BI beach habitats and the organisms living within them.

Several studies have indicated that anthropogenic response to climate change (especially sea-level rise) is of equal or more importance than the environmental factors themselves (Crawford 2008, Dugan et al. 2008). “Hard” structures, such as groins, jetties and seawalls, used to mitigate erosion caused by sea-level rise and storms have been known for years to cause destruction and eventual loss of the beach - or an adjacent beach (Pikley et al. 1998, Pilkey and Pikley-Jarvis 2008). Due to lessons learned, hard structures are illegal in some states (Schoenbaum 1982) although “soft” structures such as sand fences and sand bags are allowed. Planting vegetation to stabilize dunes is successful in some instances (Woodhouse 1978), but is ineffective if storm surge of an Extreme Episodic Storm Event (EESE) reaches a critical value (Roman and Nordstrom 1988, Feagin 2008, Koch et al. 2009).

Beach renourishment is an increasingly popular method to slow erosion but is expensive, requires continual sand inputs and negatively impacts flora and fauna (Peterson and Bishop 2005 and references therein). Sea-level has fluctuated throughout the millenia and organisms that live at the land-sea interface have often been able to migrate seaward or landward with their habitat (Dolan et al. 1980, Ehrenfeld 1990, Gilman et al. 2008). If humans continue to alter coastlines and reduce their dynamic nature, habitats and therefore organisms will not have the opportunity to relocate and extinction rates will likely rise (Feagin et al. 2005, Greaver and Sternberg 2007, Dungan et al. 2008). One promising development is the Coastal Barrier Island Network, a
recently funded (National Science Foundation) diverse group of biologists, geologists, engineers, economists and sociologists that have begun to work toward a national policy that promotes sustainable preservation, conservation and development of BI ecosystems within the natural limits imposed by a highly dynamic environment (Feagin et al. 2009)

Of the four species examined in this dissertation, *A. pumilus* is likely to be most negatively effected. *Amaranthus pumilus* was federally listed as threatened in 1993 due to extirpation from 75% of its historic range (US Fish and Wildlife Service 1993). This decline in range was mostly attributed to habitat loss due to development and hardening of the shoreline (Weakley and Bucher 1992). *Amaranthus pumilus* is a pioneering species that predominates in the driftline habitat of the barrier beach. Dispersal of seeds via overwash events and subsequent ocean currents carry *A. pumilus* to “zones of suitable habitat” which are usually accreting ends of BIs (Hancock and Hosier 2003). Due to climate change and anthropogenic factors, the future availability of such zones appears to be bleak.

*Cakile edentula* is a cool-weather annual found in lacustrine environments (Great Lakes) as well as marine environments of the East and West Coast of the United States (Barbour and Rodman 1970). The plant has a unique strategy for reproduction in that there is a proximal and distal seed for each fruit (Maun et al. 1990). The distal seed breaks off and is dispersed via ocean currents to new habitats while the proximal seed remains in place and is often buried with the parent plant. This strategy allows some seed to be distributed to new, potentially suitable habitats while some seed stays in the current, presumably suitable habitat. These, as well as other, characteristics may account for the
current extensive range of *C. edentula*. Future barrier beach habitat loss is likely to impact this species, but to a lesser extend that *A. pumilus*.

*Hydrocotyle bonariensis* grows on most barrier beaches of the Southeastern United States (Evans 1988). This species not only inhabits the foredune and primary dune, but can also be found on secondary, tertiary (etc.) dunes and throughout slacks. The greatest asset of *H. bonariensis* is probably its asexual growth via rhizomes. These rhizomes facilitate translocation of nutrients and water promoting resource acquisition in a heterogeneous environment (Evans 1988, Evans 1991). This growth pattern, along with other functional traits, will probably allow *H. bonariensis* to fare better than *A. pumilus* in the barrier beach environment of the future. In one example illustrating this idea, Fahrig et al. (1993) found that plants with a clonal growth form recovered/recolonized BI beaches more quickly than other growth forms following an overwash event.

Of the four species examined in this dissertation, *I. imbricata*, is the only one producing substantial above ground, perennial growth (wood). *Iva imbricata* can be found along the coasts of southern Virginia to the Florida Keys, Gulf Coast of the United States and on beaches of Caribbean Islands (Jackson 1960). On Topsail Island, NC (and other sandy BI beaches), *I. imbricata* defines the permanent vegetation line (i.e. foredune). For example, *I. imbricata* seedlings are found in the driftline, foredune and primary dune throughout the growing season. Winter storms, however, remove all vegetation up to a certain distance from the ocean. *Iva imbricata* seedlings that are not overwashed and removed survive into the next growing season (producing wood) and thereby define the line of permanent vegetation for the next year. *Iva imbricata*, therefore, is an excellent indicator of sea-level rise. Little attention has been paid to this
species in the past, but intensive studies documenting the seaward/landward migration and subsequent health of individual plants as well as populations would pay rich dividends concerning our knowledge of the effects (and status) of sea-level rise on BI beaches.

Figure VI-1 shows the effects of a seasonal overwash event on the driftline habitat of Topsail Island, NC. Notice that all of the driftline vegetation has been removed, but that the foredune vegetation (2\textsuperscript{nd}, 3\textsuperscript{rd}, etc. year growth of \textit{I. imbricata}) remains – defining the line of permanent vegetation. \textit{Hydrocotyle bonariensis} grows inland of this location and \textit{C. edentula} is not usually present during this time of year. This overwash event effectively ended the growing/reproductive season of \textit{A. pumilus}. What happens if storms such as this arrive earlier in the growing season? What happens as sea-level rises? What happens if storms become more intense and more frequent? Will this drive \textit{A. pumilus} to extinction? Will \textit{C. edentula}, \textit{H. bonariensis} and \textit{I. imbricata} be adversely affected? Future research should be directed to answer these questions.

**Literature Cited**


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Peterson, C.H. and M.J. Bishop. 2005. Assessing the environmental impacts of beach...


Figure VI-1. Southwestern end of Topsail Island, NC before (6 August 2001) and after (6 October 2001) a storm overwash event. Notice that all driftline vegetation has been removed, but that foredune vegetation (2\textsuperscript{nd}, 3\textsuperscript{rd}, etc. year growth of \textit{Iva imbricata}) remains – defining the permanent line of vegetation.
EDUCATION

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PUBLICATIONS


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2002. Species living on the edge: ecophysiology and survival of *Cakile edentula* (C3), *Hydrocotyle bonariensis* (C3) and the threatened *Amaranthus pumilus* (C4) on a North Carolina (USA) barrier island. Oral presentation. Association of Southeastern Biologists annual meeting.


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