COMPETITION AND FACILITATION AMONG COASTAL DUNE PLANTS IN THE SOUTHEASTERN UNITED STATES

by

STEVEN J. FRANKS

(Under the direction of Dr. Chris J. Peterson)

Competition has dominated ecological theory and the design and interpretation of experiments, but there is growing evidence that interactions among organisms can be facilitative, and that interactions range along a spectrum from negative (competitive) to positive (facilitative). One current goal in ecological research is understanding what factors affect the strength and direction of interactions within and among species. Theory suggests that facilitation may be especially important in stressful or frequently disturbed habitats and may particularly benefit individuals at the earliest life stages. The main objective of the research presented in this dissertation was to investigate factors shaping interactions among several coastal dune plant species. Vegetation and environmental sampling as well as several experiments were conducted to meet this objective. Vegetation sampling indicated positive association among several species, which is consistent with possible facilitative interactions. Seed bank sampling and a seed planting experiment in vegetated and open microsites showed that facilitation was important at early life stages, with adult plants increasing seed accumulation and seedling emergence in the field. In an experiment in which dune plant density, species richness, and a burial treatment were varied, burial disturbance shifted interactions from neutral to facilitative, supporting the hypothesis that facilitation increases with increasing stress and disturbance. An experiment examining interactions within and among two dune species showed that the presence of neighbors increased survival but decreased growth, indicating that neighbors may protect each other from sources of mortality, leading to facilitation but still compete for resources, reducing growth. These results emphasize that the outcome of interactions depend on the environmental conditions in which they occur and give further evidence that facilitation is important in communities occurring in stressful and frequently disturbed habitats.

INDEX WORDS: Competition, Disturbance, Diversity, Dune plants, Facilitation, Positive interactions, Seed bank, Stress

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DEDICATION

To my parents

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TABLE OF CONTENTS

Page

CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Rationale for research

Competition has been long regarded as one of the most important factors determining population dynamics and community structure. However, ecologists now recognize that interactions range along a spectrum from negative (competitive) to positive (facilitative) and that the net effects of neighbors may be facilitative in many natural systems (Callaway 1995). The focus of much current research on interactions is on understanding under what conditions positive effects of neighbors outweigh negative effects, resulting in facilitation. While evidence for facilitative interactions is rapidly increasing, general predictions about the conditions under which facilitation is expected to exceed competition remain largely untested. The central goal of this dissertation is to test interaction theory and increase our understanding of how different factors affect the strength and direction of plant interactions by investigating these interactions in coastal dune plant communities in the southeastern United States.

Background

Positive interactions are the general term for any interaction in which at least one organism benefits from an association with another organism (Stachowicz 2001). Facilitation is a positive interaction in which at least one organism benefits and the other organism is not harmed (Bruno and Bertness 2001), and is used interchangeably with the term positive interactions throughout this dissertation. Mutualisms are interactions in which both organisms benefit (Bronstein 1994), while in competitive interactions, both organisms are harmed. Nurse plant facilitation is a type of facilitation that occurs between established adult plants (or dead plants, as in nurse logs) and seedlings or juvenile plants (i.e. Niering et at. 1963). Keystone facilitators are organisms that facilitate many different species in a community (Hacker and Gaines 1997).

Interestingly, facilitation was thought to be an important mode of plant interactions in the early 1900's (Clements 1916). However, competition theory also became well established in the early 20th century with the work of A. J. Lotka and V. Volterra (Volterra 1926, Lotka 1932). Evidence for competition was also found in laboratory experiments (i.e. Gause 1935, Park 1948) and in field studies (Tansley 1917, Gleason 1926). From the early 1900's until the present time, competition has dominated interaction theory and the design and interpretation of experiments.

A greater appreciation of facilitative interactions has recently occurred due to many examples of such positive interactions occurring in nature and also to the development of theory that can account for mechanisms of facilitation and predict under what conditions positive interactions are likely to be found. Reviews of extensive examples of facilitative interactions can be found in Hunter and Aarenssen (1988), Callaway (1995), and Stachowicz (2001). These reviews indicate that facilitation can be found among many different types of organisms in a variety of habitats. The reviews also indicate patterns, with many examples of facilitation occurring among sessile organisms and in more extreme environmental conditions.

The existence of patterns in the occurrence of positive interactions has lead to the development of theory to explain mechanisms of facilitation, to predict under what conditions interactions are likely to be facilitative, and to model the effects of facilitation on individuals, communities, and ecosystems. Bertness and Callaway (1994) proposed that facilitation increases with increasing abiotic stress due to amelioration of environmental conditions by neighbors and that facilitation increases with increasing consumer pressure due to protection from herbivores and predators by neighbors. This model posits that mechanisms of facilitation are stress amelioration and consumer protection, which leads to the prediction that facilitation should increase as stress and predation become more intense. Brooker and Callaghan (1998) advocate a similar model that adds protection from disturbance as an additional facilitation mechanism (but see Bertness 1998). Callaway and Walker (1997) develop a model for plant interactions in which facilitation increases with both abiotic stress (as in the Bertness and Callaway (1994) model) and also with increased nurse plant size or density. Holmgren et al. (1997) present a more specific model of plant interactions that accounts for both physiological trade-offs in shade and drought tolerance and environmental covariance between light levels and soil moisture. This model predicts that facilitation under canopies will occur only when benefits due to drought reduction exceed costs due to reduced light intensity. Hacker and Gaines (1997) produced a model which demonstrates that positive interactions can increase species diversity in a community because facilitating species can allow other species to occur under conditions that would otherwise be too severe. Bruno and Bertness (2001) modeled how the relative importance of facilitation due to stress amelioration and associational defenses depend on not only levels of stress and predation but also on levels of recruitment.

While there are many examples of facilitation in the literature (Callaway 1995), direct experimental tests of the facilitation models described above are scant. Also, existing tests of some of these models have produced mixed results. For example, some studies support the hypothesis of increasing facilitation with increasing stress and disturbance (Greenlee and Callaway 1996, Callaway 1998b, Levine 2000, Pugnaire and Luque 2001, Tewksbury and Lloyd 2001) while others failed to support this hypothesis (Casper 1996, Donovan and Richards 2000, Tielborger and Kadmon 1997, 2000).

The controversy over the effects of stress and disturbance on facilitative interactions may be due in part to the fact that facilitation might be observed for some components of fitness and not others. In severe environments, neighbors may offer protection from harsh conditions, resulting in an increased probability of survival. However, the same neighbors might also compete for resources, resulting in decreased growth. The distinction between the growth and survival components of fitness in interaction studies has been elaborated (Goldberg and Novoplansky 1997), but most interaction studies examine either growth or survival (but see Levine 2000).

Because most studies of facilitation have examined the effects of only one putative facilitator species (i.e. Niering et al. 1963, Tewksbury and Lloyd 2001), whether interactions are species-specific or general across species or functional groups is an open question (Callaway 1998a). Some recent studies have found reciprocal facilitation among two or more species (Pugnaire et al. 1996, Holzapfel and Mahall1999), but comparisons of intra- versus interspecific facilitative interactions remain scant (Callaway 1995).

Based on competition theory, it is reasonable to hypothesize that heterospecific neighbors should be more facilitative (result in larger net benefits to associates) than conspecific neighbors because conspecifics are often similar in resource use patterns and may compete more intensely than heterospecific neighbors. I am aware of no studies that address this hypothesis.

Objectives

The three chapters in this dissertation describe different tests of interaction theories in coastal dunes. In Chapter 1, I use a combination of sampling methods and experimental manipulations in the field to test the effects of adult plants on seed accumulation and seedling emergence, and consider whether positive interactions at early life stages might lead to nucleated succession on dunes. Chapter 2 describes the results of a field experiment designed to test the effects of burial disturbance on interactions in both monocultures and species rich mixtures. The objectives of this experiment were to determine if facilitation increased with a burial disturbance and if facilitation increased with increased species richness. In Chapter 3, I examine competitive and facilitative interactions among two coastal dune species, *Uniola paniculata* and *Iva imbricata*, across an environmental gradient in the field. In this experiment, I tested the hypotheses that interactions at this dune site are facilitative rather than competitive, that the nature of interactions differs for growth and survival components of fitness, that facilitation increases with increasing stress and disturbance along an environmental gradient, and that facilitation is stronger among heterospecific than among conspecific individuals.

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CHAPTER 2

FACILITATION IN MULTIPLE LIFE HISTORY STAGES: EVIDENCE FOR NUCLEATED SUCCESSION IN DUNES[1]

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Abstract

Understanding plant interactions during succession is a central goal of plant ecology. The nucleation model of succession proposes that facilitative interactions lead to outward radiations of colonization from established plants. I tested the nucleation hypothesis for early successional plants on the primary dunes of barrier islands in the southeastern United States. On the coast of Florida and Georgia, I sampled the above-ground vegetation and the seed bank, and conducted a seedling emergence experiment in the field.

Vegetation sampling at both field sites showed more positive correlations in percent cover of adult species than expected by chance. At both sites, there were significantly more seeds under plants than in open microsites. Seeds of the same species as the adult plants in the vegetated microsites were removed from the analysis, so the accumulation of seeds under adults is not due simply to a seed shadow effect. Seeds of six species were added to plots under plants and in open microsites, and seedling emergence was significantly higher under plants than in the open.

The findings support the predictions of the nucleation hypothesis for the early life-history stages of seed dispersal and germination, and help to explain the clumped distribution of dune plants seen in the field. The results add further support for the contention that facilitation is an important mode of plant interaction in stressful and disturbed habitats.

Introduction

Succession theory is central to our understanding of the dynamics of natural communities. A major debate in the succession literature is the degree to which early colonizing species inhibit, have no effect on, or facilitate the establishment of new individuals (Connell & Slatyer 1977; Pickett et al. 1987). While some of the earliest models viewed facilitation to be important in succession (*i.e.* Clements 1936), competition was later thought to be more common than facilitation in successional dynamics. In fact, most recent conceptual models (Horn 1976; Tilman 1985; Tilman 1988) and computer simulations (reviewed in Urban & Shugart 1992) assume that all interactions are competitive during succession.

There is, however, growing evidence that facilitation is important in many natural communities (Hunter & Aarssen 1988; Callaway 1995; Kareiva & Bertness 1997). Facilitated succession has been found in such systems as salt marshes (Bertness & Shumway 1993; Bertness & Hacker 1994; Castellanos et al. 1994) rocky intertidal communities (Benedetti-Cecchi 2000), old fields (Li & Wilson 1998; Meiners & Gorchov 1998), and savannas (Archer 1995). Interactions during succession may be facilitative due to a variety of mechanisms, including amelioration of stress, augmentation of resources, and protection from herbivory (reviewed in Callaway 1995). Facilitation occurs during succession in many systems, but a better integration of facilitative interactions into succession theory and models is clearly needed.

One specific model of facilitated succession is the nucleation model, first proposed by Yarranton and Morrison (1974) to explain patterns of succession on the dunes of Grand Bend, Ontario, Canada. According to the nucleation hypothesis, colonists establish in an area of bare, unstable soil (Fig. 2.1). These plants then spread outward clonally and/or facilitate the establishment of persistent (late successional) species by providing suitable microsites for the accumulation and germination of seeds and the growth of seedlings. Succession proceeds outward from the nucleation centers created by the colonists, resulting in a clumped distribution of plants.

Yarranton and Morrison (1974) concluded that succession on the Grand Bend dunes fit the nucleation model based on finding a clumped distribution of plants, seedlings of persistent species under the earlier successional *Juniperus virginiana* trees, and soils higher in nutrients under *Juniperus virginiana* trees. Castellanos et al. (1994) also found nucleated succession in salt marshes in Spain, with *Spartina maritima* facilitating *Arthocnemum perenne* invasion. However, inhibition and tolerance also appeared to occur in this system. Several studies have also shown that certain species may act as perches for seed-dispersing birds or bats, resulting in a nucleated pattern of colonization (*ie*. Verdú, & García-Fayos 1996; Slocum & Horvitz 2000). Many species are also known to function as ‘nurse plants,’ facilitating establishment of other individuals (*ie*. Niering et al. 1963; Rousset & Lepart 2000). Few studies, however, have tested the nucleation hypothesis by examining interactions among plants at several life stages in the field.

The objective of this study was to test the nucleated succession hypothesis for coastal dunes in the southeastern United States. Dunes are stressful and frequently disturbed habitats (Barbour et al. 1985; Ehrenfeld 1990), making nucleation here likely since facilitation is expected to increase in frequency with increasing stress (Bertness & Callaway 1994). The nucleation hypothesis predicts that seeds should be more abundant and germination higher in vegetated microsites than in the open, leading to positive correlations in abundance among adult plants. To test these predictions, I first sampled the adult vegetation for species composition and percent cover. Second, I sampled the seed bank to determine if there were more seeds under plants than in the open. Third, I planted seeds under adult plants and in the open to determine if adults facilitate seedling emergence. Fourth, I sampled soil moisture, nutrient content, soil stability, and soil movement in vegetated and open microsites to examine variation in habitat quality and to investigate possible mechanisms of facilitation. The southern, accreting ends of Keywadin Island, Florida, and Sapelo Island, Georgia were chosen as field sites because they are currently in the relatively early stages of dune succession.

Methods

Site Descriptions

Two field sites were used in this study- Sapelo Island, Georgia, USA (31° 28'N, 81° 14'W) and Keywadin Island, Florida, USA (26° 08'N, 81° 47'W). Sapelo Island is a barrier island located on the central east coast of Georgia. Sapelo Island has long, hot and humid summers, and mild winters. The mean annual temperature is 20.5°C degrees (University of Georgia Marine Institute weather station, 1998). There is about 125cm of rainfall annually, which occurs mostly in summer. Soils are of well-drained, fine quartz sand that is low in nutrients (Mathews et al. 1980). The southern end of the island has recently been accreting (Mathews et al. 1980). Common species in the primary dunes include *Uniola paniculata*, *Panicum amaram*, *Iva imbricata*, and *Cenchrus* spp. (All nomenclature based on Wunderlin 1982; see also Duncan 1982).

Keywadin Island is located on the southwest coast of Florida. The climate on Keywadin Island is subtropical, with a mean annual temperature of 23.6°C (Twilley 1982). Mean annual precipitation is 135cm, most of which occurs in summer and fall (Chen & Gerber 1990). The soil is low in nutrients, and composed of quartz and calcareous sand and shell fragments (Johnson & Barbour 1990). The southern end of Keywadin Island has also recently been accreting, based on aerial photographs of the area. The dunes are dominated by *Uniola paniculata, Iva imbricata, Ipomoea pes-caprae, Cenchrus echinatus*, and also include the rare and endangered *Scaveola plumieri* and *Suriana maritima* (see also Johnson & Barbour 1990; Burch 1998).

Vegetation Sampling

To determine if adult plants were positively correlated in abundance, I established four belt transects each on Keywadin and Sapelo Island in the summer of 1998. Each transect spanned the primary dune vegetation (100m for Keywadin and 75m for Sapelo Island). Percent cover of each species was visually estimated in $1m^2$ quadrats (n=400 for Keywadin, 300 for Sapelo Island) every meter. Spearman's rank correlations (Sokal & Rohlf 1995) of percent cover were used to determine if species abundances were correlated. Vegetation sampling data was also used to compare the abundances of adults with abundances of seeds in the seed bank.

Seed Bank Study

To assess the composition of the seed bank under plants and in open microsites, soil samples were collected in September, 1999, on Keywadin and Sapelo Islands. At each site, I established three transects perpendicular to the shoreline and spanning the primary dune vegetation, with a random point selected every four meters. At each point, paired samples were collected from the nearest open area (less than 25% vegetation cover) and under the nearest adult perennial plant (in an area with greater than 75% cover). The samples were 5cm in depth, 5cm wide, and 5cm long ($125cm^3$), and included all soil and litter. Samples were placed in plastic bags and brought to the UGA Botany glasshouses.

Each soil sample was spread out to a depth of 1-2cm over sterile sand in subdivided flats in a randomized complete block design. The blocks were randomly assigned positions on two glasshouse benches, with blank cells of sterile sand surrounding the flats to minimize edge effects and to control for seed contamination. The flats were watered daily, fertilized with 1/4 strength Peters (15-30-15) fertilizer solution monthly, and stirred three times during the course of the study to increase germination.

Each week, the number and identity of germinated seedlings was recorded. Several individuals of each species were transplanted and grown to adults to verify identity, with these adults and several seedlings stored as vouchers. The study was terminated after nine months, when the rate of germination had drastically decreased and it appeared that the seed bank had been exhausted.

Data (total number of seedlings, number of annuals, and number of perennials) were analyzed with ANOVAs using SAS (The SAS Institute, 2000). I removed from the analysis seeds of the same species as the adult under which the sample was taken. Therefore, the number of seeds found in each microsite reflects accumulated seeds, and is not simply due to a seed shadow effect.

Seedling emergence experiment

To test the hypothesis that adult plants facilitate seedling emergence, I planted seeds of six species under adult plants and in the open on Keywadin Island in September, 1999. Seedling emergence at this subtropical site occurs year round, but appears to be concentrated in October-November (pers. obs.). Seeds were collected from Keywadin Island in the summer of 1998 and stored at 4°C until use. Species used were *Cassia chamaecrista, Chrysobalanus icaco, Iva imbricata, Scaveola plumieri, Suriana maritima*, and *Uniola paniculata*, which were chosen to represent a range in adult plant abundance and seed size.

Ten seeds of each species were planted in each of three microsites: 1) under adult *Uniola* plants, 2) under adult *Iva* plants, and 3) in open patches of bare sand between adult plants. Each microsite was replicated four times in each of three zones (foredune, mid-dune, and back dune), for a total of 2,160 seeds planted (3 zones x 4 replicates x 3 microsites x 10 seeds x 6 species). The seeds were spaced 1cm apart in a grid, and planted under 1cm of sand. Before the seeds were planted, I used a 1mm soil sieve and removed any visible seeds from the plots. In adjacent control plots where seeds were not planted, no emergence was observed. Emergence data were collected bi-weekly until November, 1999, after which no emergence was observed. Before this date (mid-October), a storm moved about 30cm sand on top of the four seaward-most plots, but did not appear to affect the other plots. No emergence was observed in these four plots, and they were removed from subsequent analyses (leaving n=1440 seeds).

I used ANOVAs in SAS (The SAS Institute, 2000) to test for the effect of canopy species (*Iva, Uniola* and none) on percent germination, and preplanned orthogonal contrasts were used to compare means. Because of the low overall rate of germination, all six seed species were pooled for the analysis.

Environmental Sampling

To test the hypothesis that environmental differences existed among microsites and examine possible mechanisms of facilitation, I sampled environmental characteristics on Keywadin and Sapelo Islands in March 1999. At each site, I established two transects perpendicular to the shoreline and spanning the primary dune vegetation. At each transect, I selected a random point every four meters and took paired measurements in the nearest open (<25% cover) and vegetated (>75% cover) microsites (N=87 for each site).

At each point, I measured soil moisture, organic content, sand movement and soil stability. I collected 125cm^3 of soil (5cm depth) and assessed moisture gravimetrically (oven-dried at 70°C) and organic content by mass lost on ignition (burned at 550°C). Soil moisture (volumetric water content) was also measured with a HydroSense Soil Content Measurement System (Campbell Scientific, Inc., Logan, Utah, USA) in vegetated and open microsites in December 2001 (n=64). To measure sand movement, a 20cm wooden stake was driven into the soil and marked at the soil surface. I measured height of the sand above or below this mark six months later. I assessed soil stability by placing eight cotton swabs vertically half way into the sand at each point and counting how many remained after six months. These swabs were approximately the same height as seedlings, but would only be removed or buried by sand movement and not experience “mortality” due to dessication, nutrient stress, or any other factor. Thus the swabs were superior to actual seedlings as indicators of soil stability.

ANOVA's in SAS (The SAS Institute, 2000) were used to determine the effect of microsite (vegetated vs. open) on proportion water content and organic content. Due to severe departures from normality, Kruskal-Wallis rank sum tests in Sigma Stat (SPSS Inc.,1997) were used to analyze the effect of microsite on remaining number of artificial seedlings and change in sand height.

Results

Vegetation Sampling

For adult plants of common dune species on Keywadin and Sapelo Islands, there were 15 positive correlations in cover (indicating that the relative abundances of two species tend to increase together) and only two negative correlations for 36 species-pair comparisons (Table 2.1). Since only two significant correlations would be expected by chance alone, there is evidence that the vegetation is strongly structured.

Seed Bank Study

A total of 1,337 seedlings of 31 species emerged during the nine month study. There were approximately 1,412 seeds/m^2 on Keywadin Island and 2,132 seeds/m^2 on Sapelo Island, however samples were only taken under dense cover or in open spaces, and may not be representative of areas of intermediate vegetation cover.

There were significantly more seeds under adult plants than in open microsites on Keywadin Island (n=150, F=23.9, $p<0.0001$) and Sapelo Island (n=150, F=6.91, $p<0.01$; Fig. 2.2), with seed density 3.6 times higher under plants than in open patches on

Keywadin Island and 2.8 times higher on Sapelo Island. Seeds of the same species as the adult cover plant were removed from the analysis to eliminate any seed shadow effect.

There was wide variability among species in seed density, with some species extremely abundant in the seed bank and others rare (Table 2.2). Most of the seeds in the seed bank at both sites were of annuals (Table 2.2), despite the fact that there were more perennial adults than annuals at both sites based on percent cover measurements described in the vegetation sampling section (Fig. 2.3). When seeds of annuals and perennials were analyzed separately, both were significantly more abundant in the vegetated than in the open microsites both on Keywadin and Sapelo Islands (Table 2.3).

Seedling Emergence Experiment

Only 5% of the seeds planted germinated and emerged. Total percent emergence was 7.0, 0, 8.3, 0.3, 0.5, and 3.6% for *Cassia chamaecrista, Chrysobalanus icaco, Iva imbricata, Scaveola plumieri, Suriana maritima*, and *Uniola paniculata*, respectively. Because of this low rate of emergence, data were pooled for all six seed species. Emergence was significantly higher under *Iva imbricata* than under *Uniola paniculata* adults, and significantly higher under adult plants of both species than in open microsites (Fig. 2.4).

Environmental Sampling

Soil moisture, as measured gravimetrically, was higher in open than in vegetated microsites on both Keywadin and Sapelo Islands, but this trend was only significant on Sapelo Island (F=32.7, 1 d.f., $p<0.0001$; Fig. 2.5a). HydroSense volumetric water content measurements were not different in vegetated and open microsites in soil moisture (Wilcoxon signed rank test, n=64, W=-161.0, p=0.071). Percent soil organic content was not significantly different in open vs. vegetated microsites, and showed opposite trends on Keywadin Island and Sapelo Island (Fig. 2.5b). The number of artificial seedlings remaining after six months was higher in vegetated than in open microsites on both Keywadin and Sapelo Islands, but this was only significant on Keywadin Island (Kruskal-Wallis rank sum test H=4.2, 1d.f., p=0.041; Fig. 2.5c). Significantly more sand accumulated in open than in vegetated microsites on Sapelo Island (Kruskal-Wallis rank sum test H=8.2, 1 d.f., p=0.003; Fig. 2.5d). On Keywadin Island, sand movement was not significantly different between open and vegetated microsites (Fig. 2.5d).

Discussion

The results of this study support the nucleated succession model for primary coastal dunes of the southeastern United States. Adult plants were positively associated, and seed accumulation and seedling emergence was greater under adults than in open microsites. These patterns appear to be caused by adult plants facilitating seed accumulation and seedling emergence by trapping seeds and protecting seedlings from severe sand movement. The results suggest that facilitation by adult plants of new colonists at early life stages through the mechanism of increased soil stability can lead to a nucleated pattern of succession on coastal dunes.

It is possible that variation in microsite quality independent of the effects of the vegetation could also produce these patterns of association, and experimental manipulations are necessary to eliminate the microsite quality explanation.

Manipulations of dune plant density in separate studies in both a common garden (Chapter 3) and in the field (Chapter 4) demonstrated facilitative interactions, giving further support for the hypothesis that field associations are due in part to facilitative interactions.

Facilitation among plants occurs when an individual changes resource levels or conditions in such a way as to benefit another individual. On dunes, the major limiting factors for plant performance are water, nutrients, salt spray, sand burial, erosion, herbivory, and seed predation (Barbour et al. 1985; Ehrenfeld 1990; Ishikawa et al. 1995; Maun 1998). Facilitation on dunes could thus occur by plants increasing the nutrient content of the soil, increasing soil moisture by shading the surface and reducing evaporation, blocking salt spray, increasing soil stability, or reducing herbivory or seed predation. While this study was not designed to elucidate mechanisms of facilitation, data on differences in environmental conditions between vegetated and open microsites can be used to investigate possible facilitation mechanisms.

Soil moisture (Fig. 2.5a) and nutrient content (Fig 2.5b) were not greater in vegetated than in open microsites. Therefore, augmentation of these resources was probably not a mechanism of facilitation. It is important to note, however, that these edaphic measurements were taken at few points in time, and that manipulations are necessary to further explore these possible mechanisms. Neither salt spray nor herbivory were quantified in this study, but both appeared to be low and unaffected by the density of the vegetation (pers. obs.) and are unlikely to be implicated in plant interactions in this system (but see Bach 1994). The most probable mechanism of facilitation appears to be the influence of plants on the stability of the substrate and the patterns of movement of sand and seeds.

Previous work has shown that dune plants cause the gradual accumulation of windblown sand (Bagnold 1954; Bressolier & Thomas 1977). It appears from this study that vegetation causes the accumulation of seeds via the same mechanism by which sand accumulates around plants. The presence of vegetation reduces extremes in sand movement, with plants attenuating wind velocity, causing gradual sand accumulation, and also stabilizing the soil through the presence of roots and rhizomes, which reduces large scale erosion and burial (Barbour et al. 1985). A moderate amount of accretion tends to benefit dune plants, while more severe burial or erosion is harmful (Maun 1998.)

More artificial seedlings remained under plants than in the open (Fig. 2.5c), probably because the artificial seedlings in the open were blown down by wind gusts or buried by shifting sand. Also, vegetated microsites tended to receive a low accumulation of sand, while open microsites received either greater burial (Sapelo Island), or net erosion (Keywadin Island) (Fig. 2.5d). Seedling emergence seems to be greater under plants than in the open because of the increased soil stability caused by the vegetation. Facilitation on these coastal dune sites thus appears to occur due to protection from the disturbances of burial and erosion rather than augmentation of resources, amelioration of stress, or protection from herbivory.

The results of this study are consistent with Yarranton and Morrison's (1974) finding of nucleated succession on the Grand Bend dunes in Ontario, Canada, and also with observations of shrubs facilitating understory plants on dunes at Cape Cod, Massachusetts, USA (Shumway 2000), but they contrast with studies of succession on other dune systems. Houle (1997) found no evidence for either competitive or facilitative interactions among three herbaceous perennials during early succession on subarctic dunes. Lichter (2000) concluded that competition occurred, and increased in intensity during succession on Lake Michigan (USA) dunes. It is likely that both facilitation and competition occur during dune succession, and that many factors, including differences in the levels of stress and disturbances among sites and life stages of the individuals sampled, influence the degree and directions of interactions observed.

Total seed density at the two coastal dune sites in this study was much greater than was found at Lake Michigan, Michigan, USA (0 seeds/m^2, Plansek & Pippen 1984) and Cape Cod, Massachusetts (337 seeds/m^2, Baptisa & Shumway 1998), but less than half that found at Perdido Key, Florida (4522 seeds/m^2, Looney & Gibson 1995). The large discrepancies among sites in seed bank density could be due to differences in total seed inputs or in seed dispersal and accumulation processes, or to differences in sampling technique. Seed densities in this study were much higher under plants than in the open, and other seed bank studies may have included many samples in unvegetated microsites. More data are needed to determine if the pattern of greater seed accumulation under plants than in open microsites holds in other dune habitats differing in species composition and environmental variables, and if any geographic trends in seed bank density exist.

While this study focused on seed accumulation and seedling emergence, many of the dominant dune plants, such as *Uniola paniculata* and *Panicum amarum*, reproduce clonally as well as by seed (Duncan & Duncan 1987). Clonal growth patterns in these species could further enhance nucleated succession by increasing outward spread from established individuals. Correlations in abundance of adult plants could also be due in part to clonal reproduction, as well as to the accumulation of seeds and enhancement of seedling emergence observed in this study. The relative importance of sexual versus asexual reproduction in dune species for population dynamics and community patterns has received little attention (Ehrenfeld 1990) and warrants further investigation.

The results of this study support the hypothesis that facilitative interactions are important in coastal dune succession. Models and management decisions involving dune plants should incorporate these facilitative interactions to aid in the conservation and restoration of valuable coastal dune habitats. The findings of this study add to the growing evidence that facilitative interactions are important in natural communities.

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Table 2.1. Spearman's rank correlation coefficients based for percent cover for the most common dune species on Keywadin and Sapelo Islands. The letters in the top row correspond to the first letter in the genus and species of the plants, and refer to the same names as in the first column. Bold type and * indicates significant correlations at the .05 level. There were 15 positive correlations and 2 negative correlations out of 36 comparisons. Nomenclature is from Wunderlin (1982).

Keywadin Island

Species	UP	II	SP	CE	FS	EP	DS
Uniola paniculata		-0.1	0.0	0.4	**-0.1**	**-0.1**	-0.2
Iva imbricata			**0.1***	**0.2***	**0.3***	**0.4***	0.1
Spartina patens				0.1	**0.1***	0.0	**0.2***
Cenchrus echinatus					**0.1***	**0.3***	0.1
Fimbristylis spathacea						**0.4***	**0.2***
Eustachys petrea							**0.1***
Distichlis spicata							

Sapelo Island

Species	UP	II	SP	PA	DS	HB
Uniola paniculata		0.0	0.0	-0.1	-0.1	**0.2***
Iva imbricata			-0.1	**0.2***	0.1	**0.2***
Spartina patens				-0.1	**0.2***	0.0
Panicum amarum					0.0	0.0
Distichlis spicata						-0.1
Hydrocotyle bonariensis						

Table 2.2. Estimated mean (SE) number of seeds/m^2 based on seed emergence in soil samples from vegetated (Veg) and open microsites on Keywadin and Sapelo Islands (n=75 samples of 125cm^3 of soil per microsite at each location). Life form (growth habitat) of each species is also given.

	Life-	Keywadin		Sapelo	
Species	form	Vegetated	Open	Vegetated	Open
ANNUALS					
Apium leptophylum	herb	0.0 (0.0)	5.1 (5.1)	5.4 (5.4)	11.1 (7.8)
Cerastium glomeratum	herb	5.1 (5.1)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Chamaesyce maculata	herb	25.3 (11.0)	35.4 (12.9)	0.0 (0.0)	5.6 (5.6)
Conzya canadensis	herb	810.1 (331.3)	187.3 (66.0)	324.3 (121.1)	227.8 (95.2)
Draba brachycarpa	herb	5.1 (5.1)	0.0 (0.0)	0.0 (0.0)	5.6 (5.6)
Geranuim spp.	herb	20.3 (9.9)	15.2 (8.7)	37.8 (15.7)	27.8 (12.1)
Gnaphallium purpurea	herb	0.0 (0.0)	15.2 (8.7)	1286.5 (438.7)	272.2 (115.4)
Hypocheris radicata	herb	10.1 (7.1)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Lamium amplexicaule	herb	5.1 (5.1)	20.3 (16.0)	5.4 (5.4)	27.8 (18.3)
Oneotheria lacinata	herb	0.0 (0.0)	5.1 (5.1)	0.0 (0.0)	5.6 (5.6)
Phyla (Lippia) nodiflora	grass	0.0 (0.0)	0.0 (0.0)	75.7 (50.9)	5.6 (5.6)
Poa annua	grass	0.0 (0.0)	0.0 (0.0)	16.2 (9.2)	0.0 (0.0)
Sebatia stellaris	herb	0.0 (0.0)	0.0 (0.0)	21.6 (13.1)	11.1 (7.8)
Stellaria media	herb	10.1 (7.1)	0.0 (0.0)	0.0 (0.0)	11.1 (11.1)
ALL ANNUALS		63.7 (24.2)	19.6 (5.2)	126.6 (32.0)	43.3 (11.0)
PERENNIALS					
Carex spp.	sedge	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	5.6 (5.6)
Cenchrus echinatus	grass	25.3 (13.2)	5.1 (5.1)	0.0 (0.0)	0.0 (0.0)
Croton punctatus	shrub	0.0 (0.0)	0.0 (0.0)	5.4 (5.4)	0.0 (0.0)
Dactyloctenium aegyptium	grass	45.6 (23.9)	25.3 (16.7)	0.0 (0.0)	0.0 (0.0)
Eustachys petra	grass	50.6 (20.8)	25.3 (15.0)	10.9 (7.6)	0.0 (0.0)
Fimbristylis spadicea	sedge	30.4 (18.8)	0.0 (0.0)	21.6 (10.6)	0.0 (0.0)
Hydrocytle bonaransis	herb	0.0 (0.0)	5.1 (5.1)	5.4 (5.4)	5.6 (5.6)
Iva imbricata	shrub	784.8 (250.8)	40.5 (26.6)	5.4 (5.4)	0.0 (0.0)
Juncus spp.	sedge	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	5.6 (5.6)
Lippia alba	herb	0.0 (0.0)	0.0 (0.0)	102.7 (74.6)	27.8 (14.4)
Paspalum setaceum	grass	50.6 (37)	30.4 (21.3)	0.0 (0.0)	0.0 (0.0)
Triplassis purpurea	grass	5.1 (5.1)	10.1 (7.1)	145.9 (47.2)	5.6 (5.6)
Uniola paniculata	grass	81.0 (36.3)	10.1 (7.1)	5.4 (5.4)	0.0 (0.0)
ALL PERENNIALS		71.6 (18.1)	10.5 (2.9)	20.2 (6.0)	3.7 (1.3)
Unknown		319.0 (105.3)	86.1 (35.1)	1291.9 (371.1)	183.3 (82.2)
ALL SPECIES		76.1 (14.9)	17.4 (3.1)	112.3 (20.9)	28.1 (5.9)

Table 2.3. ANOVA table for the effect of microsite (vegetated vs. open) on the number of annual and perennial seeds emerging from the Keywadin Island and Sapelo Island samples.

	Annuals			Perennials		
Source	d.f.	F	p	d.f.	F	p
Keywadin Island						
Microsite	1	4.62	0.03	1	20.67	<0.0001
Sapelo Island						
Microsite	1	5.04	0.02	1	5.26	0.02

Figure Legends

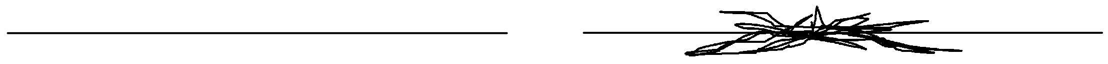
Figure 2.1. Diagram of the proposed nucleation model of succession on dunes.

Figure 2.2. Mean seed densities (±SE). There were significantly more seeds in vegetated than in open microsites on Keywadin Island ($n=150$, $F=23.9$, $p<0.0001$) and Sapelo Island ($n=150$, $F=6.91$, $p<0.01$).

Figure 2.3. Relative frequency of annuals (black bars) and perennials (grey bars) in the seed bank compared with the adult community.

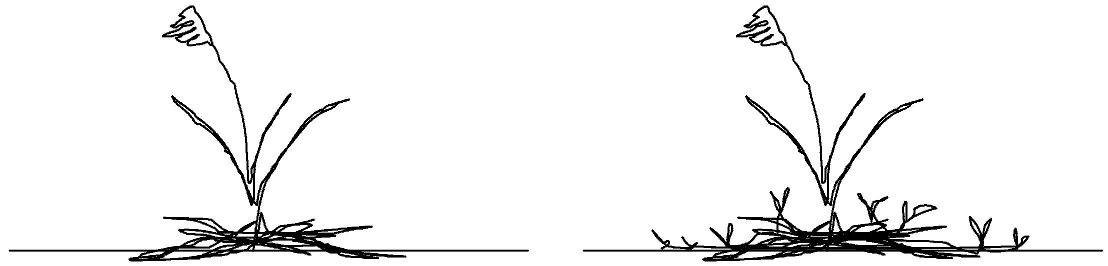
Figure 2.4. Percent germination of all six seed species pooled under *Iva imbricata* (IVIMB) and *Uniola paniculata* (UNPAN) canopies, and in open microsites (NONE). Letters indicate significant ($p<0.05$) differences among treatment groups ($n=1440$).

Figure 2.5. Edaphic characteristics in open (grey bars) and vegetated (black bars) microsites. Shown are means (±SE) of percent water content (a), percent organic content (b), number of artificial seedlings (out of 8 initial) remaining after six months (c), and net soil movement after six months (d), all for both Keywadin Island and Sapelo Island ($n=87$ for each). Asterisks (*) denote significant ($p<0.05$) differences between microsites.



1) Bare sand

2) Stabilization



3) Establishment

4) Seed accumulation and germination

Figure 2.1.

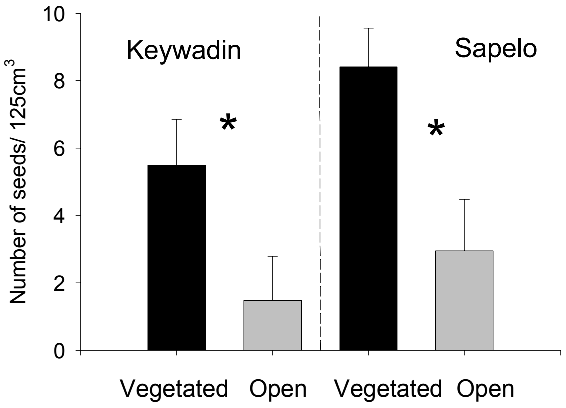

10
8
6
4
2
0
Number of seeds/ 125cm3
Keywadin
Sapelo
*
*
Vegetated
Open
Vegetated
Open

Figure 2.2

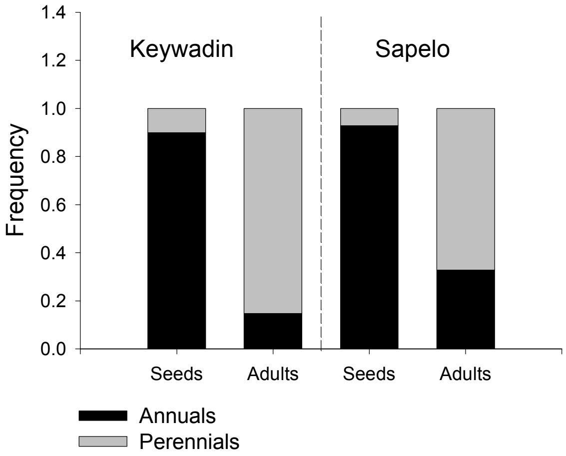

1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
Frequency
Keywadin
Sapelo
Seeds
Adults
Seeds
Adults
Annuals
Perennials

Figure 2.3.

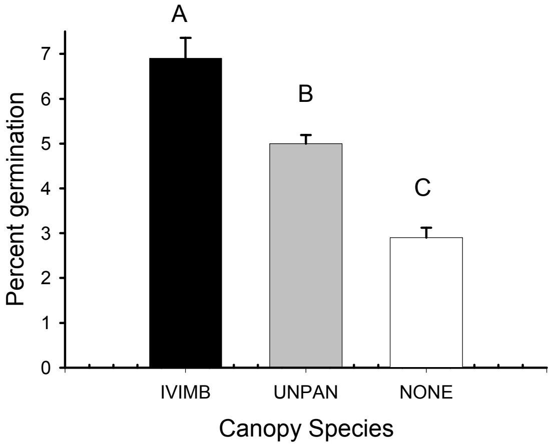

A
B
C
Percent germination
0
1
2
3
4
5
6
7
IVIMB
UNPAN
NONE
Canopy Species

Figure 2.4.

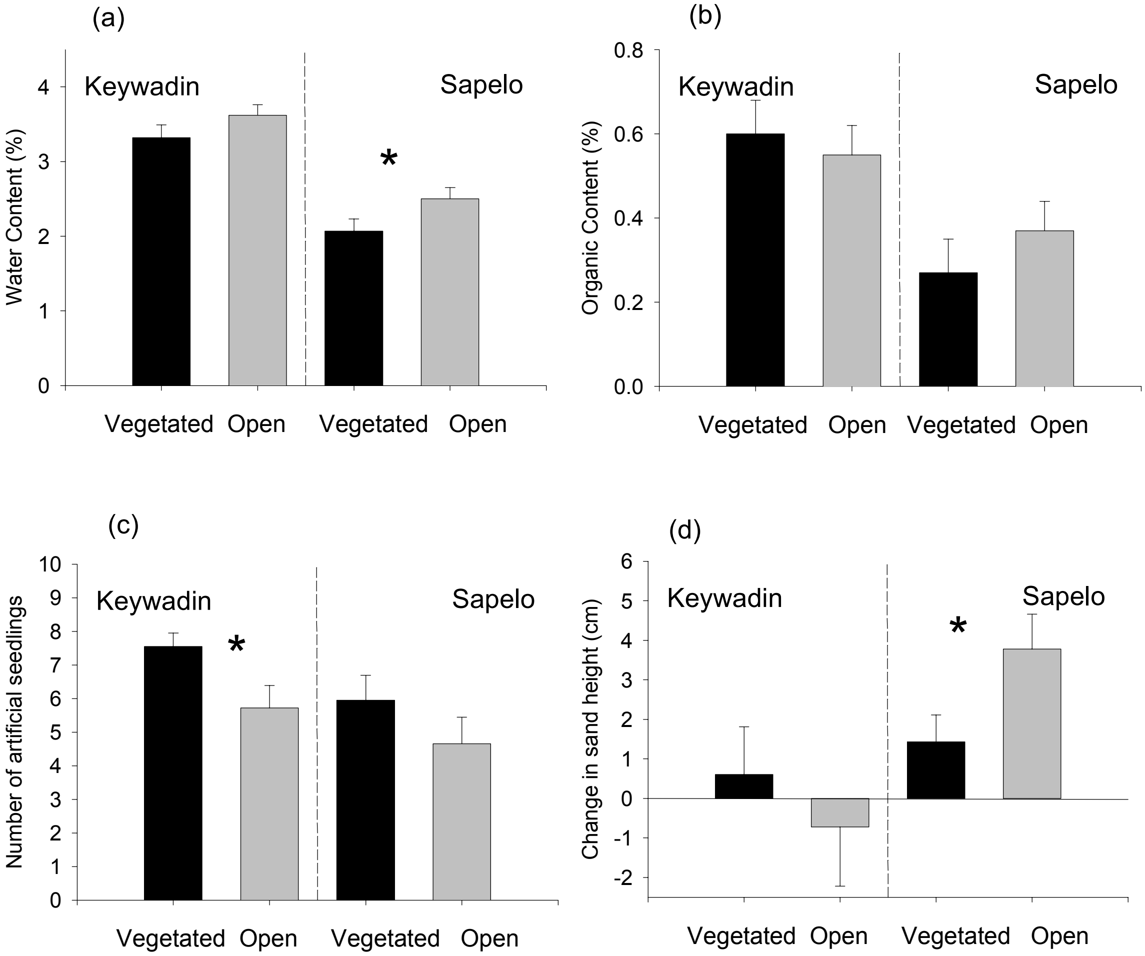

(a)
Keywadin
Sapelo
Water Content (%)
0
1
2
3
4
*
Vegetated
Open
Vegetated
Open
(b)
Keywadin
Sapelo
Organic Content (%)
0.0
0.2
0.4
0.6
0.8
Vegetated
Open
Vegetated
Open
(c)
Keywadin
Sapelo
Number of artificial seedlings
0
1
2
3
4
5
6
7
8
9
10
*
Vegetated
Open
Vegetated
Open
(d)
Keywadin
Sapelo
Change in sand height (cm)
-2
-1
0
1
2
3
4
5
6
*
Vegetated
Open
Vegetated
Open

Figure 2.5

CHAPTER 3

BURIAL DISTURBANCE LEADS TO FACILITATION IN A COASTAL DUNE PLANT EXPERIMENT[1]

---

[1] SJ Franks and CJ Peterson.

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Abstract

There is growing evidence that interactions among plants can be facilitative as well as competitive, but knowledge of how disturbances influence these interactions and how they vary with species diversity is lacking. We manipulated plant density, species richness, and a burial disturbance in a controlled, complete factorial experiment, allowing critical tests of theories about the relationships among species interactions, disturbance, and diversity. The hypotheses tested were 1) burial disturbance reduces plant performance at all levels of density and richness, 2) burial disturbance can cause net plant interactions to become more facilitative, and 3) facilitation increases with species richness. Burial decreased plant survival by 60% and biomass by 50%, supporting the hypothesis that burial reduces plant performance. In the control (unburied) treatment, there was no difference in proportion survival or per plant biomass between low and high density plots, meaning that neither competition nor facilitation was detected. In the buried treatment, however, high density plots had significantly greater survival and per plant biomass than the low density plots, indicating net facilitative interactions. Thus facilitation occurred in the buried treatment and not in the unburied control plots, supporting the hypothesis that facilitation increases with increasing disturbance. The hypothesis that facilitation increases with increasing species richness was not supported. Richness did not affect survival or biomass, and there was no richness by burial treatment interaction, indicating that richness did not influence the response of the community to burial. The influence of the disturbance on plant interactions was thus consistent across levels of richness, increasing the generality of this relationship.

Introduction

While facilitative interactions have long been recognized as potentially important in natural plant communities (Clements et al. 1926; Connell & Slayter 1977), competition has historically dominated ecological theory and the design and interpretation of experiments (Bertness & Callaway 1994). There is, however, growing evidence that facilitation is common in many communities (Callaway 1995; Hunter & Aarssen 1988; Brooker & Callaghan 1998). Understanding what factors influence the balance between competitive and facilitative interactions among organisms is a major goal of current research.

Previous investigators have suggested that the frequency of facilitative interactions should increase with increasing stress (Bertness & Callaway 1994; Callaway & Walker 1997) and increasing disturbance (Brooker and Callaghan 1998). Studies in salt marshes (Bertness & Shumway 1993; Bertness & Hacker 1994; Bertness & Yeh 1994), cobble beaches (Bruno 2000), subalpine heath (Gerdol et al. 2000), and deserts (Greenlee & Callaway 1996) have supported this hypothesis. However, several studies have failed to find an increase in facilitation with increased disturbance and/or stress. Removal experiments on early successional subarctic coastal dunes failed to show positive or negative interactions among plants (Houle 1997). Casper (1996) and Donovan & Richards (2000) failed to find either facilitation or competition in desert plants. In contrast to their predictions, Tielbörger & Kadmon (2000) found that desert annuals benefited more from the presence of shrubs in wetter years than in drier years. The effect of stress and disturbance on positive and negative plant interactions is thus still unclear.

Disturbances, which are punctuated events resulting in biomass reduction and mortality, have been distinguished from stresses, which are also abiotic and reduce plant fitness, but are not punctuated events (Grime 1979; Rykiel 1985; White & Pickett 1985). Both models and empirical studies of abiotic effects on plant interactions have tended to focus on environmental stress rather than disturbances (Brooker & Callaghan 1998 but see Bertness 1998). Mechanisms of facilitation, however, may be fundamentally different depending on whether the plant interaction is affected by a stress or a disturbance.

In stressful habitats, such as dry or low-nutrient environments, plants can ameliorate conditions by, for example, reducing evaporation or promoting nitrogen fixation. In contrast, facilitation during a disturbance, such as storm or fire, could occur if plants either directly protected each other from the disturbance, or improved post-disturbance recovery. Despite the importance of disturbances and biotic interactions in structuring communities (Connell 1978; Grime 1979; Huston 1979; Menge & Sutherland 1987; Tilman 1988), few experimental studies have directly manipulated a disturbance and examined the resulting effects on plant interactions .

Studies of facilitation have also usually examined either one or two species, so the extent to which these interactions are species-specific is unknown (Callaway 1998). Some research has shown differences among species in their benefits to an associate (Kellman 1985; Day & Wright 1989; Callaway & D'Antonio 1991; Valiente-Banuet et al. 1991; Suzán et al. 1996), but others found benefits to be less specific (e.g. Steenberg & Lowe 1969; Greenlee & Callaway 1996). While it is likely that interactions may shift more toward facilitation as diversity increases due to reduced resource competition among different species (Hooper 1998), direct tests of this hypothesis are scant. Also, many examples of facilitation are found in communities of relatively low diversity, such as salt marshes (Bertness & Shumway 1993; Bertness & Hacker 1994; Bertness & Yeh 1994) and deserts (Niering et al. 1963; Turner et al. 1966; Franco & Nobel 1989), though this relationship may be due to stress rather than diversity.

The dynamic nature of dune habitats and the strong zonation patterns exhibited by the vegetation have long made dune communities model systems for the study of succession and plant interactions (Cowles 1899; Oosting & Billings 1942; Olson 1958; Lichter 1998). Dunes are stressful, frequently disturbed habitats, with plants experiencing low nutrients, frequent drought and high temperatures, and erosion as well as burial (Ranwell 1972; van der Valk 1977; Barbour et al. 1985; Erenfeld 1990; Maun 1998). The stressful, frequently disturbed nature of dunes may make facilitation likely in this habitat, since plants may ameliorate these conditions. However, previous work has revealed both facilitative (Yarranton & Morrison 1973; Maun 1998) and competitive (Mack & Harper 1977; Silander & Antonovics 1982) dune plant interactions.

We conducted an experiment using coastal dune plants to test three hypotheses regarding the relationships among disturbance, density, and richness: 1) burial disturbance reduces plant performance at all levels of density and richness, 2) burial disturbance can cause plant interactions to shift to facilitative, and 3) facilitation increases at higher levels of richness. We transplanted plants to a common garden, creating communities that differed in both density and richness. After establishment, we subjected half of the plots to a sand burial disturbance, which is one of the most important factors in structuring coastal dune communities (Barbour et al.1985; Moreno-Cassola 1986; Maun 1998). We predicted that plants would protect neighbors from the effects of burial, and that facilitation would be found in the high density, buried plots. This could occur by plants either directly shielding each other from burial damage, or through a reduction in soil compaction in the high-density plots, which would allow increased regrowth following burial. Because dune plant species differ in burial tolerance (Barbour et al. 1985; Maun 1998), we also predicted that the high richness plots would be more likely to contain at least some disturbance-tolerant species and would thus experience greater post-disturbance recovery.

Methods

Site Description

The study was conducted at the Rookery Bay National Estuarine Research Reserve in Naples, Florida (25°62'N and 80°25'W). The local climate is subtropical, with a mean annual temperature of 23.6°C (Twilley 1982). Mean annual precipitation is 1346mm, most of which occurs in summer and fall (Chen & Gerber 1990). The soil is composed of calcareous sand and shell fragments. The experimental site was a sandy area outside of the Rookery Bay headquarters, approximately 3km from Naples Beach and Keywadin Island.

Species used in the experiment were chosen to represent a range of growth characteristics of plants found across the open beach, primary dunes, and slacks (low-lying areas between dunes) of coastal southwest Florida (Table 3.1). Dunes in this area are typically less than one meter tall, with zonation patterns across the dune environment as follows (Table 3.1; Nomenclature is from Wunderlin (1998)). *Ipomoea pes-caprae* often spreads across the open beach and foredune areas. Farther inland, *Uniola paniculata* dominates the primary dunes, with *Cenchrus echinatus, Chamaesyce* *mesembrianthemifolia,* and *Iva imbricata* interspersed. *Eustachys petraea, Fimbristylis spathacea,* and *Sesuvium portulacastrum* are primarily found in slacks, which are frequently flooded. Behind the dunes, there is usually either mangrove forest in areas flooded with salt water or tropical hardwood hammocks in upland areas.

Experimental Design

To determine the levels of density and richness to be used in the experiment, we sampled natural plant communities at Naples Beach (3km from study site) and Cape Canaveral National Seashore (300km from study site, but a more protected and natural area). At each site, 30 1m^2 quadrats were randomly placed along a transect, and the percent cover and number of individuals of each species were visually estimated. Maximum density was found to be 16 plants/m^2, and maximum richness was 7 species/m^2 (Table 3.2).

We then conducted a factorial experimental with 2 levels of each of 3 factors: plant density (4 or 16 plants/m^2), species richness (monoculture or mixture), and burial (buried or control) (Figure 1), with 10 replicates for a total of 80 1m^2 plots. The plots were arranged in a completely randomized design, with buffer zones of 1m between each plot. The distance between a plant and its nearest neighbors within a plot were 50 cm in the low density plots and 20 cm in the high density plots. In the low richness plots, one species was chosen at random with replacement from a pool of the 8 species listed above. In the high richness plots, each plant in the plot was randomly selected with replacement from the species pool. Due to the nature of this method of plant selection, plots in the same treatment groups differed in species composition. This prevents richness from being confounded with composition (Tilman 1997), but also precludes an analysis of the effect of species composition.

Plants were collected from Keywadin Island (3km from the experimental site) in the spring of 1998, maintained in pots outdoors in the shade, and then removed from the pots and transplanted to the experimental site. Existing vegetation at the site was removed with a tiller and by hand two weeks before the experimental plants were introduced on June 7, 1998. Burial treatments were applied on July 8, one month after the plants were established in the experimental site. There was no mortality of the experimental plants before the burial treatment was applied. For the burial treatment, sterile sand was shoveled onto the plots to a height of 8cm, which was 1/2 the height of the existing vegetation.

While natural burial occurs by sand blowing onto plants, there were several reasons for burying the plots by shoveling sand rather than blowing sand. First, shoveling sand provided a uniform, consistent, and repeatable treatment. Second, our treatment isolated the effect of burial itself from sand abrasion and wind stress. Third, burial by hand has been performed in other experiments on dune plants (e.g. Bach 1998), making our results more comparable to these studies. While windblown sand would have been more realistic, shoveling sand was more controllable and appropriate for the main objectives of this study.

The height and width of each plant was measured at the beginning of the experiment, before and after the burial treatment, and at the end of the experiment. All plants were harvested on August 15-17, 1998. At this point, surviving plants had more than doubled in height and more than quadrupled in width, indicating extensive post-disturbance recovery. Additionally, many plants had grown enough that they were beginning to encroach on neighboring plots, making harvesting at this time necessary. Plants were washed, and roots and shoots were separated, dried at 65 C, and weighed. Because the plants were grown in the field, some fine root material was likely lost. However, the same collection protocol was used for all plants, and the small amount of root material lost was unlikely to bias the results. Final plant root and shoot biomass and the proportion of plants surviving to the end of the experiment within a plot were used as indicators of disturbance response.

Analysis

All analyses were performed with the SAS statistical software (SAS Institute, 1990). The effects in the analyses were density, richness, burial, and their interactions, and the dependent variables were survival, biomass, and root:shoot ratio. Survival (arcsine square root transformed) was analyzed using an analysis of variance (ANOVA). Biomass (final, per plant) was analyzed using a mixed model analysis of covariance (ANCOVA), with plot nested within treatments a random effect, treatments fixed effects, and species, initial plant height, and initial width entered as covariates to account for initial size differences (data were log-transformed). Degrees of freedom were adjusted to give the appropriate F-tests based on N=80 plots (experimental units) rather than 800 plants. Root:shoot ratio was log-transformed and analyzed with a mixed model ANOVA. Because the high density, high richness plots could have more species than the low density, high richness plots, richness was treated as nested within density.

To test the effects of density on response to burial, the interaction term was examined. A significant density*burial interaction would indicate that the response to burial differed between the high and low density plots. Within each burial treatment, the effect of density was then analyzed with planned orthogonal contrasts (α=0.05). Competition was indicated if survival or biomass decreased with increasing density. Facilitation was indicated if survival or biomass increased with increasing density. The interaction between richness and burial was examined to test the effect of richness on burial response.

Results

To determine the effects of burial, richness, density, and species on plant performance, the main effects in the ANOVA were examined. A comparison of buried and unburied (control) plots showed that burial significantly reduced survival ($F_{1,72}$ = 112.1, $p <$ 0.0001; Table 3.3) and biomass ($F_{1,63}$ = 34.2, $p < 0.0001$; Table 3.4), but did not affect root:shoot ratio ($F_{1,63}$ = 0.11, $p = 0.746$; Table 3.4). Percent survival of plants in unburied (control) plots was 96.5% (SE = 0.036), while percent survival of buried plants was 42.9% (SE = 0.036). Average per plant biomass was 2.3g (SE = 0.059) for plants that were not buried and 1.7g (SE = 0.096) for buried plants. Richness and density did not affect survival (Table 3.3), biomass, or root:shoot ratio (Table 3.4).

Interaction terms in the ANOVA were examined to determine whether the effects of burial differed at different levels of density and richness. There was a significant burial*density interaction for survival ($F_{2,72}$ = 7.53, $p = 0.008$; Table 3.3) and per plant biomass ($F_{2,63}$ = 7.32, $p = 0.009$; Table 3.4). Planned orthogonal contrasts showed that in the unburied (control) treatment, high density and low density plots did not significantly differ in survival ($F_{1,72} = 1.55$, $p = 0.217$; Fig. 3.2a) or per plant biomass ($F_{1,63} = 2.24$, $p = 0.124$; Fig. 3.2b). However, in the buried treatment, high density plots had greater survival ($F_{1,72} = 6.94$, $p = 0.010$; Fig. 3.2a) and per plant biomass ($F_{1,63} = 4.81$, $p = 0.032$; Fig. 3.2b) than the low density plots. There was not a significant richness by burial treatment interaction for either survival ($F_{2,72} = 0.11$, $p = 0.895$; Table 3.3) or biomass ($F_{2,63} = 1.22$, p 0.301; Table 3.4), meaning that burial had the same effect at both high and low levels of richness.

Discussion

The results of this study support the hypothesis that facilitation increases with burial. In the unburied (control) treatments, plants in the high and low density plots did not significantly differ in survival and biomass, indicating that the interactions were either too weak to be detected or that competition and facilitation balanced each other out, resulting in net neutral interactions. In contrast, in the buried treatments, survival and per plant biomass were greater in the high density than in the low density plots, suggesting facilitation in the buried plots (Fig. 3.2).

This study is the first, to our knowledge, to experimentally manipulate both density and a burial treatment to test the hypothesis that facilitation increases with increasing disturbance. Other researchers have, based on density manipulations and environmental measurements, inferred that facilitation occurred by protection from disturbance. For example, Levine (2000) showed that *Carex* facilitated other species in a riparian community in California, presumably by protecting them from flooding events in the winter. Also, Bruno (2000) found that *Spartina alterniflora* facilitated coble beach plants in New England by stabilizing the substrate. Our study adds experimental evidence that facilitation can increase with increasing disturbance.

This experiment was not designed to determine the mechanisms of facilitation among dune plants, and the reasons why facilitation occurred in the buried plots but not in the unburied controls remains unclear. The facilitation observed in this experiment is probably linked to burial, since facilitation was only observed in the buried plots. It is unlikely that the facilitation observed in the buried plots was caused by high-density plots having more disturbance-tolerant species because there was no effect of richness and because the three most disturbance-tolerant species, *U. paniculata, I. pes-capre, and C. echinatus* (these three species had the least reduction in growth and survival by burial in this experiment) were not planted more frequently in the high density plots than the other species (77% of the plants of the disturbance-tolerant species were in the high density plots, and 81% of the plants of the other species were in the high density plots). It is also unlikely that facilitation occurred by plants protecting each other from abrasion, since sand was shoveled onto the plots and no visible signs of abrasion were observed.

It seems that the most likely explanation for positive interactions under buried conditions in this experiment is that plants protected each other from the weight of the sand after burial. In plots with higher plant density, the sand added in the burial treatment may have been less compacted, allowing buried plants to better grow though the added sand. While sand compaction was not measured in this experiment, measurements with a penetrometer in the field on Keywadin Island in 26 vegetated and 26 open microsites showed that the soil was significantly more compact in unvegetated areas than in high density areas (t-test d.f.=50, t=3.38 p<0.001). This result would be expected if dune plants reduce soil compaction, which could facilitate growth of buried neighbors. However, further experimental work is necessary to determine more conclusively the mechanisms of facilitation among dune plants.

In contrast to our predictions, richness did not affect productivity or survival, or the response of the communities to disturbance. This result conflicts with other findings. For example, Tilman & Downing (1994) found that more diverse grassland communities were more resilient following drought than less diverse communities. It is important to note, however, that diversity and a nutrient treatment were confounded in the Tilman & Downing study (Huston 1997). Additionally, Tilman et al. (1997) and Hector et al. (1999) found that increased diversity increased primary productivity.

The lack of a richness effect in our study could be due to several factors. It could be that the experiment was not continued for long enough to detect an effect of richness. However, the objective of the study was to examine the response of the plants to a disturbance, and the extensive growth of the plants following burial indicated that sufficient post-disturbance recovery had occurred. In fact, so much growth occurred that plants were beginning to grow into adjacent plots, making the termination of the experiment at this time necessary. The lack of a richness effect could also have been due to composition being more important than diversity in determining productivity, as others have suggested (Hooper & Vitousek 1997; Hooper 1998).

In reviewing the literature on the effects of sand burial on dune plants, Maun (1998) found that low levels of burial tended to stimulate plant growth but that high levels of burial were inhibitory. Since a large amount of sand was added to the plots at one time in our study, the reduced growth observed in our burial treatment is consistent with the detrimental effects of rapid sand burial. The plants used in this study may benefit from gradual sand additions, but our study suggests that burial *disturbance* (an acute and severe event), as could be experienced in a severe storm, has negative effects.

In summary, burial reduced overall survival and biomass, and caused net interactions among dune plants to shift from neutral to facilitative. The hypothesis of facilitation increasing with increasing disturbance was thus supported. This effect of burial on the plant interactions held for different levels of richness, increasing the generality of this relationship. These results emphasize the importance of abiotic factors in influencing interactions among organisms, and give further evidence that facilitation is important in communities occurring in stressful and frequently disturbed habitats.

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Figure Legends

Figure 3.1. Experimental design. Symbols represent different species. Each of eighty 1m^2 plots contained either 4 plants or 16 plants, which were the two density treatments. Each plot was either a monoculture of one species chosen at random with replacement from the pool of eight species (see Table 1), or a mixture in which each plant was chosen at random with replacement from the species pool. Forty plots were buried, and the other forty were unburied controls. There were 10 replicates of each density by richness by burial treatment combination.

Figure 3.2. The effect of burial (buried and control treatments) on plots of low (gray bars) and high (black bars) density. Shown are mean proportion survival per plot (a) and mean per plant biomass (b) ± SE. An * indicates a significant difference in means ($p < 0.05$) based on preplanned orthogonal contrasts.

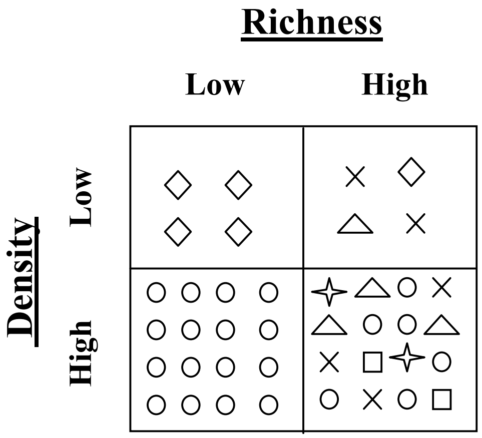

Fig. 3.1

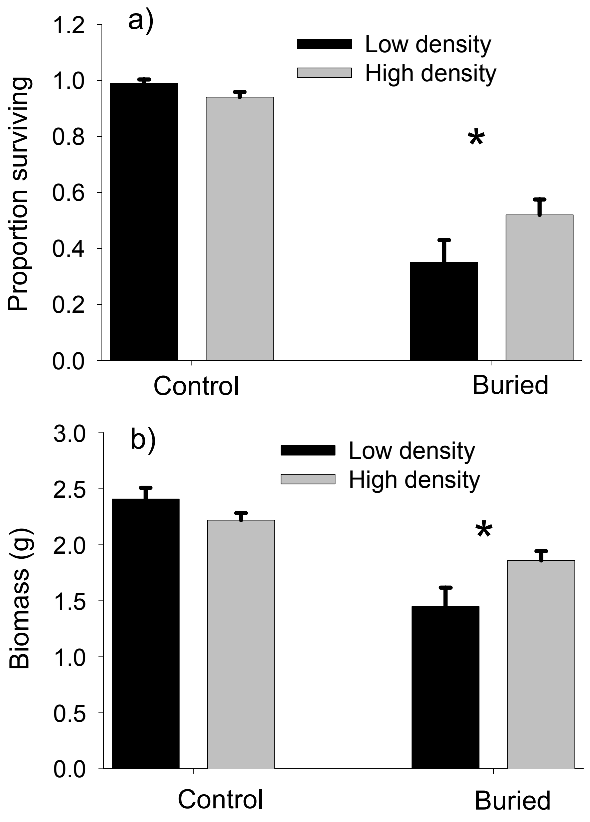

Fig. 3.2a, Fig. 3.2b.

Table 3.1. Species used in the experiment. Shown are genus and species, family, general growth form, the vegetation zone in which the plant is generally found, and the relative abundance (dominance) of this species compared to others in the community. Nomenclature is from Wunderlin (1998).

Name	**Family**	**Growth Form**	**Zone and Dominance**
Cenchrus echinatus	Poaceae	Sprawling grass, rooting at nodes	Primary dune subordinate
Chamaesyce mesembrianthemifolia	Euphorbiaceae	Prostrate perennial herb	Primary dune subordinate
Eustachys petraea	Poaceae	Tall grass	Dune and slack subordinate
Fimbristylis spathacea	Cyperaceae	Bunch graminoid	Dune and slack subordinate
Ipomoea pes-caprae	Convolvulaceae	Sprawling vine	Open beach dominate, primary dune subordinate
Iva imbricata	Asteraceae	Herb or short, woody shrub	Primary dune subordinate
Sesuvium portulacastrum	Aizoaceae	Succulent, prostrate herb	Dune and slack subordinate
Uniola paniculata	Poaceae	Tall rhizomatous grass	Primary dune dominant

Table 3.2. A comparison of the density and richness levels used in the experiment (EX) with those found in two natural communities in 1998: Naples Beach, Florida (NB) and Cape Canaveral National Seashore, Florida (CS).

	Density (plants/m^2)			**Richness (species/m^2)**		
	Average	Minimum	Maximum	Average	Minimum	Maximum
NB (n=20)	5.04	0	15	1.55	0	4
CS (n=30)	5.50	0	16	2.27	0	7
EX (n=80)		4	16		1	8

Table 3.3. ANOVA table for the effects of burial, density, and richness nested within density on the proportion of plants surviving per plot (arcsine square root transformed). The contrasts are preplanned orthogonal means comparisons.

Source	**DF**	**F**	**p**
Burial	1	112.11	**<0.0001**
Density	1	0.96	0.3295
Richness (Density)	2	2.03	0.1392
Burial* Density	1	7.53	**0.0076**
Burial* Richness (Density)	2	0.11	0.8951
Error	72		
Contrasts			
Density in Buried	1	6.94	**0.0103**
Density in Control	1	1.55	0.2166

Table 3.4. Mixed model ANCOVA table for the effects of burial, density, and richness nested within density on total final biomass per plant and root:shoot ratio. Initial plant height and width were covariates in the biomass model. Biomass and root:shoot ratio were natural logarithm transformed. The contrasts are preplanned orthogonal means comparisons. N/A indicates effects or contrasts not used in an analysis.

Source			**Biomass per plant**		**Root:shoot ratio**	
	NDF	**DDF**	**F**	**p**	**F**	**p**
Burial	1	63	34.18	**<0.0001**	0.11	0.7455
Density	1	63	0.99	0.3248	0.13	0.7223
Richness (Density)	2	63	0.30	0.7410	0.12	0.7315
Burial* Density	1	63	7.32	**0.0088**	1.84	0.1756
Burial* Richness (Density)	2	63	1.22	0.3010	0.32	0.5738
Species	7	465	33.29	**<0.0001**	9.90	**<0.0001**
Initial height	7	465	18.85	**<0.0001**	N/A	N/A
Initial width	7	465	121.37	**<0.0001**	N/A	N/A
<u>Contrasts</u>						
Density in Buried	1	63	4.81	**0.0319**	N/A	N/A
Density in Control	1	63	2.24	0.1235	N/A	N/A

CHAPTER 4

COMPETITIVE AND FACILITATIVE INTERACTIONS AMONG TWO COASTAL DUNE PERENNIAL SPECIES[1]

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Abstract

While there is growing evidence for facilitation, hypothesized relationships between facilitative interactions and such factors as stress, disturbance, and species identity remain controversial. In a coastal dune system where facilitative interactions have been previously demonstrated, I tested the hypotheses that: 1) facilitative interactions should increase with increasing stress and disturbance, 2) neighbors may facilitate survival but still compete for resources, reducing growth, and 3) facilitative interactions should be stronger among heterospecific than among conspecific individuals. At two field sites, I transplanted *Uniola paniculata* and *Iva imbricata* individuals into plots along with four conspecific neighbors, four neighbors of the other species, or no neighbors, at three zones across an environmental gradient on the dunes. The plants were harvested after two growing seasons. The presence of neighbors significantly increased the survival of targets, suggesting facilitation. In contrast, growth of targets was either unchanged or reduced by the presence of neighbors, suggesting neutral or competitive interactions, respectively. Unexpectedly, competition was greatest in the zone purported to be most stressful and disturbed (foredune). For these two coastal dune plant species, the outcome of interactions differed for growth and survival components of fitness and depended on position along the environmental gradient but not neighbor identity.

Introduction

Competition has been long regarded as one of the most important factors determining population dynamics and community structure. However, ecologists now recognize that interactions range along a spectrum from negative (competitive) to positive (facilitative) and that the net effects of neighbors may be facilitative in many natural systems (Hunter and Aarenssen 1988, Bertness and Callaway 1994, Bruno and Bertness 2001). The focus of much current research is on understanding under what conditions positive effects of neighbors outweigh negative effects, resulting in facilitation. While evidence for facilitative interactions is rapidly increasing (Callaway 1995), general predictions about the conditions under which facilitation is expected to exceed competition remain largely untested.

Several recent hypotheses have suggested that facilitation may increase with increasing stress (Bertness and Callaway 1994, Callaway and Walker 1997, Holmgren et al. 1997) and disturbance (Brooker and Callaghan 1998). Many examples of facilitation come from stressful or disturbed habitats (Callaway 1995), but the hypothesis that facilitation should increase with increasing stress or disturbance has been explicitly tested by only a few studies in the field, and the results have been mixed. Studies supporting the hypothesis of increasing facilitation with increasing stress and disturbance include Greenlee and Callaway (1996), Callaway (1998b), Levine (2000), Pugnaire and Luque (2001), and Tewksbury and Lloyd (2001). Casper (1996), Donovan and Richards (2000), and Tielborger and Kadmon (1997, 2000) failed to support this hypothesis.

The controversy over the effects of stress and disturbance on facilitative interactions may be due in part to the fact that facilitation might be observed for some components of fitness and not others. In severe environments, neighbors may offer protection from harsh conditions, resulting in an increased probability of survival. However, the same neighbors might also compete for resources, resulting in decreased growth. The distinction between the growth and survival components of fitness in interaction studies has been elaborated (Goldberg and Novoplansky 1997), but most interaction studies examine either growth or survival (but see Levine 2000).

Because most studies of facilitation have examined the effects of only one putative facilitator species (i.e. Niering et al. 1963, Tewksbury and Lloyd 2001), whether interactions are species-specific or general across species or functional groups is an open question (Callaway 1998a). Some recent studies have found reciprocal facilitation among two or more species (Pugnaire et al. 1996, Holzapfel and Mahall1999), but comparisons of intra- versus interspecific facilitative interactions remain scant (Callaway 1995). Based on competition theory, it is reasonable to hypothesize that heterospecific neighbors should be more facilitative (result in larger net benefits to associates) than conspecific neighbors because conspecifics are often similar in resource use patterns and may compete more intensely than heterospecific neighbors. I am aware of no studies that address this hypothesis.

In this study, I examine competitive and facilitative interactions among two coastal dune species, *Uniola paniculata* and *Iva imbricata*, across an environmental gradient. I tested the following hypotheses 1) interactions at this dune site are facilitative rather than competitive, 2) the nature of interactions differs for growth and survival components of fitness, 3) facilitation increases with increasing stress and disturbance along an environmental gradient and 4) facilitation is stronger among heterospecific than among conspecific individuals.

Materials and methods

Study sites and species

The experiments were conducted on the southern, accreting ends of two barrier islands: Keywadin Island, Florida (26° 08'N, 81° 47'W), and Sapelo Island, Georgia (31° 28'N, 81° 14'W). The climate on Keywadin Island is subtropical, with rainfall abundant in the summer and fall. The soils are composed of coarse sand of limestone and shell fragments. Sapelo is a temperate barrier island with a cooler climate (though rarely at or below freezing) and finer sands. In coastal dunes, plants experience such stresses as low nutrients and salt spray and disturbances such as sand burial and erosion (Barbour et al. 1985; Ehrenfeld 1990; Ishikawa et al. 1995; Maun 1998). Stress and disturbance on dunes tend to decrease with distance from the shoreline (Oosting and Billings 1942, Barbour 1978, Ranwell 1972, Ehrenfeld 1990).

Species used (referred to hereafter by genus) were *Uniola paniculata* L. (Poaceae) and *Iva imbricata* Walt. (Asteraceae) (nomenclature follows Wunderland 1982). *Uniola* is a rhizomatous perennial C4 grass that dominates primary coastal dunes in much of the southeastern United States, and *Iva* is a small woody perennial C3 shrub common in primary coastal dunes.

Transplant experiment

In January 1999, juvenile *Uniola* and *Iva* individuals were transplanted into plots along with four conspecific neighbors, four neighbors of the other species, or no neighbors in a randomized complete block design. Transplanted plants were an average of 14cm and 20cm tall for *Iva* and *Uniola*, respectively. For targets with neighbors, the four neighbors were placed one in each cardinal direction and were approximately 5cm from the target. Targets were marked with flagging tape. Group of plants (targets plus neighbors) within blocks were separated by at least 50cm. At each site (Keywadin and Sapelo Islands), there were four replicates of each block in each of three zones: foredune, mid-dune, and rear dune. These zones correspond to, respectively, the shoreward edge of the vegetation, the mid point between the foredune and rear dune zone, and the landward edge of the primary dune vegetation (approximately 0, 50, and 100m from the high tide mark). I refer here to the rear dune as the area shoreward of the occurrence of large woody shrubs (such as *Myrica cerifera*) or trees. There were 144 target individuals (2 species x 3 neighbor treatments x 3 zones x 4 replicates x 2 sites = 144).

The plots were fertilized once per week with 15-30-15 (N-P-K) Peters fertilizer diluted to 1/8 strength and watered with fresh water three times per week for the first three weeks of the experiment to aid establishment, but were not supplemented afterwards. Individuals that died during the first three weeks were replaced. Throughout the experiment, I clipped or removed by hand any plants other than the experimental individuals that occurred within the plots, taking care not to disturb the experimental plants. Height, total number of leaves, and survival of all target and neighbor plants were measured at the beginning and end of the experiment. All plants were harvested in October 2000, dried at 60 C to constant weight, and weighed. Franks and Peterson (unpublished data) showed that the root:shoot ratio of these species was not affected by density or burial, so aboveground biomass should be an accurate indicator of total biomass.

Analysis

Analyses were conducted using SAS (Version 8.02, The SAS Institute, Cary, NC). Target survival was analyzed with logistic regression, with target identity, neighbor treatment, site, zone, and initial target size as main effects. Final size (biomass and leaf number, both natural logarithm transformed) of targets was analyzed with an analysis of covariance (ANCOVA), with neighbor treatment, site, and zone as main effects and initial target size and final neighbor biomass as covariates. When *Iva* and *Uniola* targets did not differ in their response ($p>0.05$), the results were pooled, with the species term removed from the analysis. Results were also pooled across sites when the sites were not different or when the directions of the statistical interaction terms were the same at both sites. Preplanned orthogonal contrasts (Sokal and Rohlf 1995) were used to compare means within the neighbor treatments and zones. A regression of neighbor biomass on target biomass was used to test for per-gram effects of neighbors.

Results

Survival and Growth

The presence of neighbors significantly increased survival of target plants (logistic regression d.f.=1, Wald χ^2=8.6, p=0.003; Table 4.1). The odds ratio indicated that targets were 11 times more likely to survive if neighbors were present. There was not a significant difference in survival probability between *Uniola* and *Iva* targets (Table 4.1).

While survival was greater on Sapelo than Keywadin, the effects of neighbors was consistent across sites (no significant site*neighbor interaction; Table 4.1).

The results for growth contrasted with the results for survival. On Sapelo Island, the presence of neighbors significantly reduced final biomass of *Uniola* targets (planned contrast d.f.=1, F=16.6, p=0.015; Table 4.2). *Uniola* targets without neighbors had 4.0 times the biomass of targets with neighbors (Fig. 4.1a). Biomass of *Iva* was not reduced by neighbors on Sapelo (planned contrast d.f.=1, F=0.74, p=0.40; Table 4.2). However leaf number, which may be a better indicator of fitness for this woody shrub, was reduced by neighbors on Sapelo (planned contrast d.f.=1, F=6.1, p=0.019; Fig. 4.1b). On Keywadin Island, there was not a significant effect of neighbors on biomass of *Uniola* (planned contrast d.f.=1, F=0.1, p=0.737; Table 4.2) or *Iva* (planned contrast d.f.=1, F=0.03, p=0.878; Table 4.2). Neighbor size did not significantly affect size of target plants for either species at either site. A linear regression for both species at both sites showed no per-gram effects of neighbors (n=18, MS=0.56, F=1.46, p=0.25, r^2=0.08).

Interactions across the gradient

To determine the effect of the position along the environmental gradient on overall plant performance, I examined the main effect of zone in a logistic regression for survival and in an ANOVA for biomass. Survival was significantly lower closer to the shore (d.f.=2, χ^2=6.7, p=0.035; Table 4.1), but zone did not significantly affect biomass (d.f.=2, F=0.21, p=0.82). Survival was lowest at the foredune (planned orthogonal contrast d.f.=1, χ^2=4.4, p=0.036) and did not differ between the mid and rear dune zones (d.f.=1, χ^2=0.3, p=0.581).

To test the hypothesis that interactions changed along the environmental gradient, the zone*neighbor treatment interaction term was examined. There was not a significant zone*neighbor treatment interaction for survival (Fig. 4.2a), indicating that interactions did not change along the gradient. There was a significant zone*neighbor treatment interaction for biomass (d.f.=2, F=3.4, p=0.047), with competition greatest at the foredune zone and no significant competition or facilitation at the mid-dune or rear dune zones (Fig. 4.2b).

Intraspecific versus interspecific interactions

Neighbor species did not influence target performance. For *Iva* and *Uniola* targets with neighbors at both sites, the species of the neighbor did not significantly affect target survival (Table 4.1) or size (Table 4.2). Thus there was no difference between intra- and interspecific interactions.

Discussion

Responses to neighbors

The results of this study indicate that interactions among *Uniola* and *Iva* in dunes can be competitive, neutral, or facilitative depending on conditions. The presence of neighbors reduced target plant size at one site, suggesting competition, but increased the probability of target survival at both sites, suggesting facilitation. Interactions were in some cases neutral or too weak to be detected, with no significant effects of neighbors on target biomass on Keywadin Island and in both the mid and rear dune zones on Sapelo Island.

A key finding of this study is that interactions were facilitative when survival was the measure of fitness but competitive or neutral when growth was considered. This result is likely due to neighbors protecting targets from environmental extremes, enhancing survival, but still competing for resources, reducing growth. A similar result was reported by Levine (2000), who showed that in a riparian community in California, *Carex* competed with associated species by reducing biomass but facilitated neighbors by protecting them from mortality during winter disturbances. The fact that neighbors can affect the survival and growth components of fitness differently was pointed out by Goldburg and Novoplansky (1997) in their theoretical work on competition in temporally heterogeneous environments. Facilitation may be generally more important for survival than for growth, but more studies examining both fitness components are necessary to test this idea.

Previous studies have reported competition, facilitation, and a lack of interactions among dune plants. Yarranton and Morrison (1974) reported that facilitative interactions occurred among dune plants and were responsible for a nucleated pattern of succession. Silander and Antonovics (1982) found both positive and negative responses of dune plants to neighbor removals. Lichter (2000) found that the intensity of competition increased during succession on Lake Michigan sand dunes. Shumway (2000) found that *Myrica* shrubs facilitated seedling growth. Houle (1997) found neither competition nor facilitation in subarctic dunes. It appears that interactions among dune plants range along a spectrum from competitive to facilitative, and that the direction and magnitude of interactions depend on characteristics of the plants and of the environment, and on the fitness components measured.

Interactions and gradients

On coastal dunes, nutrient, drought, and salt spray stresses as well as disturbances due to burial, erosion, and storm overwash generally tend to decrease with distance from the shore (Oosting and Billings 1942, van der Valk 1977, Barbour 1978, Kachi and Hirose 1983, Moreno-Casasola 1986, Ehrhefeld 1990, Hesp 1991, Olff et al. 1993, Ishikawa et al. 1995, Maun and Perumal 1999). Based on this trend on the dunes and on the hypothesis that facilitation increases with increasing stress (Bertness and Callaway 1994, Callaway and Walker 1997) and disturbance (Brooker and Callaghan 1998), I predicted that facilitative interactions would be greatest closest to the shore. In contrast to this prediction, competition, measured by biomass, was greatest near the shore and was lower (and not significantly different from neutral) in the mid and rear dune zones (Fig. 4.2a). In addition, there was not a significant effect of zone on plant interactions as measured by survival (neighbor*zone interaction, Table 4.2). The hypothesis of increasing facilitation with increasing stress and disturbance was thus not supported, possibly because the dune gradients may be more complex than previously thought (Franks, unpublished data).

Intra- vs. interspecific interactions

In this study, there were no differences between intra- versus interspecific interactions as measured by survival (Neighbor identity factor in Table 4.1) or size (*Uniola* vs. *Iva* neighbors contrasts in Table 4.2) at both sites. The hypothesis that facilitation would be greater among heterospecifics than among conspecifics was not supported. This result was somewhat surprising in light of the fact that these two species (one rhizomatous C4 grass and one woody C3 shrub) differ in growth form, rooting patterns, photosynthetic pathway, and other characteristics (Brown and Gracen 1972, Duncan and Duncan 1987).

It appears that in this dune system, the presence or absence of neighbors may be more important than their identity. This result would be expected if amelioration of stress or protection from disturbance caused by neighbors is a function of physical presence rather than specific environmental effects. In dunes, any physical structures stabilize the soil. Thus if facilitation occurs by a mechanism such as soil stabilization, species of neighbor might not be expected to affect the outcome of interactions. In systems where facilitation is caused by such mechanisms as nitrogen fixation by a particular species, neighbor identity would be expected to influence the outcome in the interactions. Thus understanding the mechanism of facilitation is critical for predicting under what conditions facilitation is expected.

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Table 4.1. Logistic regression table for survival of both target species pooled (N=144).

Neighbors refers to the presence or absence of neighbors.

Effect	**DF**	**Wald Chi-square**	**p**
Site	1	4.0	**0.046**
Zone	2	6.7	**0.035**
Initial height	1	4.2	**0.040**
Neighbors	1	8.6	**0.003**
Site*neighbors	1	0.1	0.741
Neighbors*zone	1	0.2	0.916
Target species	1	0.0	0.997
Neighbor species	2	3.7	0.156
Target species* Neighbor species	2	3.5	0.173
Foredune vs other	1	4.4	**0.036**
Mid vs rear dune	1	0.3	0.581

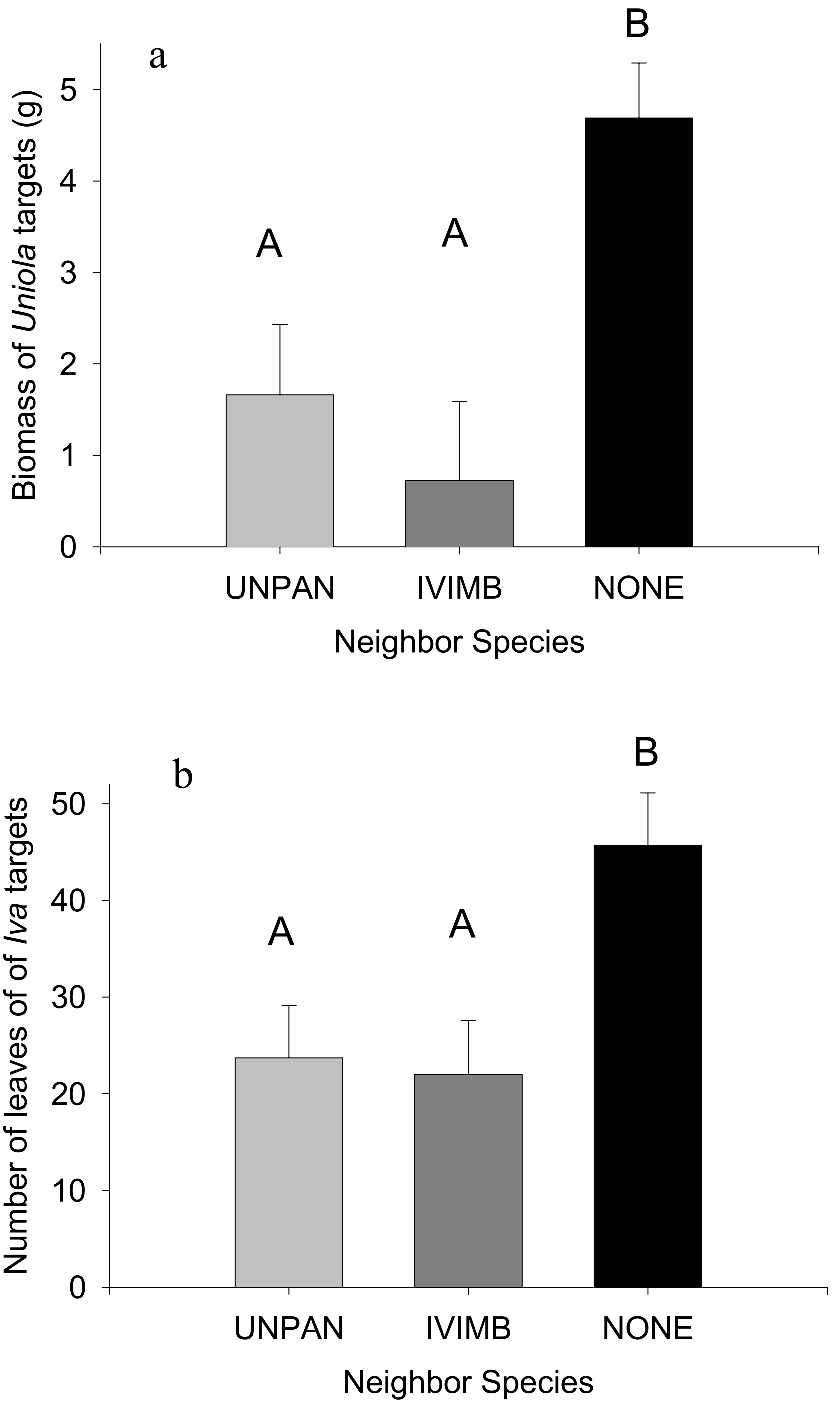
Table 4.2. ANCOVA table for biomass of *Uniola* on Keywadin (N=7) and Sapelo Islands (N=8) and biomass of *Iva* on Keywadin (N=9) and Sapelo Islands (N=19). The three neighbor treatments were alone, *Uniola* neighbors, and *Iva* neighbors. The neighbors vs. alone planned orthogonal contrast tests for significant competition or facilitation, and the *Uniola* vs. *Iva* neighbors contrast compares intra- vs. interspecific interactions.

	Keywadin Island				**Sapelo Island**			
	DF	MS	F	p	DF	MS	F	p
Uniola								
Neighbor treatment	2	59.3	1.9	0.300	2	0.35	8.3	**0.037**
Initial target height	1	36.2	1.2	0.363	1	0.17	4.1	0.113
Error	3	31.6			4	0.04		
Neighbors vs. alone	1	4.29	0.1	0.737	1	0.69	16.6	**0.015**
Uniola vs. *Iva* neighbors	1	110	3.5	0.159	1	0.04	0.9	0.403
Iva								
Neighbor treatment	2	0.01	0.03	0.971	2	1.33	1.57	0.240
Initial target height	1	0.31	1.08	0.347	1	0.45	0.53	0.482
Error	5	0.28			15	15.53		
Neighbors vs. alone	1	0.01	0.03	0.878	1	0.62	0.74	0.405
Uniola vs. *Iva* neighbors	1	0.01	0.04	0.852	1	2.29	2.71	0.121

Figure Legends

Figure 4.1. The effect of neighbor treatment on (a) biomass of *Uniola* targets (N=8) and on (b) number of leaves of *Iva* targets (N=19) on Sapelo Island. The neighbor treatments are *Uniola* neighbors (UNPAN), *Iva* neighbors (IVIMB), and no neighbors (NONE). Different letters indicate significant ($\alpha<0.05$) differences in means based on planned orthogonal contrasts.

Figure 4.2. Survival (a) (N=144) and biomass (b) (N=72) of target plants (*Iva* and *Uniola* pooled) with (gray bars) and without (black bars) neighbors at the foredune, mid dune, and rear dune zones (both sites pooled). An * indicates significant ($\alpha<0.05$) differences in means based on planned orthogonal contrasts.


a
B
A
A
5
4
3
2
1
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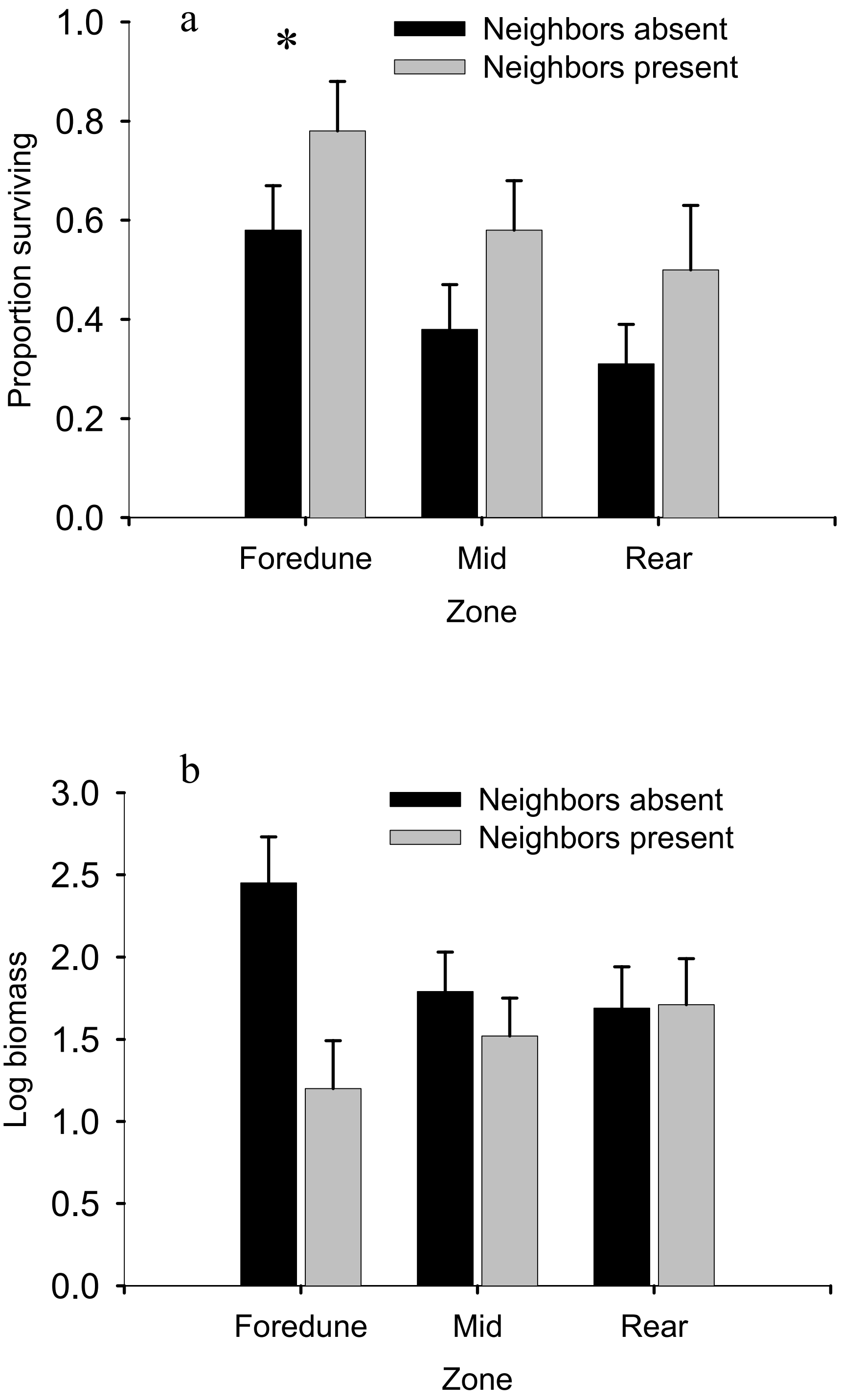
Biomass of *Uniola* targets (g)
UNPAN
IVIMB
NONE
Neighbor Species
b
B
A
A
50
40
30
20
10
0
Number of leaves of of *Iva* targets
UNPAN
IVIMB
NONE
Neighbor Species

Figure 4.1.


a
*
Neighbors absent
Neighbors present
1.0
0.8
0.6
0.4
0.2
0.0
Proportion surviving
Foredune
Mid
Rear
Zone
b
Neighbors absent
Neighbors present
3.0
2.5
2.0
1.5
1.0
0.5
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Log biomass
Foredune
Mid
Rear
Zone

Figure 4.2.

CHAPTER 5

CONCLUSIONS

The results of the research presented in this dissertation suggest that facilitation can occur on coastal dunes and that the strength of facilitation can increase with increasing disturbance, that facilitation is important at early life stages, that interactions can be positive for survival but negative for growth, and that species identity was not important for determining the outcome of interactions in this system. Additionally, there is evidence that facilitation occurs among dune plants due to protection from disturbance, but additional manipulative experiments are necessary to definitively test this purported mechanism.

The set of studies presented in Chapter 2 support the nucleated succession model for coastal dunes of the southeastern United States. Adult plants were positively associated, and seed accumulation and germination was greater under adults than in open microsites. These patterns appear to be caused by adult plants facilitating seed accumulation and germination by trapping seeds and protecting seedlings from severe sand movement. The results suggest that facilitation by adult plants of new colonists at early life stages through the mechanism of increased soil stability leads to a nucleated pattern of succession.

The results of Chapter 2 are consistent with Yarranton and Morrison's (1974) finding of nucleated succession on the Grand Bend dunes, and also with observations of shrubs facilitating understory plants on dunes at Cape Cod (Shumway 2000), but they contrast with studies of succession on other dune systems. Houle (1997) found no evidence for either competitive or facilitative interactions among three herbaceous perennials during early succession on subarctic dunes. Lichter (2000) concluded that competition occurred, and increased in intensity during succession on Lake Michigan dunes. It is likely that both facilitation and competition occur during dune succession, and that many factors, including differences in the levels of stress and disturbances among sites and life stages of the individuals sampled, influence the degree and directions of interactions observed.

The results of Chapter 3 support the hypothesis that facilitation increases with burial. In the unburied (control) treatments, plants in the high and low density plots did not significantly differ in survival and biomass, indicating that the interactions were either too weak to be detected or that competition and facilitation balanced each other out, resulting in net neutral interactions. In contrast, in the buried treatments, survival and per plant biomass were greater in the high density than in the low density plots, suggesting facilitation in the buried plots.

In contrast to my predictions, species richness did not affect productivity or survival or the response of the communities to disturbance in the experiment described in Chapter 3. This result conflicts with other findings. For example, Tilman & Downing (1994) found that more diverse grassland communities were more resilient following drought than less diverse communities. It is important to note, however, that diversity and a nutrient treatment were confounded in the Tilman & Downing study (Huston 1997).

Additionally, Hector et al. (1999) found that increased diversity increased primary productivity.

The lack of a richness effect in the experiment in Chapter 3 could be due to several factors. It could be that the experiment was not continued for long enough to detect an effect of richness. However, the objective of the study was to examine the response of the plants to a disturbance, and the extensive growth of the plants following burial indicated that sufficient post-disturbance recovery had occurred. In fact, so much growth occurred that plants were beginning to grow into adjacent plots, making the termination of the experiment at this time necessary. The lack of a richness effect could also have been due to composition being more important than diversity in determining productivity, as others have suggested (Hooper & Vitousek 1997; Hooper 1998). The lack of a diversity effect is consistent with the lack of a species effect found in the experiment described in Chapter 4.

The results of the experiment described in Chapter 4 indicate that interactions among *Uniola* and *Iva* in dunes can be competitive, neutral, or facilitative depending on conditions. The presence of neighbors reduced target plant size at one site, suggesting competition, but increased the probability of target survival at both sites, suggesting facilitation. Interactions were in some cases neutral or too weak to be detected, with no significant effects of neighbors on target biomass on Keywadin Island and in both the mid and rear dune zones on Sapelo Island.

A key finding of this study is that interactions were facilitative when survival was the measure of fitness but competitive or neutral when growth was considered. This result is likely due to neighbors protecting targets from environmental extremes, enhancing survival, but still competing for resources, reducing growth. A similar result was reported by Levine (2000), who showed that in a riparian community in California, *Carex* competed with associated species by reducing biomass but facilitated neighbors by protecting them from mortality during winter disturbances. The fact that neighbors can affect the survival and growth components of fitness differently was pointed out by Goldburg and Novoplansky (1997) in their theoretical work on competition in temporally heterogeneous environments. Facilitation may be generally more important for survival than for growth, but more studies examining both fitness components are necessary to test this idea.

Previous studies have reported competition, facilitation, and a lack of interactions among dune plants. Yarranton and Morrison (1974) reported that facilitative interactions occurred among dune plants and were responsible for a nucleated pattern of succession. Silander and Antonovics (1982) found both positive and negative responses of dune plants to neighbor removals. Lichter (2000) found that the intensity of competition increased during succession on Lake Michigan sand dunes. Shumway (2000) found that *Myrica* shrubs facilitated seedling growth. Houle (1997) found neither competition nor facilitation in subarctic dunes. It appears that interactions among dune plants range along a spectrum from competitive to facilitative, and that the direction and magnitude of interactions depend on characteristics of the plants and of the environment, and on the fitness components measured.

Overall, the results of this dissertation show that facilitation can occur among dune plants and that several factors, including levels of stress and disturbance, plant life stage, and indicator of fitness used, can influence the strength and direction of these interactions. The findings of these studies give further support for the growing evidence that facilitative interactions are important in natural communities. The results also emphasize the fact that interactions are often conditional, and depend on abiotic conditions. Furthermore, many subcomponents combine to produce the net outcome of interactions. For example neighbor effects could be positive for soil moisture retention but negative for nutrient uptake. The strength and direction of neighbor effects will thus depend on the total net effect of each subcomponent, which will vary depending on environmental conditions. Investigations of interaction subcomponents, how they are affected by abiotic factors, and how they combine to produce net neighbor effects would be fruitful areas of future research.

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