COMMUNITY STRUCTURE, PLANT INTERACTIONS, SEEDLING PERFORMANCE AND SEED BANK COMPOSITION OF SALT MARSHES ALONG AN ESTUARINE GRADIENT IN COOS BAY, OREGON

by

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A DISSERTATION

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DISSERTATION ABSTRACT

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Salt marshes are intertidal communities dominated by halophytic vascular plants that are subjected periodically to tidal inundation. These species have developed various adaptations to this stress, including tolerances of fluctuating salinity, extended periods of inundation and intervals of anoxic conditions. The marshes are divided into zones of different plant communities based on species' tolerances of ambient estuarine conditions. Abiotic stresses change along the estuarine salinity gradient (marine to riverine), potentially altering development and composition of plant communities.

Abiotic gradients associated with tides are not the only factors that contribute to development of plant community composition in salt marshes. Both negative (competition) and positive (facilitation) biological interactions are also important. Factors that influence community structure in salt marshes, particularly on the eastern North American seaboard, have been well studied. In contrast, salt marshes along the Oregon coast are smaller and more discrete and have received comparatively little attention.

The community structure and seed bank composition of six marshes along an estuarine salinity gradient were evaluated. Four major community types dominated marshes that varied in the salinity of inundating tidal waters. Community types were relatively consistent throughout the estuary despite the distances between the marshes. Unlike the emergent plant communities, marsh seed bank composition was more similar within a marsh than within a community type.

The low and high marsh community types were separated by a distinct boundary in the marine marshes. Although abiotic factors influence the physical separation of communities, competitive interactions commonly determine the upper limit of a species. In Metcalf marsh, however, the upper boundary for two dominant low marsh species was not determined by competition with the high marsh dominant species.

Positive biotic interactions between seedlings and existing vegetation in a community are important factors in determining species distributions, particularly in stressful estuarine environments. In salt marshes, where abiotic stress can be harsh, presence of existing vegetation can ameliorate these conditions and enhance germination and seedling establishment. However, interaction between seedlings and the emergent marsh community was highly competitive, though germination of one species was enhanced in the presence of existing vegetation.

This dissertation includes un-published co-authored material.

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CHAPTER I

GENERAL INTRODUCTION

At mid to high latitudes throughout the world, salt marshes exist at the interface between terrestrial and marine ecosystems (Chapman 1960). They are restricted to areas with regular tidal influences, and do not extend into continually submerged environments. These marshes are dominated by communities of halophytic vascular plants that must contend with harsh environmental conditions associated with salt water inundation and associated gradients of physical factors, such as waterlogging and suboxic or anoxic conditions, that have considerable detrimental impact on the vegetation. Marshes are often clearly delineated into zones, by to tidal elevation, dominated by a particular species or group of species (Vince and Snow 1984, Bertness and Ellison 1987, Bertness 1991a). Zonation of a particular species may be indicative of physiological constraints which prevent the species from expanding beyond a specific zone, as well as competitive interactions which displace the species to a more stressful marsh zone (Snow and Vince 1984, Ewing 1986, Earle and Kershaw 1988).

Abiotic Influence on Salt Marsh Plant Distribution

Physiological stress can be manifested in many ways in a salt marsh. Abiotic factors such as salinity (Mahall and Park 1976a, Bertness and Ellison 1987, Bertness et al. 1992, Pennings and Callaway 1992, Rogel et al. 2000, Konsiky and Burdick 2004), sediment grain size (Ewing 1986, Adam 1990, Zhou et al. 2007), inundation (Mahall and Park 1976b, Vince and Snow 1984, Bertness and Ellison 1987, Campbell and Bradfield 1989, van Diggelen 1991, Grace and Jutila 1998, Kunza and Pennings 2008), soil redox potential (Ewing 1986, Lindthurst 1979, Howes et al. 1981, Glough and Grace 1998), soil carbon and nitrogen content (Valiela and Teal 1974, Lindthurst 1979, Lindthurst and Seneca 1981, Tyler et al. 2003, Sala et al. 2008, Orwin et al. 2010), and pH (Bertness and Ellison 1987, Rogel et al. 2000, Piernik 2005, Koretsky et al. 2006) influence the distribution of salt marsh vegetation. These abiotic characteristics differ along an intertidal gradient from low to high elevation within individual marshes. Species' zonal distributions are usually associated with tolerance of environmental attributes of zones within the marshes.

These factors which influence plant distribution have been explored primarily in marshes on the east coast of North America (Bertness and Ellison 1987, Bertness 1991, Hacker and Bertness 1994, 1999, Sala et al, 2008), Europe (Adam 1978, Armstrong et al. 1985), Alaska (Snow and Vince 1984, Vince and Snow 1984, Price et al. 1988), and California (Mahall and Park 1976a,b, Callaway and Davis 1993) but relatively few studies have examined salt marshes within the Pacific Northwest, particularly in Oregon (Hoffnagle 1980, Taylor et al. 1983, Cornu and Sadro 2002, Rumrill and Sowers 2008). Along much of the west coast of the United States, the geomorphological profile of the coastal plain is not conducive to the development of large, expansive marshes typical of Europe or the east coast of North America. The steep offshore topography in the northwest restricts development sites to the degree that salt marshes tend to be rather small and isolated (Chapman 1960, Callaway and Zedler 2009). Salt marshes in this region are located within estuaries and the plant communities often reflect differences in the salinity of the water column. Composition of salt marsh communities changes from marine-dominated marshes near the mouth of the embayment to riverine-dominated marshes close to the river input (Odum 1988, Kincheloe and Stehn 1991, Crain et al. 2004, Rumrill and Sowers 2008).

Competition and Facilitation in Salt Marshes

In the past, the distribution of species within salt marshes was attributed primarily to these physiological factors but more recently, the role of competitive (negative) and facilitative (positive) interactions with neighboring plants has been recognized as critical in the structure of salt marsh communities (Levine et al. 1988, Emery et al. 2001, Bertness and Ewanchuk 2002). Boundaries between zones of dominant species are influenced by the 'competitive-physiological-exclusion principle', which states that plants are excluded from neighboring zones by competitive interactions with vegetation in that zone or physiological constraints which do not allow growth into that zone (Bockelmann and Neuhaus 1999). Generally, plants that are able to tolerate abiotic stresses tend to be ill-adapted to successfully compete for space or light (Grime 1977, Bertness 1991b). As abiotic stress decreases with increased intertidal elevation, levels of competition increase as more species are able to tolerate the physiological conditions (Wilson and Keddy 1986, Bertness and Ellison 1987, Sanchez et al. 1996, Hacker and Bertness 1999). Therefore, the lower boundary of a species is defined by the physiological tolerance of that species to the ambient abiotic conditions while the upper boundary of the species is defined by the competitive ability of the species (Bertness and Ellison 1987, Bertness 1991b).

Not all interactions between vascular plants within salt marshes are negative. Facilitative interactions between plants species frequently occur in areas of high abiotic stress (Bertness and Shumway 1993, Pugnaire et al. 1996). Amelioration of harsh environmental conditions is an important element in the structure of plant communities in salt marshes (Bertness and Shumway 1993, Hacker and Gaines 1997, Hacker and Bertness 1994, 1999, Pennings et al. 2003). Neighboring plants can decrease the anoxic conditions of the sediment (Snow and Vince 1984, Hacker and Bertness 1999) as well as shade hypersaline soils (Bertness 1991b, Bertness et al. 1992, Shumway and Bertness 1994), both of which have the potential to alter the abiotic environment and allow growth of species which would otherwise be physiologically excluded from the marsh.

Seed Banks in Salt Marshes

The structure of salt marsh communities is based on other factors in addition to the impact of abiotic and biotic factors on the adult plants. Presence and distribution of seeds in the seed banks of these marshes can also influence the distribution of salt marsh plants in both space and time. Seed banks are defined as the viable seeds present in the soil for less than one year (“transient”) to many years (“persistent”) (Leck and Graveline 1979, Fenner 1985, Ungar and Woodell 1996). Plant recruitment, especially after a disturbance that clears existing vegetation, is based on seed production, ability of the seeds to germinate in the existing conditions, longevity of the seeds in the soil, survival of the seeds until germination and survival of the germinated seedlings (Fenner 1985). Seeds of salt marsh species must tolerate highly saline conditions either through the ability to germinate under high salt conditions or to remain viable through long periods of enforced dormancy (Ungar 1995, Ungar 2001). Most seeds of salt marsh species exhibit the highest levels of germination during periods of or areas with low salinity (Hutchinson and Smythe 1986, Shumway and Bertness 1992, Ungar 2001), so coastal salt marshes have high variability in number of seeds and composition of seed banks between zones

(Jefferies et al. 1981, Hartman 1988, Ungar 1995). Areas with lower salinity allow more germination, leaving fewer seeds within the seed bank.

Seed banks in salt marshes do not usually reflect the patterns of the emergent marsh vegetation (Ungar and Woodell 1993, Maranon 1998). This relationship is often closely associated with the amount of freshwater in the marsh (Leck and Graveline 1979, Leck and Simpson 1987, Baldwin et al. 1996) and the dominance of perennial versus annual species (Hopkins and Parker 1984, Bertness and Shumway 1993, Unger and Woodell 1993).

Scope and Objectives

My primary objective in developing this dissertation project was to examine the role of abiotic factors, competitive and facilitative interactions and seed bank composition on the structure and development of the emergent salt marsh communities of six marshes along an estuarine salinity gradient within the South Slough branch of the Coos estuary, in Oregon.

Chapter II describes a quantitative investigation of community composition and corresponding abiotic conditions of six salt marshes along the estuarine gradient in South Slough, Coos Bay, Oregon. Although typical zonation patterns of community structure are apparent with casual observation, the underlying factors contributing to these patterns had not previously been explored. In this chapter, measurements of species cover and biomass yield are described from plots in each marsh from marine to mesohaline and riverine. The structure of the marsh communities is compared to a suite of physical and chemical abiotic factors that were measured at each sampling site. Abiotic parameters include site elevation, peak month inundation time, sediment texture, percent carbon, percent nitrogen, redox potential, and pore water salinity and pH. Chapter II describes the relationship of the marsh communities present in South Slough to each other and with the abiotic conditions within individual marshes and positions of the marshes along the estuarine gradient.

Chapter III investigates the role of competition in maintaining the high/ low marsh boundary in one marine-dominated marsh in the South Slough. Previous studies suggest that the upper boundary of low marsh species is dictated by competition with high marsh dominant species and that the lower edge of the high marsh zone is determined by the physiological constraint on the high marsh species (Bertness and Ellison 1987, Bertness 1991a,b, Hacker and Bertness 1995, 1999). High marsh species, therefore, do not extend into the low marsh due to an inability to tolerate the more stressful, low marsh conditions (Wilson and Keddy 1986, Bertness and Ellison 1987, Bockelmann and Neuhaus 1999). The purpose of this chapter is to test the validity of this paradigm in a Pacific Northwest salt marsh. The high/low marsh boundary in the study marsh is defined by one high marsh species, *Carex lyngbyei*, and two low marsh species, *Distichlis spicata* and *Salicornia virginica*. The interactions among the three dominant species were examined through reciprocal transplants in two consecutive summer growing seasons (2009 and 2010), across the high/low marsh boundary. The role of competition was examined by comparison of the growth of transplanted ramets of all three species into vegetated plots and plots cleared of existing marsh vegetation.

Chapter IV examines the composition of seed banks in the same six marshes (as Chapter II) along the South Slough. Seed banks in salt marshes along the west coast of Oregon have been largely unexplored and though previous studies indicate that there may be considerable heterogeneity in the seed bank of salt marshes (Milton 1939, Ungar and Riehl 1980, Hopkins and Parker 1984, Hutchings and Russell 1989, Ungar 1995), studies of marsh seed banks along an estuarine gradient are scarce. This chapter evaluates the seed density, field emergence and viability of seed banks along the estuarine salinity gradient. Seed density was determined from manual seed counts under light microscopy. These counts were compared with paired samples allowed to germinate as an estimate of viability of salt marsh seeds. Field emergence was also examined in a subset (three of six) of the marshes.

Chapter V explores the interaction between germinating seedlings and the emergent marsh community in three marshes along the estuarine salinity gradient in South Slough. This chapter examines germination and survival of out-planted seeds of five salt marsh species (*Plantago maritima, Triglochin maritima, Distichlis spicata, Salicornia virginica* and *Atriplex patula*) in paired plots, with and without neighboring vegetation, established in three marshes along South Slough with arrays in each of three intertidal heights. Both positive and negative interactions between species are important in influencing the structure of plant communities, but facilitation (positive interactions) is more often prevalent in areas of high stress, including salt marsh environments (Bertness and Callaway 1994, Hacker and Bertness 1995, 1999, Pennings et al. 2003, Hacker 2009). Possible facilitative effects of the emergent marsh community on germination and survival of seedlings are described. Chapter V was written by H. Keammerer with S. D. Hacker as a co-author. Changes to the original method (as suggested by S.D. Hacker), experimental installation, data collection and analyses were all carried out by H. Keammerer. The chapter was written with input and suggestions from S. D. Hacker.

CHAPTER II

ENVIRONMENTAL FACTORS AND SALT MARSH COMMUNITY STRUCTURE ALONG AN ESTUARINE SALINITY GRADIENT

Introduction

Patterns of community structure in coastal salt marshes have long been of interest to ecologists (Chapman 1960, Beeftink 1977, Odum 1988). Although it is widely understood that plant communities are responsive to changes in the physical environment, the spatial distribution of plant communities does not always correspond closely to the physiological tolerances of the component species. In addition, the patchy distribution exhibited by many plant communities does not always correspond with variability in abiotic factors (Bertness and Ellison 1987, Callaway and Davis 1993, Pulliam 2000, Orwin et al. 2010). Zonation within salt marshes is generally a response to location along the intertidal gradient and is based on the ability of a given species to tolerate environmental conditions, particularly those driven by regular inundation (Adam 1990, Schroder et al. 2002). Regular tidal inundation affects the lower elevation regions of the marsh to a greater extent than higher elevation regions. The associated environmental variables, particularly salinity and oxygen availability (redox potential), also vary along the gradient from low to high intertidal (Vince and Snow 1984, Bertness and Ellison 1987, Schat et al. 1987, Campbell and Bradfield 1989, Ungar 1998, Baldwin and Mendelssohn 1998, Bhattacharjee et al. 2009, Thomas et al. 2009, Alberti et al. 2010). Within these marshes, other abiotic factors, such as pH, sediment texture and nutrient availability, can also influence the development of community zonation (Kortesky et al. 1996, Boyer and Zedler 1999, Zhou et al. 2007, Sala et al. 2008). Although these factors are known to influence community structure within salt marshes, little is known about their role in Pacific Northwest coastal salt marshes.

The intertidal gradient is not, however, the only environmental gradient of importance in marshes along the Pacific coast. In contrast to the expansive marshes of the East Coast of the US (Bertness and Ellison 1987, Bertness 1991, Bertness et al. 2004), Europe (Adam 1978, Armstrong et al. 1985), Alaska (Snow and Vince 1984, Vince and Snow 1984, Price et al. 1988), or California (Mahall and Park 1976), Oregon's marshes are relatively small (Chapman 1960, Rumrill 2006). Few studies have examined the changes in salt marsh community structure in the context of the estuarine salinity gradient between the estuary mouth and the riverine input (Odum 1988, Crain et al. 2004, Rumrill and Sowers 2008, Sharpe and Baldwin 2009). While some of the edaphic stresses associated with salt marsh zonation, such as high salinity, change along the estuarine salinity gradient, others, such as low oxygen availability, may not. Therefore, the environmental variables which are most important in dictating community structure in a marsh in the marine-dominated portion of the estuary may not be the same as those dictating community structure in more riverine-dominated marshes.

The objectives of this study were to examine the vegetation structure and composition and associated abiotic factors in northwest Pacific marshes along an estuarine gradient. I expected plant community composition to vary according to the position of the marsh along the estuarine salinity gradient. I predicted that the estuarine gradient, manifested by factors such as salinity and sediment texture, will be the most important factor in structuring plant communities and therefore creating large-scale patterns in plant community structure within the estuary. Secondly, I expected plant species distributions within the marsh to be primarily determined by their physical tolerances. As a result plant communities with similar species composition may reflect a particular range of environmental variables regardless of marsh position along the estuarine salinity gradient.

Methods

Site Descriptions

Metcalf marsh and Collver Point marsh are both located near the mouth of Coos estuary (4.4 and 5.0 km from the mouth respectively) (Figure 2.1, Appendix A). These marine-dominated marshes are exposed to tidal salinities ranging from 20 to 31 g/kg. Lower elevations in Metcalf marsh are dominated by large patches of *Salicornia virginica* and *Distichlis spicata* intermixed with *Triglochin maritima*, *Jaumea carnosa* and occasionally *Atriplex patula* and *Plantago maritima*. Higher elevations are dominated by *Deschampsia caespitosa* and *Carex lyngbyei*. *Salicornia virginica* covers the majority of Collver Point marsh, in monotypic stands and mixed with *D. spicata*. Parasitic dodder (*Cuscuta salina*), which depends on *S. virginica* and occasionally *J. carnosa*, is also common. Both *D. caespitosa* and *C. lyngbyei* are present but occur only in small patches.

Valino Island and Hidden Creek salt marshes are located within the mesohaline region of South Slough (7.1 and 9.2 km from the mouth of Coos estuary, respectively) where tidal salinities range from 15 to 28 g/kg. These marshes are dominated by *D. caespitosa* with small patches of *S. virginica*, *D. spicata*, and *C. lyngbyei* communities. Danger Point marsh and Tom’s Creek marsh are located within the riverine dominated portion of South Slough (10.6 and 11.2 km from the mouth of Coos estuary, respectively) where tidal salinities range from 0 to 21 g/kg. Both of these marshes are covered almost exclusively with communities dominated by *D. caespitosa* and *C. lyngbyei*. In these marshes, the introduced grass *Agrostis stolonifera* constitutes a larger proportion of the cover than in the other study marshes. Although *D. spicata* is present, it accounts for limited amounts of cover within the marsh and *S. virginica* is almost entirely absent.

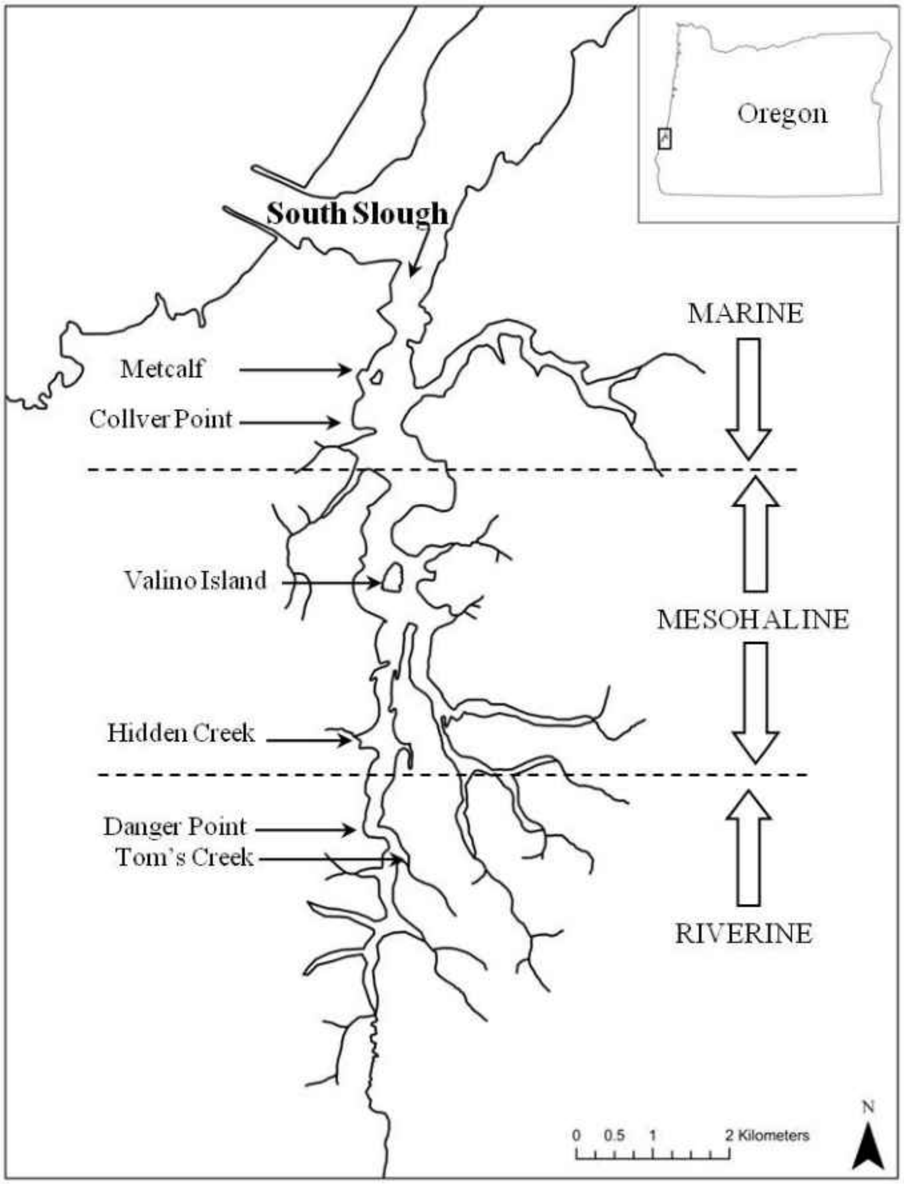

Figure 2.1. Map of the locations of the six study marshes within South Slough, Coos Bay, Oregon. South Slough mouth is indicated with the arrow; the slough itself continues to the south and drains from south to north.

Vegetation and Environmental Sampling

Plant communities and associated environmental variables were sampled in six tidal marshes along the length of South Slough, Coos Bay on the southwest Oregon coast during the summer of 2008 (Figure 2.1). Although all the sites have sustained minor anthropogenic disturbances, only Tom's Creek marsh was diked, although the marsh was never used for agriculture. Tidal circulation was restored there over 25 years ago (Cornu and Sadro 2002). All of the study sites are regularly inundated by tides, the magnitude of which are determined by the proximity to the mouth of the slough. Salinity regime (salinity of the tide water inundating the marsh) in the tidal marsh varies based on marsh position in the slough (Figure 2.1). The marshes are classified as marine (Metcalf and Collver Point marsh), mesohaline (Valino Island and Hidden Creek marsh) and riverine (Danger Point and Tom's Creek marsh) (Rumrill 2006, Rumrill and Sowers 2008). Vegetation structure and composition and characteristics of the pore water and sediment were sampled at 121 locations within the six marshes.

Preliminary reconnaissance of the marshes suggested that four major community types were present at the study sites. Two of these community types, based on the abundance of *Salicornia virginica* and *Distichlis spicata*, do not occur in the riverine marshes. Both *S. virginica* and *D. spicata* are highly salt tolerant, tend to be poor competitors, and are therefore excluded from higher elevation parts of marshes as well as the riverine marshes at the upper end of the slough (Bertness 1991b, Shumway and Bertness 1994, Tolley and Christian 1999). The other two main communities are dominated by high marsh species, *Carex lyngbyei* and *Deschampsia caespitosa*. Both are found only in the upper portions of marine and mesohaline marshes, but dominate the riverine marshes over broad elevation ranges (especially *C. lyngbyei*). In order to evenly sample these disparate community types, I haphazardly placed six plots in areas dominated by each species in each marsh (24 plots per marsh). An extra *Carex* dominated plot was established within the Metcalf salt marsh. Only 12 plots were sampled in the two riverine marshes since the *S. virginic*a and *D. spicata* community types were absent.

Vegetation sampling occurred during peak growing season, July-August. Percent cover and peak standing biomass were measured at each of the sampling locations. Cover was estimated within a one meter square area using an optical point sampling method (Figure 2.2; see also Goodall 1952, Phillips 1959, Winkworth and Goodall 1962, Morrison and Yarranton 1970). The optical point-frame with 20 preset points was sampled at two locations within the one square meter area for a total of 40 points per sample plot. Species within the sampling area not encountered during cover sampling were recorded as <1% cover. Taxonomic nomenclature follows Kozloff (2005).

Figure 2.2. Photograph of optical point sampling device and sampling bar. Photo W. Keammerer.

Plant annual yield (biomass) was determined for each plot. A 25 cm x 25 cm subplot was placed outside three of the corners of the 1 m square cover plot. All growth within each 25 cm plot was clipped at ground level, sorted by species, and bagged. Biomass from the three clipped subplots was combined. Samples were dried until mass had reached a constant value (approximately 48 hours at 80°C). The final mass was recorded.

Sediment cores (2.5 cm diameter) were extracted to a depth of 15 cm at the four corners and center of the cover plot. Sediment samples were dried at 105°C until a constant weight was attained and then divided into three equal portions. One third was dry sieved to determine proportions (by mass) of sand (2.0-0.02 mm diameter), silt (0.02-0.002 mm diameter) and clay (<0.002 mm diameter). Total carbon and nitrogen were determined from the second dried and ground portion of sediment using a Costech Analytical Technologies 4010 elemental combustion analyzer (Valencia, CA, USA). Total organic matter in the final portion was estimated through loss on ignition (LOI) in a muffle furnace (Thermolyne 62700) at 400° C.

Characteristics of the soil pore water were measured at each plot at five different sampling times. In addition to collecting these data during the summer of 2008 concurrent with the other sampling, the collection process was repeated over a neap tidal cycle and the following spring tidal cycle in both the summer of 2009 and the winter of 2010. A sediment core, approximately 14 cm in diameter and 20 cm deep was removed, and the hole was allowed to fill with interstitial pore water. Salinity of this water was measured with a refractometer while pH and redox potential were measured with a YSI pH100 portable meter (YSI Environmental, Yellow Springs, OH, USA). Prior to analysis, pH, salinity and redox potential from the five time intervals were condensed into four measures for each variable at each plot; the mean of all summer measurements (Sum), the mean of both winter measurements (Win), the overall mean (Mean) and the range in values (Range).

Surface elevation of each plot was determined at the central point using a TRIMBLE Real-Time Kinematic Global Positioning System with a stationary base and mobile receiver in August 2009. As inundation time is a better predictor of plant community structure than elevation (Bockelmann et al. 2002), elevations were compared to recorded tidal data from three lunar months (January 8-February 7; March 7-April 6; August 1- August 30) in 2008 to calculate inundation time for each plot (n=121). Inundation times for all three months were highly correlated (January to March: $r = 0.97$, $p<0.0001$; January to August: $r = 0.99$, $p<0.0001$; March to August: $r = 0.98$, $p<0.0001$). Therefore only one month of data (January 8, 2008- February 7, 2008) was arbitrarily chosen and was used for analyses.

Statistical Analyses

Cluster analysis was used to evaluate the similarity of all 121 plots based on vegetation cover data. The analysis was conducted using the relative Euclidian distance measure and Ward's method was performed using PCORD (Version 4; MjM Software Design, Gleneden Beach, OR). Prior to analysis, uncommon species (occurrence in fewer than 5 plots) were removed (McCune and Grace 2002, Austin et al. 2007, Sharpe and Baldwin 2009). Indicator species analysis was used to further characterize clusters (McCune and Grace 2002). This method identifies species which are important in differentiating among groups based on frequency and relative abundance (Sharpe and Baldwin 2009). A Monte Carlo test was used to determine significance of the indicator species ($p < 0.05$) based on 1000 permutations of randomized data.

Total yield was combined for all species in a given plot and compared among all community subgroups with the Kruskal-Wallis test. Post-hoc analyses were performed using Games-Howell method due to constraints of unequal variance and sample size (Day and Quinn 1989). Differences in abiotic factors among groups were also compared using the same method.

Community Analysis

Variation in plant community structure and composition among marshes and community types was evaluated using nonmetric multidimensional scaling (NMS) which utilizes ranked distances between sites in species space (Kruskal 1964, Mather 1976, Clark 1993, Waichler et al. 2001, McCune and Grace 2002). This method determines the best distribution of plots on *k*-dimensions (axes) while minimizing the stress of the configuration (Petersen and Stringham 2009). 'Stress' is defined as the departure from monotonicity, or the difference between the dissimilarity matrix from the original plant data and the distribution in ordination space (Waichler et al. 2001, Petersen and Stringham 2009). Although larger stress values (departure from monotonicity) decrease the interpretability of the results, values smaller than 15 are satisfactorily small and values approaching 20 are still interpretable (McCune and Grace 2002). Prior to analysis, percent cover data were arcsine square root transformed. All analyses were performed using PCORD.

NMS ordinations were developed using all plots and for each dominant vegetation type as identified by the cluster analysis. For each analysis, an initial run was performed to determine the number of dimensions to use based on plots of instability versus stress for all six possible dimensions (McCune and Grace 2002). For all plots together, a three-dimensional configuration was determined to be optimal. Two-dimensional configurations were chosen for separated *Carex*, *Deschampsia*, *Distichlis* and *Salicornia* dominated community plots as increased dimensions did not significantly decrease stress (McCune et al. 1997). For each NMS analysis, a Sorensen (Bray-Curtis) distance measure was used with a 0.00001 stability criterion. Final runs for each species matrix were derived with 150 iterations and a randomly selected starting configuration (McCune and Grace 2002).

Abiotic Factors

Marsh communities were compared to environmental variables in two ways. First, a second matrix of the environmental variables was compared to the axes generated by the NMS analysis. Abiotic factors measured as percent (organic content, sand, silt, clay, total carbon, total nitrogen) were arcsine square root transformed. Environmental factors which correlated significantly ($p<0.05$) with community distributions on each axis were displayed using a joint plot. Second, each abiotic factor was compared to the NMS axes using multiple linear regression. Prior to analysis, variables were removed if they were highly autocorrelated (> 80 % correlated). The backward method was used to determine which abiotic factors were significant predictors of community structure. NMS axes for all plots, *Carex* dominated, *Deschampsia* dominated, *Distichlis* dominated and *Salicornia* dominated communities were analyzed separately using SPSS 19 for Windows.

Results

Community Type Distribution and Description

Cluster analysis returned four major community types defined primarily by abundance of four major species: *Carex lyngbyei*, *Deschampsia caespitosa, Distichlis spicata/Salicornia virginica*, and *Salicornia virginica* (Figure 2.3). The more salt tolerant communities, the *Salicornia* and *Salicornia/Distichlis* community types, were most closely related. The *Deschampsia* and *Carex* community types were more distinct, both from one another and from the *Distichlis/Salicornia* and *Salicornia* types. Cluster analysis also determined that the four major groups were divided by 13 subgroups (Figure 2.4; See Appendix B for detailed descriptions of composition). While the finer branches of the dendrogram are explained by indicator species, the four major vegetation types show strong relationships with the measured environmental parameters (Figures 2.5, 2.6).

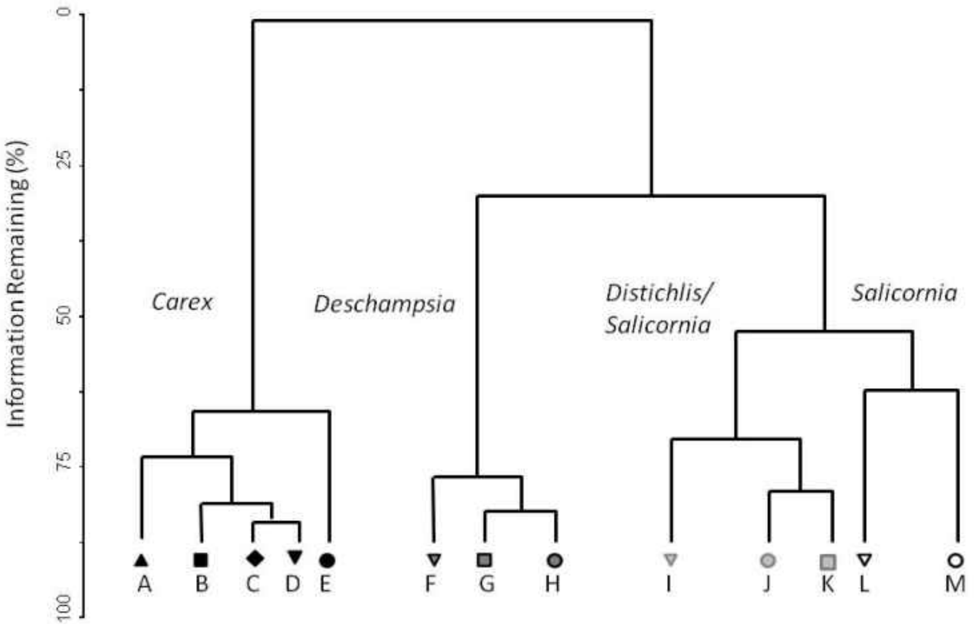

Figure 2.3. Dendrogram of the four major community types and 13 subgroups based on the cluster analysis.

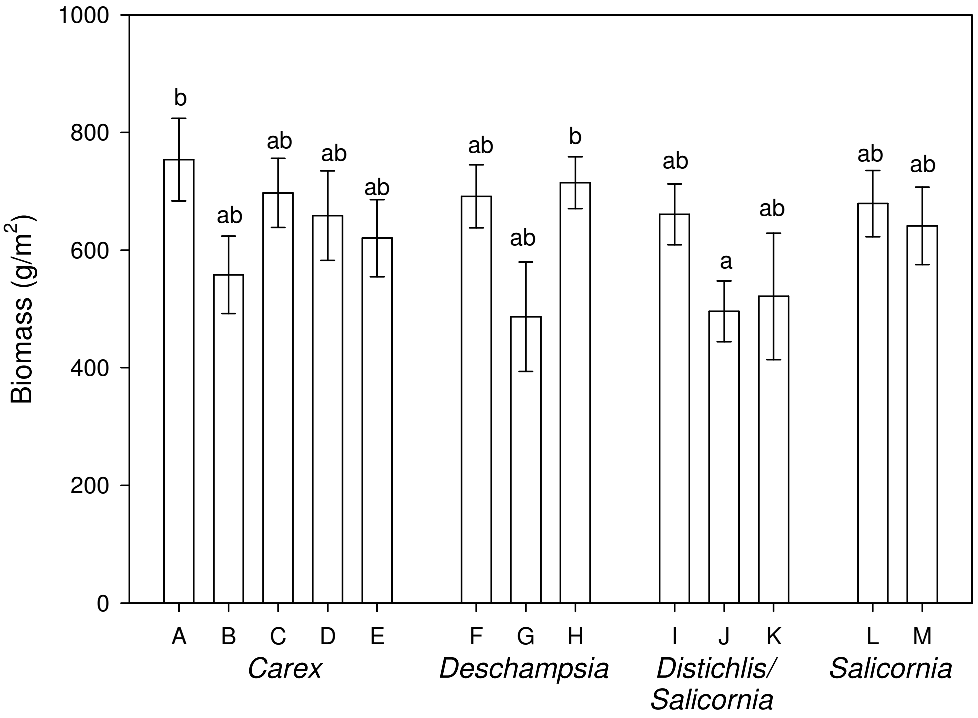

Figure 2.4. Mean total yield of plots within each sub-group separated into the four major community types based on the dominant vegetation (*Carex lyngbyei, Deschampsia caespitosa, Distichlis spicata/Salicornia virginica*, and *Salicornia virginica*). Error bars represent standard error of the mean. Bars with different letters are statistically different (post hoc: Games-Howell: $p<0.05$).

Carex Community Type

The major community type dominated by *Carex lyngbyei* is present in all six study marshes. Cluster analysis split this major community type into five subgroups (A, B, C, D, and E), but every subgroup was not present in every marsh (Figure 2.3, Table 2.1). Subgroup A had higher total yield than the other subgroups within the *Carex* communities, but the difference was not significant (Figure 2.4). The *Carex* communities experience lower summer and mean salinity values than the other three major community types (Figure 2.5a, c). Average winter pH was significantly higher in the *Carex* communities than in the *Distichlis/Salicornia* communities, but did not differ from the *Deschampsia* or *Salicornia* communities (Figure 2.5f). Summer redox potential was more reducing in the *Carex* communities than the *Deschampsia* communities, but not significantly, and less reducing than in the *Salicornia* communities (Figure 2.5g). The *Carex* community type had significantly higher percent organic, percent carbon and percent nitrogen and significantly lower January inundation time and percent silt than the *Salicornia* community type (Figure 2.6).

Table 2.1. Species lists for community types and sub-groups in observed plots as determined by cluster analysis. Marshes are listed when the community type was present in that marsh.

Group	Sub-group	Marshes	Species
Carex	A	Hidden Crk Danger Pt. Tom’s Crk.	*Agrostis stolonifera**; *Carex lyngbyei*; *Deschampsia caespitosa*; *Distichlis spicata*; *Glaux maritima*; *Jaumea carnosa*; *Juncus arcticus* ssp. *balticus*; *Triglochin maritima*; *Trifolium wormskjoldii*
	B	Collver Pt. Valino Is. Danger Pt.	*Agrostis stolonifera*; *Atriplex patula*; *Carex lyngbyei*; *Deschampsia caespitosa*; *Distichlis spicata*; *Eleocharis parvula*; *Jaumea carnosa*; *Plantago maritima*; *Potentilla anserina* ssp. *pacifica*; *Salicornia virginica*; *Triglochin maritima*
	C	Metcalf Collver Pt. Hidden Crk. Danger Pt. Tom’s Crk.	*Agrostis stolonifera*; *Carex lyngbyei**; *Deschampsia caespitosa*; *Distichlis spicata*; *Eleocharis parvula*; *Grindelia integrifolia*; *Jaumea carnosa*; *Limonium californicum*; *Potentilla anserina* ssp. *pacifica*; *Triglochin maritima*; *Trifolium wormskjoldii*
	D	Metcalf Collver Pt. Hidden Crk. Danger Pt.	*Agrostis stolonifera; Atriplex patula; Carex lyngbyei; Cuscuta salina; Deschampsia caespitosa; Distichlis spicata; Glaux maritima; Hordeum brachyantherum*; *Jaumea carnosa*; *Salicornia virginica*; *Triglochin maritima*; *Trifolium wormskjoldii*
	E	Metcalf Valino Is. Hidden Crk.	*Agrostis stolonifera*; *Atriplex patula*†; *Carex lyngbyei*; *Cuscuta salina*; *Deschampsia caespitosa*; *Distichlis spicata*; *Glaux maritima*; *Jaumea carnosa*; *Juncus arcticus* ssp. *balticus*; *Plantago maritima*; *Salicornia virginica*; *Spergularia marina*; *Triglochin maritima*

Table 2.1 Continued

Group	Sub-group	Marshes	Species
Deschampsia	F	Metcalf Collver Pt. Hidden Crk. Danger Pt. Tom's Crk.	*Agrostis stolonifera*; *Atriplex patula*; *Carex lyngbyei*; *Cuscuta salina*; *Deschampsia caespitosa*; *Distichlis spicata*; *Grindelia integrifolia*; *Hordeum brachyantherum*; *Jaumea carnosa*; *Lilaeopsis occidentalis*; *Salicornia virginica*; *Triglochin maritima*
	G	Valino Is. Tom's Crk.	*Agrostis stolonifera*; *Carex lyngbyei*; *Cuscuta salina*; *Deschampsia caespitosa**; *Distichlis spicata*; *Eleocharis palustris*; *Eleocharis parvula**; *Glaux maritima**; *Grindelia integrifolia**; *Jaumea carnosa*; *Juncus arcticus* ssp. *balticus**; *Limonium californicum*; *Plantago maritima**; *Potentilla anserina* ssp. *pacifica*; *Salicornia virginica*; *Spergularia marina*; *Triglochin concinna*; *Triglochin maritima*; *Trifolium wormskjoldii*
	H	Metcalf Collver Pt. Hidden Crk. Valino Is. Danger Pt. Tom's Crk.	*Agrostis stolonifera*; *Atriplex patula*; *Carex lyngbyei*; *Cuscuta salina*†; *Deschampsia caespitosa* ; *Distichlis spicata*; *Eleocharis parvula*; *Glaux maritima*; *Grindelia integrifolia*; *Hordeum brachyantherum*; *Hordeum jubatum*; *Jaumea carnosa*; *Juncus arcticus* ssp. *balticus*; *Juncus gerardii*; *Limonium californicum*; *Plantago maritima*; *Salicornia virginica*; *Triglochin maritima*
Distichlis/ Salicornia	I	Metcalf Collver Pt. Valino Is. Hidden Crk.	*Atriplex patula*; *Cordylanthus maritimus* ssp. *palustris*; *Cuscuta salina*; *Deschampsia caespitosa*; *Distichlis spicata**; *Hordeum brachyantherum*; *Jaumea carnosa*; *Salicornia virginica*; *Spergularia marina*; *Triglochin maritima*
	J	Metcalf Collver Pt. Valino Is.	*Atriplex patula*; *Cordylanthus maritimus* ssp. *palustris*; *Cuscuta salina*; *Deschampsia caespitosa*; *Distichlis spicata*; *Glaux maritima*; *Jaumea carnosa*; *Lilaeopsis occidentalis*; *Limonium californicum*; *Salicornia virginica*‡; *Spergularia marina*; *Triglochin maritima*
	K	Metcalf	*Atriplex patula; Cuscuta salina; Distichlis spicata; Salicornia virginica; Triglochin maritima**; *Trifolium wormskjoldii*†
Salicornia	L	Collver Pt. Valino Is.	*Cuscuta salina*; *Distichlis spicata*; *Salicornia virginica**
	M	Metcalf Valino Is. Hidden Crk.	*Atriplex patula*; *Deschampsia caespitosa*; *Distichlis spicata*; *Jaumea carnosa**; *Salicornia virginica*; *Spergularia marina**; *Triglochin concinna*; *Triglochin maritima*

* Significant indicator species for the subgroup ($p < 0.01$), † Significant indicator species for the subgroup ($p < 0.10$)

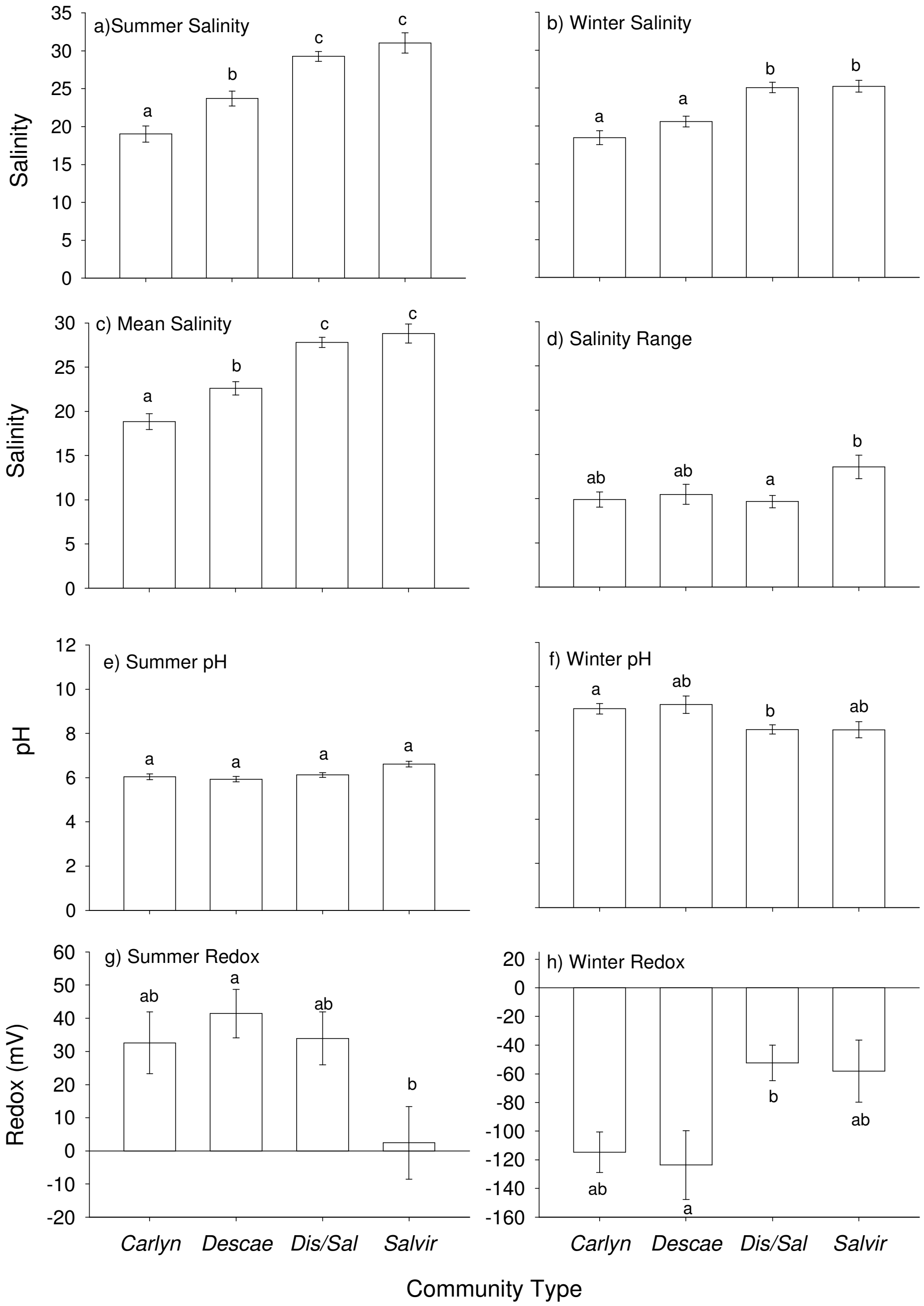

Figure 2.5. Mean values for calculated averages of salinity in g/kg (a-d), pH (e, f) and redox potential (g, h) throughout all six marshes for the four major community types. Error bars represent standard error of the mean. Results of Kruskal-Wallis variable by community type: a) χ^2 =53.60, p<0.001, b) χ^2 =37.10, p<0.001, c) χ^2 =58.03, p<0.001, d) χ^2 =8.434, p=0.04 e) χ^2 =12.76, p=0.005 f) χ^2 =7.59, p=0.135 g) χ^2 =4.42, p=0.22, h) χ^2 =7.01, p=0.07. For each variable, bars with different letters are statistically different (post hoc: Games-Howell p<0.05). Overall mean and range for pH and redox were omitted as community types did not differ.

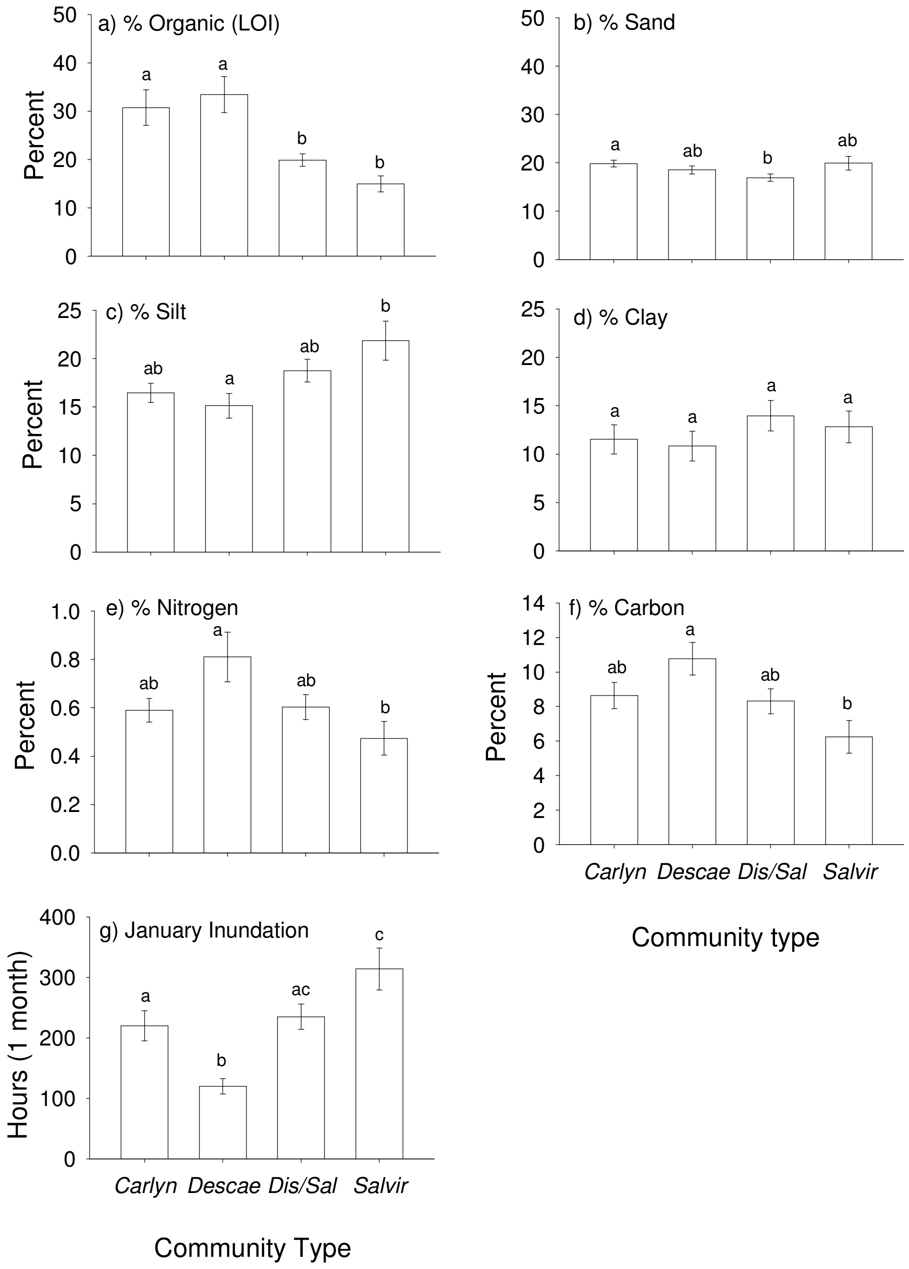

Figure 2.6. Mean values for calculated averages of sediment characteristics and January inundation throughout all six marshes for the four major community types. Error bars represent standard error of the mean. Results of Kruskal-Wallis variable by marsh: a) $\chi^2 = 20.79$, $p<0.001$, b) $\chi^2 = 8.48$, $p=0.04$, c) $\chi^2 = 11.29$, $p=0.01$, d) $\chi^2 = 7.70$, $p=0.06$ e) $\chi^2 = 10.79$, $p=0.01$ f) $\chi^2 = 13.23$, $p=0.004$ g) $\chi^2 = 26.81$, $p<0.001$. For each variable, bars with different letters are statistically different (post hoc: Games-Howell $p<0.05$). Note: range of Y-axis varies between plots.

Deschampsia Community Type

The *Deschampsia* community type was separated into three subgroups (F, G, and H) by the cluster analysis (Figure 2.3). Group H had higher total yield than the other two groups in the *Deschampsia* community type, but the difference was not significant (Figure 2.4). Summer and mean salinity within this community differed significantly from the other three community types (Figure 2.5a, c). pH values within the *Deschampsia* community type were generally intermediate between, but not statistically different from those measured in the *Carex* community and the *Distichlis*/*Salicornia* and *Salicornia* types (Figure 2.5e, f). The measured redox potential was significantly higher (more oxidizing) in this community during the summer than in the *Salicornia* community and was significantly more reducing than the *Distichlis/Salicornia* community in the winter (Figure 2.5g, h). The *Deschampsia* community type experienced statistically less inundation in January than the other communities (Figure 2.6).

Distichlis/Salicornia Community Type

This community type was separated into three subgroups (I, J, and K) by the cluster analysis (Figure 2.3) and occured in the four marine and mesohaline marshes closest to the mouth of Coos Bay (Metcalf, Collver Pt., Valino Is., and Hidden Creek; Figure 2.1, Table 2.1). Within all community types, group J had low overall yield compared with all subtypes, but differed only from subgroups A (*Carex* type) and H (*Deschampsia* type) (Figure 2.4). Summer, winter and mean salinity were higher within the *Distichlis*/*Salicornia* community type and were higher than either the *Carex* or *Deschampsia* community type, but were similar to the *Salicornia* type (Figure 2.5a-c). The salinity range within the *Distichlis/Salicornia* community was significantly lower than in the *Salicornia* community (Figure 2.5d). The winter pH was slightly lower than the pH measured in other community types, but was only significantly different from the *Carex* communities (Figure 2.5f). The *Distichlis*/*Salicornia* community type had the least reducing winter redox potentials overall, but was only significantly different from the *Deschampsia* communities (Figure 2.5h). Most of the sediment characteristics within this community type were not significantly different from those within the other community types (Figure 2.6). However, the *Distichlis*/*Salicornia* community type had significantly lower percent sand than the *Carex* community and significantly lower percent organic than either the *Carex* or *Deschampsia* community types (Figure 2.6a, b).

Salicornia Community Type

The *Salicornia* community type was divided into only two subgroups (L and M) (Figure 2.3, Table 2.1). The total yield of groups within the *Salicornia* community was not significantly different from other groups (Figure 2.4). The summer, winter and mean salinity were higher within this community type compared to the *Carex* and *Deschampsia* communities (Figure 2.5a-c), but pH was not significantly different from the other community types (Figure 2.5e, f). The *Salicornia* communities experienced more reducing sediment conditions than the *Deschampsia* community during the summer months (Figure 2.5g). Winter redox potential within the *Salicornia* community did not differ from the other communities (Figure 2.5h). The *Salicornia* type community developed in sediments with the highest percent silt and January inundation time as well as the lowest percent carbon and percent nitrogen (Figure 2.6).

In summary, the *Salicornia* community type experienced high salinity values relative to the other community types as well as a large range in salinity values (Figure

2.5) and longer inundation time (Figure 2.6). While the *Distichlis/ Salicornia* community also had high salinity, it had the smallest measured range of values. The soils associated with these two communities also had relatively low percent organic matter, percent nitrogen and percent carbon (Figure 2.6). Both the *Carex* and *Deschampsia* communities had relatively low measured pore water salinity, but highly variable redox potential, with weakly reducing environments in the summer and strongly reducing environments in the winter. Soils in both *Carex* and *Deschampsia* communities had high percent organic matter, percent nitrogen and percent carbon. The *Deschampsia* community type experienced the least inundation time of all communities within the marshes of South Slough.

Plant Community Structure and Environment

Relationships between plant community structure and environmental factors were evaluated using NMS ordination techniques (McCune and Grace 2002). An initial ordination based on cover data from all 121 plots resulted in a three dimensional model with a final stress of 10.57 after 126 iterations (Figure 2.7). These axes accounted for 92.6% of the total variation in the cover data matrix; Axis 1 accounted for 50.4%, Axis 2 31.2% and Axis 3 11.0%. Overall, the sample plots are arranged not only into the four major community types (*Carex, Deschampsia, Distichlis/Salicornia* and *Salicornia*) but also into subgroups. Axis 1 was positively correlated with salinity and redox potential (Table 2.2). The first axis was negatively correlated with winter and mean pH as well as percent organic matter and percent sand (Table 2.2). Species with high left oriented loadings on Axis 1 include *Agrostis stolonifera* and *Carex lyngbyei* (Figure 7a, c). Axis 2 was also positively correlated with salinity, percent silt, and inundation, but negatively with summer redox potential, percent organic matter, percent nitrogen and percent carbon (Table 2.2). Salt tolerant species, such as *Salicornia virginica* and *Spergularia marina* loaded more heavily toward the positive end of this axis (Figure 2.7a, b). The third axis accounted for relatively little of the variation in the overall community, but was positively correlated with percent organic and negatively correlated with winter salinity and inundation (Table 2.2). Regression analyses of the relationship among axes and environmental variables were different from correlations with the axes (Table 2.3). The model explained 50.2% of Axis 1, 47.6% of Axis 2 and 24.6% of Axis 3. The most important predictors of community type were summer salinity (Axis 1, Axis 2) and winter salinity (Axis 3) which reiterates the importance of pore water salinity on the distribution of different community types.

When plots within the *Carex* communities were separated into their own ordination model, two axes accounted for 83.5% of the variance of the community. Axis 1 accounted for 53.2% and Axis 2 accounted for 30.3% of the variance (Figure 2.8a). The overall stress of the ordination was 16.11 after 102 iterations. Axis 1 was negatively correlated with salinity and positively correlated with organic content and percent silt of the sediment (Figure 2.8a, Table 2.2). Axis 2 was positively correlated with organic content and winter pH, but negatively correlated with winter redox potential and inundation (Table 2.2). High marsh species loaded heavily at the positive ends of both axes (Figure 2.8a). Regression model for community structure based on environmental variables for axes position accounted for 44.6% (Axis 1) and 22.3% (Axis 2) (Table 2.3). Percent organic content and percent clay were the most important predictors for Axis 1 while percent sediment nitrogen was the only predictor for Axis 2.

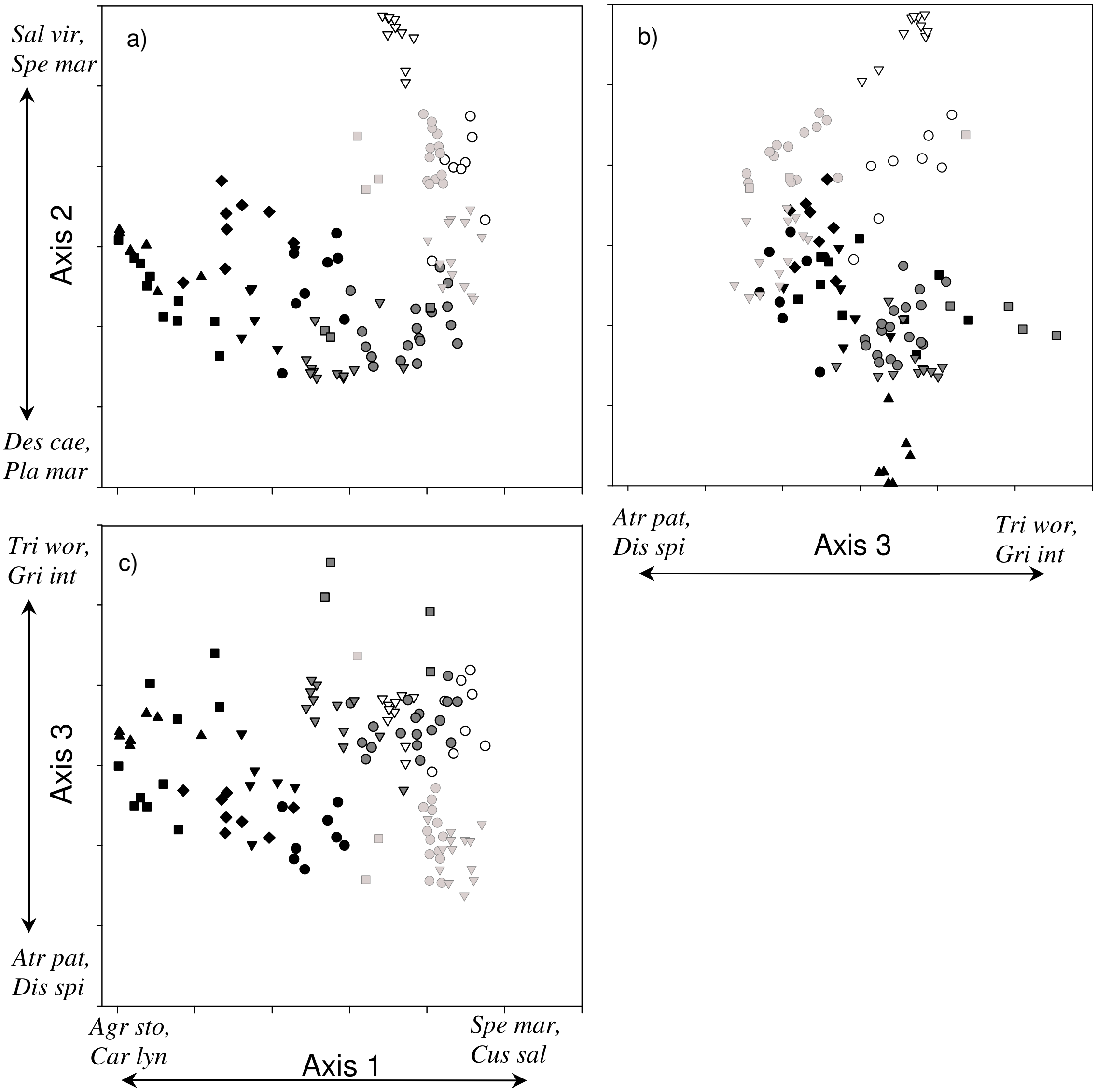

Figure 2.7. Three dimensional NMS representation of the salt marsh communities by sub-group of all six marshes based on percent cover. Axes represent 92.6% of the total variance. When indicated, species have increased presence (higher % cover) along the noted axis e.g. plots to the left along Axis 1 have higher percent cover of *Agrostis stolonifera* (*Agr sto*) and *Carex lyngbyei* (*Car lyn*) than those to the right. Other species: *Atriplex patula (Atr pat), Cuscuta salina (Cus sal), Distichlis spicata (Dis spi), Deschampsia caespitosa (Des cae), Grindelia integrifolia (Gri int), Plantago maritima (Pla mar), Salicornia virginica (Sal vir), Spergularia marina (Spe mar), Trifolium wormskjoldii (Tri wor).* Group symbols: A= ▲; B= ■; C= ◆; D= ▼; E= ●; F= ▼; G= ■; H= ●; I= ▽; J= ●; K= ■; L= ▽; M= ○. Dominant cover species for each group is indicated by shade of the symbol: black: *Carex lyngbyei*; dark grey/black outline: *Deschampsia caespitosa*; Light grey: *Distichlis spicata*; white/black outline: *Salicornia virginica.*

Table 2.2. Correlation coefficient (r) of given measured environmental variables against axes derived from NMS using arcsine square root transformed percent cover for all plots (All Cover) and plots dominated by the four primary marsh species. Environmental variables: mean summer pH (salinity, redox): Sum pH (Sal, Rdx); mean winter pH (salinity, redox); Win pH (Sal, Rdx); overall mean pH (salinity, redox): Mean pH (Sal, Rdx); sediment organic content based on LOI (% Organic); percent sediment particle size (% sand, % silt, % clay); sediment nitrogen (%N) and carbon (%N); inundation time January 7, 2008- February 8, 2008 (Inundation)

NMS Axis	All Cover			*Carex*		*Deschampsia*		*Distichlis/Salicornia*		*Salicornia*	
	1	2	3	1	2	1	2	1	2	1	2
Sum pH	0.082	0.357	-0.063	0.168	0.017	-0.096	-0.437*	0.226	-0.027	0.774*	0.195
Win pH	-0.307*	-0.312	0.097	0.179	0.330*	0.554**	0.256	-0.36	-0.043	0.167	-0.065
Mean pH	-0.190*	-0.037	0.052	0.245	0.159	0.401*	0.090	-0.333	-0.108	0.115	-0.238
Sum Sal	0.621**	0.503**	-0.018	-0.421*	-0.211	-0.783**	0.046	0.171	0.294	0.820*	0.354
Win Sal	0.583**	0.445**	-0.289*	-0.477**	-0.437**	-0.388*	-0.407*	0.483**	0.102	0.825*	0.194
Mean Sal	0.660**	0.523**	-0.114	-0.494**	-0.322	-0.780**	-0.125	0.391*	0.203	0.860*	0.301
Sum Rdx	0.018	-0.315*	0.036	-0.234	-0.164	0.079	0.473**	-0.222	0.127	-0.902**	-0.134
Win Rdx	0.319**	0.304**	-0.114	-0.203	-0.335*	-0.523**	-0.252	-0.089	0.213	-0.091	0.053
Mean Rdx	0.256**	0.062	-0.068	-0.25	-0.287	-0.470**	-0.034	-0.204	0.225	-0.550*	-0.034
% Organic	-0.391*	-0.366*	0.238*	0.429*	0.390*	0.534*	0.323	-0.525**	0.330	-0.370	0.138
% Sand	-0.246*	-0.115	0.156	0.222	0.121	0.601*	0.424*	0.233	-0.300	-0.250	-0.305
% Silt	0.036	0.314**	-0.006	0.343*	0.299	0.246	-0.122	0.109	-0.043	0.316	-0.556*
% Clay	0.053	0.180	-0.084	-0.057	0.267	0.201	-0.157	-0.355	0.035	0.413	-0.165
% N	0.040	-0.275*	0.013	-0.131	0.088	0.299	-0.242	-0.386*	0.228	-0.555*	-0.247
% C	-0.021	-0.336*	0.024	-0.089	0.003	0.340*	-0.154	-0.372*	0.185	-0.496*	-0.191
Inundation	0.093	0.310**	-0.245*	-0.099	-0.447**	0.770**	0.056	0.338	-0.395*	-0.628**	-0.508*

* p<0.05, ** p<0.005

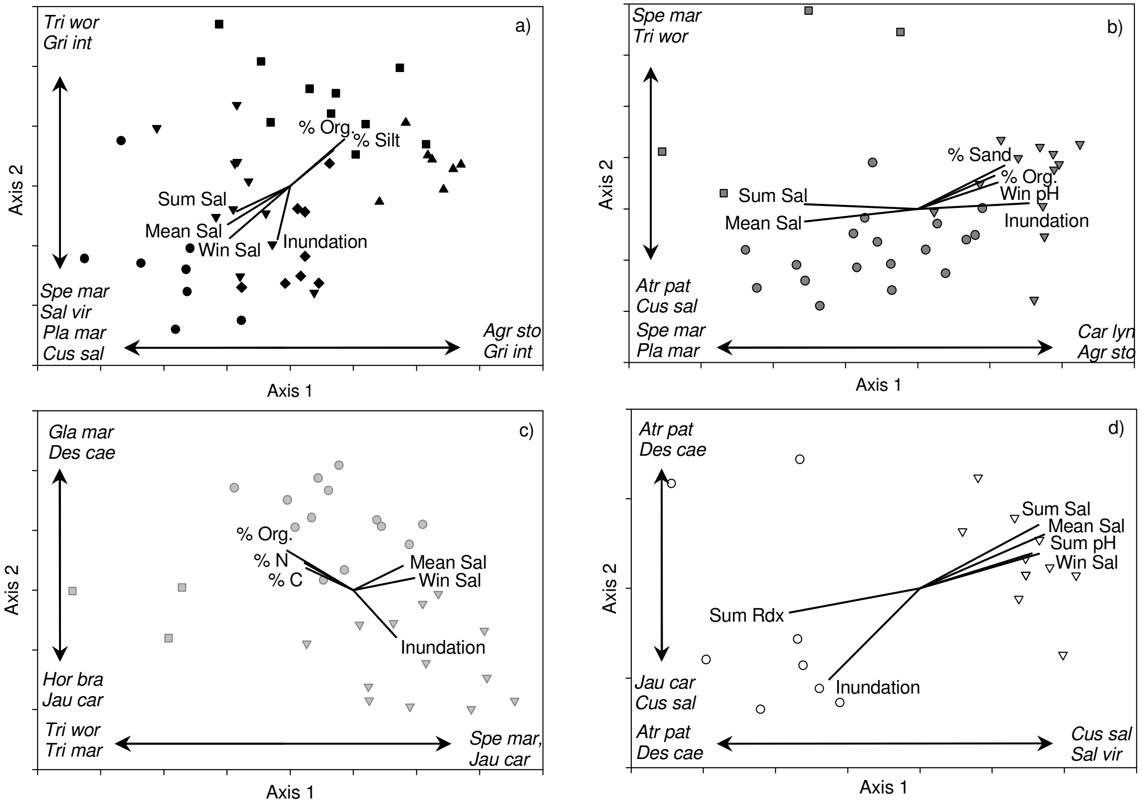

Figure 2.8. NMS ordination of communities by sub-group within community type a) *Carex*, b) *Deschampsia*, c) *Distichlis/Salicornia*, d) *Salicornia*. Axes represent a) 83.5%; b) 87.5%; c) 91.8%; d) 97.8% of the total variance for each distribution. Correlation vectors ($p<0.05$) at origin represent strength and direction of the relationships between the six most significant environmental variables and the axes. When indicated, species have higher % cover along the noted axis. Species: *Agrostis stolonifera*, *Atriplex patula, Carex lyngbyei*, *Cuscuta salina, Distichlis spicata, Deschampsia caespitosa, Grindelia integrifolia, Hordeum brachyantherum, Jaumea carnosa, Plantago maritima, Salicornia virginica*, *Spergularia marina, Trifolium wormskjoldii*. Group symbols: A= ▲; B= ■; C= ◆; D= ▼; E= ●; F= ▼; G= ■; H= ●; I= ▽; J= ●; K= ■; L= ▽; M= ○.

Table 2.3. Standardized coefficients of significant ($p<0.05$) predictors from backward regression of axes derived from NMS using arcsine square root transformed percent cover for all plots (All Cover) and plots dominated by the four primary marsh species. Environmental variables: mean summer pH (salinity, redox): Sum pH (Sal, Rdx); mean winter pH (salinity, redox); Win pH (Sal, Rdx); overall mean pH (salinity, redox): Mean pH (Sal, Rdx); sediment organic content based on LOI (% Organic); percent sediment particle size (% sand, % silt, % clay); sediment nitrogen (%N) and carbon (%N); inundation time January 7, 2008- February 8, 2008 (Inundation) Autocorrelated variables were not included in the analysis: pH range, mean salinity, summer redox, winter redox and mean redox removed.

		all			*Carex*		*Deschampsia*		*Distichlis/Salicornia*		*Salicornia*	
	NMS Axes	1	2	3	1	2	1	2	1	2	1	2
Predictor	Inundation	--	0.273	-0.281	--	--	--	0.317	--	--	-0.323	--
	Sum pH	--	0.333	--	--	--	-0.430	--	--	-0.409	-0.369	--
	Win pH	-0.119	--	--	--	--	--	--	--	--	0.355	--
	Mean pH	--	-0.185	0.208	0.272	--	--	--	--	-0.525	--	-0.589
	Sum Sal	0.400	0.393	0.266	--	--	--	--	--	-0.438	0.511	-0.475
	Win Sal	0.268	--	-0.342	--	--	--	--	--	0.563	--	--
	Range Sal	--	0.146	0.248	--	--	-0.295	--	0.311	0.468	0.297	-0.318
	Range Rdx	--	--	--	--	--	--	--	--	0.211	--	--
	%OrganicLOI	-0.207	--	--	0.536	--	--	0.636	-0.517	--	--	--
	% Sand	--	--	0.242		--	-0.430	--	0.719	-0.387	0.543	--
	% Clay	--	--	--	-0.493	--	-0.330	--	--	0.497	0.350	0.415
	% Silt	--	0.203	--	--	--	--	--	--	--	--	--
	% Carbon	0.246	--	--	--	--	--	-0.308	--	--	0.615	-2.193
	% Nitrogen	--	--	--	--	-0.479	-0.372	--	--	--	--	2.884
Model	Overall r^2	0.523	0.502	0.283	0.489	0.243	0.315	0.557	0.647	0.915	0.850	0.635
	Adjusted r^2	0.502	0.476	0.246	0.446	0.223	0.192	0.512	0.592	0.867	0.775	0.514

The ordination of the *Deschampsia* type returned two axes which accounted for 87.5% of the total variation in the cover data matrix, with 46.4% accounted for by Axis 1 and 41.1% by Axis 2 (Figure 2.8b). The overall stress was relatively low (15.31) after 125 iterations. Salinity (summer, winter and mean) and redox potential (winter and mean) were significantly negatively correlated with Axis 1 (Table 2.2). Summer pH negatively correlated while summer redox potential positively correlated with Axis 2. The introduced grass, *Agrostis stolonifera*, loaded positively on Axis 1 while the indicator species for group L, *Plantago maritima*, loaded negatively along the same axis (Figure 2.8b). Summer pH and percent sand were equally significant predictors for community structure along Axis 1, but the model only accounted for 19.2% of the variability. Percent organic content and inundation time predicted community composition along Axis 2 and the model accounted for 51.2% of the variability (Table 2.3).

The two dimensional NMS distribution (stress: 11.7, 104 iterations) of the *Distichlis/Salicornia* community type accounted for 91.8% of the variation in the community with 66.2% loaded onto Axis 1 and 25.5% onto Axis 2 (Figure 2.8c). Percent organic content, percent nitrogen, percent carbon, mean salinity and inundation correlated with these axes (Figure 2.8c, Table 2.2). Separation of plots in the *Distichlis/Salicornia* community was related to high cover contributions of *Jaumea carnosa* and *Spergularia marina* (positive of Axis 1) and plots with high cover contributions of *G. maritima* and *D. caespitosa* (positive of Axis 2). The regression model fit environmental variables to Axis 1 accounted for 59.2% of the variation in the cover data and was defined primarily by percent sand and percent organic content (Table 2.3). The relationship between Axis 2 and the environmental variables accounted for more of the variation (86.7%), and mean pH and winter salinity were the most significant predictors.

The distribution of *Salicornia* subtypes fit well into two dimensional space with a stress of 4.25 after 54 iterations (Figure 2.8d). The majority of variation in the community was described by two axes (97.8%) with 91.1% on Axis 1 and 6.7% on Axis 2. The community subgroups separated clearly with *Cuscuta salina* and *S. virginica* (indicator species, group K) loaded positively and clustered to the right on Axis 1. *Jaumea carnosa*, the indicator species for group M, negatively loaded onto Axis 2, with *C. salina* while *A. patula* and *D. caespitosa* contributed more cover in plots distributed toward the positive end of that axis (Table 2.1, Figure 2.8d). Inundation, percent carbon, percent nitrogen and mean redox potential were negatively correlated with Axis 1 while percent silt negatively correlated with Axis 2 (Table 2.2). Percent sand and percent sediment carbon were the most significant predictors for Axis 1 (77.5% of the variation) while percent nitrogen and percent carbon in the sediment were the best predictors for Axis 2 (51.4% of the variation; Table 2.3).

Discussion

Plant community composition in the South Slough estuary was strongly related to the intertidal gradient within marshes and other small-scale factors rather than to the location of the marsh. This was evident from the high variability within community types for each marsh and the general lack of large-scale patterns in marsh vegetation structure within the estuary.

Many of the subgroups identified by the cluster analysis had disjunct distributions within the slough (e.g. subgroups E and M were absent from Collver Pt. but present in

Metcalf, Valino Is. and Hidden Creek and subgroup G was present only in Valino Is. and Tom’s Creek; Table 2.1). This indicates that most of the community subgroups were not confined to one section of the slough as defined by the salinity of the water column (marine, mesohaline or riverine); only one (subgroup K) was found within a single section of the slough (Table 2.1, Figure 2.1). There were similarities between these observed community types and early salt marsh observations from the region (Jefferson 1975, Hoffnagle 1976, Hoffnagle 1980, Taylor 1983, Rumrill and Sowers 2008). In contrast to the current study, Rumrill and Sowers (2008) found marsh communities in the lower estuary to be more similar than to a riverine marsh. In the present work, marshes located within the same region of the slough did not necessarily have the same types of communities. Additionally, vegetation development was more a function of the environmental characteristics of the patches within the marsh than the position of the marsh along the estuarine salinity gradient.

Unlike previous ordination studies of marshes (e.g. Schroder et al. 2002, Silvestri et al. 2005, Capers and Les 2005, Peirnik 2005), the NMS ordination accounted for the majority of the variation within the plant community cover data (Figure 2.7). Salinity, inundation duration and organic matter were important in determining the community type of the vegetation based on the NMS distribution of communities (Figures 2.7, 2.8). These factors correlated more often with the NMS axes (Table 2.2), but only salinity consistently contributed to regression models (Table 2.3). Sediment texture, percent nitrogen and percent carbon in the sediment were important predictors (Tables 2.2, 2.3). Although the other abiotic factors measured were variable, they contributed less to the overlying community structure.

In support of the secondary hypothesis that community types would be associated with particular ranges in abiotic factors, the four major community types described in the current study were primarily determined by their physical tolerances and were found in areas characterized by different abiotic conditions (Figures 2.5, 2.6). The *Carex* community type was generally found in less saline and slightly more basic environments (Figure 2.5). The annual biomass within the *Carex* community was similar to biomass from previously sampled *Carex lyngbyei* dominated communities within South Slough (Gilman 1993). The pH values observed for this community were similar to those reported for a diked marsh (Taylor 1983), but were more basic than other reported values (Stephens and Billings 1967). Previous studies indicate that *C. lyngbyei* does not tolerate anoxic conditions (Ewing 1986), however, this species is common in the lower riverine marshes of South Slough (Danger Point and Tom's Creek), occasionally under waterlogged conditions (Stephens and Billings 1967, Campbell and Bradfield 1989). In the current study, *Carex* dominated communities grew in sediments which were strongly reduced during the winter (Figure 2.5).

The low marsh/low slough communities, *Distichlis/Salicornia* and *Salicornia*, were found under the most saline conditions. Dominance in highly saline environments is common for other species within the same family as *Salicornia* (Chenopodiaceae) (Ewing 1983, Rogel et al. 2000, Piernik 2005), but the group is also commonly limited by low redox potentials (Schat et al. 1987). These low marsh communities had less variation in redox potential by season, and though frequently inundated, the sediments were less reducing than the higher marsh communities in the winter.

The high marsh community types (*Carex* and *Deschampsia*) were impacted by salinity and other pore water characteristics. Based on the average condition of the environment (Figures 2.5, 2.6), it is apparent that the salinity and duration of inundation influence the extent of particular vegetation types within the six study marshes, particularly the distribution of *Carex* and *Deschampsia* dominated communities. These high marsh communities were present in the lower estuarine (marine) marshes, but they were limited to the upper edges of the lower estuarine (marine) marshes.

Salinity and soil texture were important factors in determining community structure in the South Slough marshes. These factors have been shown to be predictors of growth and distribution in other marshes (Ewing 1983, Ewing 1986). Salinity, in particular, has been associated with community structure and distributions (Jefferson 1975, Hutchinson 1982, Vince and Snow 1984, Baldwin and Mendelssohn 1998, Schroder et al. 2002, Bantilan-Smith et al. 2009). High levels of salinity can have strong negative consequences even for species adapted to saline environments including decreased total chlorophyll and efficiency of photosynthesis (Lee et al. 2004), but the effect can be somewhat ameliorated when sediments have high nutrient and oxygen availability (Lindthurst and Seneca 1981). Lower species richness in low marsh communities and the strong correlation between the distributions of the *Distichlis/Salicornia* and *Salicornia* communities suggest that salinity has a major impact in the marshes within South Slough (Figure 2.8, Table 2.1, 2.2, Appendix B). This observation is consistent with earlier observations of decreased taxonomic richness in salt marsh plant communities at lower tidal elevations within the South Slough estuary (Ewing and Seebacher 1997, Rumrill 2006)

Inundation and redox potential are closely associated and both had a significant impact on the distribution of communities within the South Slough marshes (Figure 2.8, Tables 2.2, 2.3). Under inundated conditions, atmospheric oxygen is slow to replenish oxygen lost at depths within the sediment greater than 5-10 mm (van Diggelen 1991), so plant roots are quickly subjected to reduced sediment conditions (Armstrong 1978, Gambrell and Patrick 1978, Thomas et al. 2009). Inundation has been shown to be a major factor dictating community structure in many marsh studies from other locations (Mahall and Park 1976, Vince and Snow 1984, Bertness and Ellison 1987, Campbell and Bradfield 1989, van Diggelen 1991, Grace and Jutila 1998, Kunza and Pennings 2008). Likewise, redox potential has been closely associated with species distributions (Lindthurst and Seneca 1981, Adam 1990, Baldwin and Mendelssohn 1998, Schroder et al. 2002, Bantilan-Smith et al. 2009, Alberti et al. 2010) and is highly dependent on season as well as the presence or absence of vegetation (Ewing 1986, Koretsky et al. 2003, 2005, Bhattacharjee et al. 2009). Low redox potentials decrease biomass production (Lindthurst 1979, Howes et al. 1981, Glough and Grace 1998). Despite the high frequency and duration of inundation, the *Distichlis*/*Salicornia* and *Salicornia* communities experience redox potential levels that were less variable across seasons than within the *Carex* or *Deschampsia* communities (Figure 2.5). This is likely due to the regular tidal flushing of those portions of the marsh, which re-oxygenates the sediment (Silvestri et al. 2005).

Previous work by Gilman (1993) described longer inundation periods for the low marsh communities (*Distichlis/Salicornia* and *Salicornia*) than I calculated in the current study. However, the method used to determine inundation time differed significantly.

Gilman extrapolated inundation time from observation of the tide in the field while I compared precise elevations to known tidal elevation data. It is possible that my estimates were slight overestimates in the high marsh communities due to a small degree of lag associated with friction of the inundating water against the marsh plants. However, I do not believe that these minor differences would appreciably alter the inundation times calculated for this study.

pH was relatively stable within the marshes of South Slough, but values were slightly more basic during the winter and slightly more acidic in summer (Figure 2.5). This pattern is consistent with observed seasonal patterns in pH within saturated sediments (Koretsky et al. 2006). Within marshes of South Slough, pH did contribute to the structure of community and was correlated with the distribution of the *Deschampsia* community (Table 2.2). This abiotic factor is usually fairly consistent through time between and among sites in salt marshes (Bertness and Ellison 1987, Koretsky et al. 2006) and can contribute significantly to the structure of plant communities (Rogel et al. 2000, Piernik 2005).

Sediment texture was a particularly important predictor of the presence of the *Distichlis/Salicornia* community type. In previous studies sediment texture has been linked with marsh community structure (Ayyad and El-Ghareeb 1982, Earle and Kernshaw 1989, van Diggelen 1991, Middelburg et al. 1997, Zhou et al. 2007). Ewing (1986) considered soil texture to be an important predictor of community development only in less saline environments. In contrast, sediment texture was more important in the low marsh (more saline) communities of South Slough (Table 2.3). Finer sediments collect in the higher portions of the marsh (Adam 1990), and these areas are often associated with organic content (Ewing 1983, Zhou et al. 2007). High organic content (percent carbon) is usually associated with high marsh communities (Figure 2.6; see also Ewing 1983, Cartaxana and Catarinno 1997, Bhattacharjee et al. 2009) and is often observed to be highly correlated with community structure (Ewing 1983, Tyler et al. 2003, Capers and Les 2005).

Percent nitrogen in the sediment was significantly related to the *Salicornia* community type (Table 2.3). While many previous studies have indicated the importance of nitrogen in determining plant communities (Valiela and Teal 1974, Lindthurst 1979, Lindthurst and Seneca 1981, Cartaxana and Catarinno 1997, Tyler et al. 2003, Sala et al. 2008, Orwin et al. 2010), others show weak correlation with this factor (Boyer and Zedler 1999, Alberti et al. 2010). Salt marshes are commonly nitrogen limited, as illustrated by studies showing increased biomass with added nitrogen (Boyer and Zedler 1999, Orwin et al. 2010). Concentrations of nitrogen in the sediment were low in salt marshes in South Slough (Figure 2.6). However, nitrogen addition studies in Oregon salt marshes have not supported the hypothesis that nitrogen is a limiting resource in these marshes (J. Kaldy, personal communication).

The distributions of the four major community types in South Slough salt marshes were affected by small-scale intertidal and within-marsh factors. However, salt marsh communities in South Slough were complex and varied. The dominance and distribution of communities did shift along the estuarine salinity gradient from marine-dominated marshes largely covered by salt tolerant species, to communities with higher species richness and reduced salt tolerance, which dominate the riverine marshes. Along the estuarine salinity gradient, community types developed in areas with particular ranges of environmental variables of which salinity, pH and sediment texture were particularly important.

Bridge I

Chapter II described the relationship between the emergent marsh communities and the gradient of abiotic factors present in the salt marshes along the estuarine salinity gradient in South Slough. The abiotic environment is not, however, the only important factor which contributes to the structure and composition of salt marshes; interactions between plants can also have a strong impact on marsh structure. Chapter III focuses on the competitive interactions of three of the dominant emergent marsh species within and between the high and low marsh zones in a marine-dominated marsh.

CHAPTER III

ROLE OF COMPETITION IN MAINTAINING THE HIGH/LOW MARSH BOUNDARY IN A MARINE SALT MARSH

Introduction

The zonation patterns exhibited by salt marsh plant communities have long been of note to ecologists (Chapman 1960, Adams 1963). Early work attributed the zonation patterns of the gradient to abiotic stresses, such as salinity and anoxia, which are associated with periods of tidal inundation (Chapman 1960, Adams 1963, Cooper 1982). Lower areas of salt marshes are inundated more frequently and for longer periods than the higher elevations of the marsh. Although these abiotic stresses have been shown to contribute to zonation (Huckle et al. 2000, La Peyre et al. 2001, Sanderson et al. 2008), interactions between the plants have also been shown to be important determinants of these patterns (Austin and Austin 1980, Pennings and Callaway 1992, Gaudet and Keddy 1995, Ungar 1998). Biotic and abiotic factors have generally been shown to influence zonation in predictable ways. That is, the upper boundary for a particular species within a marsh is dictated by biotic interactions with other species, usually competitive, while the lower boundary of a species is determined by the physiological tolerances of that species to the abiotic stresses associated with the low marsh environment (Snow and Vince 1984, Bertness and Ellison 1987, Keddy 1989, Bertness 1991, Pennings and Callaway1992, Sanderson et al. 2008, Luo et al. 2010). Tolerance to stressful conditions is thought to be a trade off with competitive ability (Grime 1977, Ungar et al. 1979, Grace 1990, Huckle et al. 2000, Emery et al. 2001). Conditions of high stress (e.g. salinity and extreme temperatures) may restrict the ability of plants to acquire necessary resources such as light, water and nutrients and therefore limit productivity (Grace 1991, Callaway and Walker 1997, Elmendorf and Moore 2007).

Competition, the utilization of shared resources in short supply (Grace 1960), is an important factor that affects the structure of plant communities. The dynamics of competitive interactions are known to differ along gradients in productivity (Wilson and Keddy 1986, Wilson and Tilman 1991, Gaudet and Keddy 1995, Twolan-Strutt and Keddy 1996, Peltzer et al. 1998) succession (Parrish and Bazzaz 1982) and salinity (Snow and Vince 1984, Bertness and Shumway 1993, Crain et al. 2004). Salt marshes are particularly conducive to experimentation with competition across natural stress gradients (Bertness and Ellison 1987, Bertness 1991, Bertness and Shumway 1993). Removal experiments conducted in salt marshes at the boundary between community zones demonstrate that removal of upper marsh neighbors allows low marsh species to expand toward the upland edge of the marsh. These field experiments indicate that under natural conditions, low marsh species are competitively excluded from the more benign environment of the upper marsh habitats (Bertness and Ellison 1987, Bertness 1991, Shevtsova et al. 1995, Levine et al. 1998, Dormann et al. 2000, Pennings et al. 2002).

This phenomenon, sometimes called ‘competitive-physiological-exclusion’ (Bockelmann and Neuhaus 1999) has been observed in several salt marshes along the Atlantic coast (Bertness and Ellison 1987, Bertness 1991, Gerry and Wilson 1995, Pennings et al. 2002). This concept has not, however, been widely explored in Pacific coast salt marshes (Snow and Vince 1984, Seliskar 1985, Taylor et al. 1997). Salt marshes along the West Coast of the United States are generally small pocket and fringing marshes within estuaries. Within the South Slough of the Coos Bay estuary in

Oregon, salt marshes close to the mouth of the estuary are dominated by very few species which clearly divide the marshes into horizontal swaths that differ in intertidal elevation (Chapter II). The primary purpose of this study was to explore though a reciprocal transplant experiment, the role of competition in maintaining the boundary between the high and low marsh. If the generalized 'competitive-physiological-exclusion' theory is correct, then two predictions should be fulfilled; specifically, (i) high marsh dominant species transplanted to the low marsh should exhibit decreased biomass and growth compared to high marsh transplants and (ii) low marsh species transplanted to the high marsh habitat should exhibit increased growth when high marsh neighbors are removed.

Methods

Site Description

Metcalf marsh is a marine salt marsh located near the mouth of the South Slough in the Coos Bay estuary, Oregon (Chapter II, Figure 2.1, Appendix A). This small pocket marsh is located 4.4 km from the mouth of Coos Bay and is frequently inundated with seawater, which ranges in salinity seasonally from 20 to 31 g/kg. Most of the marsh is covered by the low marsh community type which is dominated by the highly salt tolerant chenopod herbaceous forb, *Salicornia virginica* (pickleweed; hereafter '*Salicornia*') intermixed with the grass, *Distichlis spicata* (spikegrass; hereafter '*Distichlis*'). These two species account for most of the cover in the low marsh (1.9 m – 2.0 m NAVD), though other salt tolerant species such as *Atriplex patula* and *Jaumea carnosa* also occur under the condition of regular periods of tidal inundation. The high marsh (2.1 m- 2.2 m NAVD) is dominated primarily by the sedge, *Carex lyngbyei* (slough sedge; hereafter '*Carex*'), which co-occurs with patches of the bunchgrass (*Deschampsia caespitosa*) and associated species (Chapter II). The two communities are separated by a distinct boundary, which delineates the high marsh from the low marsh.

Experimental Transplant Design

To evaluate the role of competition in maintaining the boundary between the high and low marsh species, in the spring of 2009 and 2010 I conducted reciprocal transplants of the three major species (*Carex, Salicornia* and *Distichlis*). Growth of the transplanted individuals was monitored throughout each growing season. For each species, individual ramets were transplanted into both vegetated (n=8) and artificially cleared (n=8) plots in the high and low marsh (Figure 3.1). Ramet is defined here as the functional unit for a plant, usually a section of root or rhizome with some aboveground tissue (Keddy et al. 2002). In the case of *Carex* and *Distichlis*, the aboveground tissue generally consisted of several leaves, while for *Salicornia*, the aboveground portion was a section of stem bearing one or two succulent lateral branches. In 2010, larger plugs of *Distichlis* 'sod' (5-10 connected ramets) were also transplanted (Appendix C).

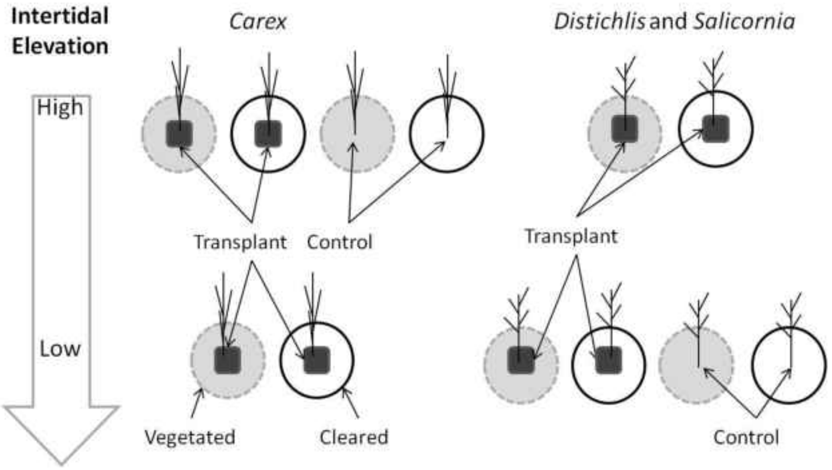

Figure 3.1. Experimental design of reciprocal transplant of three species (*Carex lyngbyei*, *Distichlis spicata* and *Salicornia virginica*) in two intertidal elevations (High and Low) into cleared (empty circles) and vegetated (filled circles) plots. Controls were established in high (*Carex*) and low (*Distichlis* and *Salicornia*) marsh intertidal elevations.

The cleared plots were created six weeks prior to transplanting by removal of all aboveground vegetation in a 30 cm diameter area. Sediment was removed to a depth of approximately 20 centimeters and all large root and rhizome material was manually removed before sediment was replaced. To prevent re-incursion of the cleared plot by neighboring vegetation, a plastic ring (30 cm diameter, 6 cm height) was inserted into the sediment until the ring was level with the marsh surface. In late spring (May 2009, April 2010) individual plants that were previously established in the marsh were transplanted into cleared and vegetated plots in the high and low marsh. For the vegetated treatment, transplanted individuals were inserted into existing vegetation with minimal impact to the neighboring plants. For each species (*Carex*, *Salicornia* and *Distichlis*), 32 transplant plots were created (8 each for vegetated and cleared plots in the high and low marsh). In addition, control plants (n=8) for each species were monitored (Figure 3.1). These were marked for identification, but were left with existing neighboring vegetation (vegetated control). In 2010, a cleared control treatment was added where a plastic ring was inserted around the chosen control ramet and all neighboring vegetation within the 30 cm diameter was clipped at ground level. Below ground competition was not eliminated as this would have disturbed the control individual. The controls (both vegetated and cleared) for all species occurred only in the high (*Carex*) or the low (*Salicornia* and *Distichlis*) marsh where growth of each species occurs naturally. All transplants were monitored bi-weekly throughout the growing season. At the conclusion of the summer growing season (end of August 2009, 2010), transplanted and control individuals were harvested (clipped at sediment surface), dried to constant mass (approximately 24 hours) at 80°C (Huckle et al. 2002) and weighed.

At the conclusion of the study, measurements of biomass (dry grams) and plant growth (mm/day) were used to evaluate differences between high and low, vegetated and cleared treatments. Plant growth was calculated as the increase in total height from the beginning of the experiment to the period of peak plant height (millimeters) divided by the number of days to that point. The date of peak height differed between years and between species. Peak height for *Carex* occurred in early July 2009 and the end of August 2010 while the peak height for *Salicornia* and *Distichlis* occurred at the end of August both years.

Differences between treatments for each species were examined with separate two-way ANOVAs with intertidal elevation (low, high or control) and vegetation (vegetated or cleared) as fixed factors. Distribution of biomass data for all three species in both years was non-normal, which violated the assumption of homogeneity of variance for the ANOVA. To reduce the increased likelihood of Type I errors associated with this violation, the alpha was changed to the more stringent level of $\alpha = 0.025$ (Keppel and Wickens 2004, Gamst et al. 2008). Similarly, in 2009, the growth rate data for *Distichlis* were non-normal even after transformation (square root), so again, the alpha was adjusted to $\alpha = 0.025$. For both years, *Carex* growth rate was transformed to fit assumptions (2009: fourth root transformed, 2010: square root transformed). Growth rate of *Salicornia* did not require transformation in either year nor did the growth rate of *Distichlis* in 2010.

In addition to comparison of growth factors, the effect of neighboring vegetation on the biomass of the transplanted individual was examined using an index of Relative Neighbor Effect (RNE) based on the measurements of dry biomass at the conclusion of the field experiment (Markham and Chanway 1996, Goldberg et al. 1999). It should also be noted that comparisons between vegetated and cleared plots allows for an evaluation of apparent competition as other effects of neighboring vegetation are possible, such as impact of herbivory or likelihood of mycorrhizal infection. For this reason, the relative effect of the neighboring vegetation was measure with RNE. This was calculated as:

$$\text{RNE}= (X_{\text{vegetated}}-X_{\text{cleared}})/\max\ (X_{\text{vegetated}} \text{ or } X_{\text{cleared}})$$

where X is dry biomass of the target individual at the conclusion of the study from either the plots with existing vegetation ($X_{\text{vegetated}}$) or the cleared plots (X_{cleared}). The denominator of the equation, based on the maximum value of either the vegetated or cleared plot, creates a symmetric distribution of possible values around zero from -1 to 1 (Armas et al. 2004). Negative values of RNE indicate competitive interactions while positive values of RNE indicate positive interactions (facilitation) between the transplanted individuals and the existing vegetation. RNE values close to zero indicate no effect of existing vegetation. The mean RNE based on the dry mass of the transplants ($\text{RNE}_{\text{biomass}}$), for each species was compared to zero with a one-sided t-test.

Results

The elevation within the salt marsh (height) and presence or absence of neighboring vegetation had a significant effect on the growth rate and the dry mass of the transplanted species in both years (Table 3.1). The effect of intertidal elevation was significant for *Carex* only in 2009, when the control plants had significantly more biomass at the end of the growing season (Figure 3.2 a, b). In 2010, though neither the effect of intertidal elevation nor the effect of vegetation was significant for *Carex*, a significant interaction between the two occurred (Table 3.1) indicating a difference in the impact of neighboring vegetation depending on the intertidal elevation of the transplant.

The overall mass of *Salicornia* at the end of the growing season was significantly impacted by intertidal elevation and the interaction of elevation and neighboring vegetation in both years (Table 3.1, Figure 3.2 c, d). In the low marsh, individuals transplanted into cleared areas exhibited significantly greater biomass at the end of the season than those growing with neighboring vegetation. However, the presence of neighbors did not impact the growth of *Salicornia* in the high marsh (Figure 3.2 c, d). In 2010, *Distichlis* transplanted within the low marsh exhibited higher mass at the end of the season (Table 3.1), though the effect was only significant for individuals without neighboring vegetation (Figure 3.2f). *Distichlis* 'sod' transplants exhibited similar growth patterns to the individual *Distichlis* ramets (Appendix C). Overall dry mass for all three species at the end of the growing season was higher in 2010 than in 2009, most likely due to interannual differences in the local climate.

Table 3.1. ANOVA (F-ratio) results for full model (all treatments separately), intertidal elevation (low, high, control), vegetation (cleared, vegetated) and the interaction of elevation and vegetation (E x V) for all three species in both years.

Species	df		*Carex*		*Salicornia*		*Distichlis*	
Year	2009	2010	2009	2010	2009	2010	2009	2010
Sources of Variation								
Dry mass								
Model	4	5	9.610**	2.557	18.239**	14.587**	15.974**	4.942**
Elevation	2	2	17.165**	1.513	11.755**	13.824**	28.401**	9.545**
Vegetation	1	1	0.311	1.694	24.205**	0.095	1.137	0.050
E x V	1	2	0.311	4.033†	18.843**	22.595**	2.707	2.786
Error	35	42						
Growth rate								
Model	4	5	15.206**	10.091**	3.845*	4.045**	3.284†	2.800*
Elevation	2	2	26.365**	23.270**	1.238	0.602	6.036†	6.640**
Vegetation	1	1	1.097	0.733	4.098*	6.952*	0.795	0.007
E x V	1	2	4.016	1.085	5.002*	4.662*	0.639	0.356
Error	35	42						
$RNE_{dry\ mass}$								
Elevation	1	2	0.253	1.606	4.242	8.079**	0.695	0.316
Error	14	21						

** $p<0.005$; † $p<0.025$; * $p<0.05$

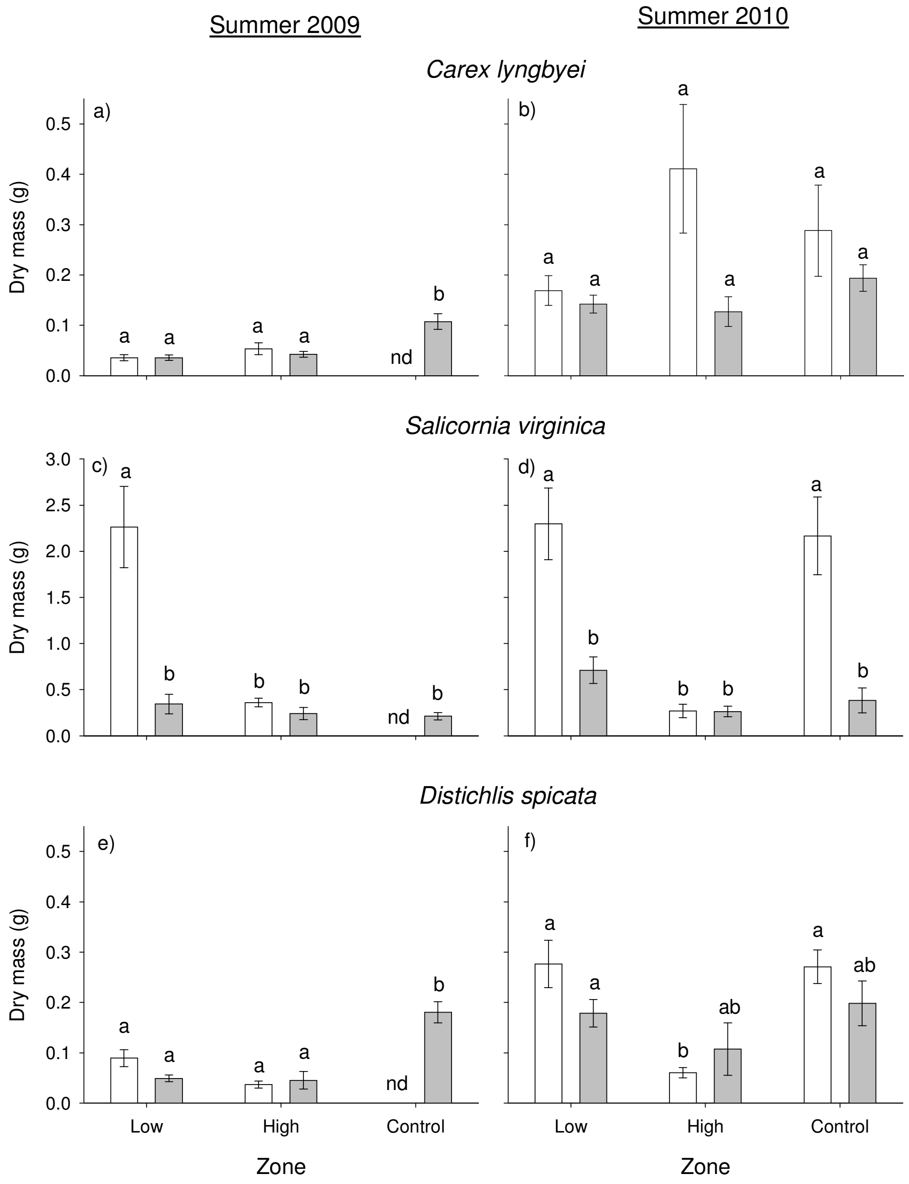

Figure 3.2. Biomass (dry grams) of the three transplanted species (*Carex*: a, b; *Salicornia*: c, d; *Distichlis:* e, f) at the conclusion of the summer growing season for both years in cleared (empty bars) and vegetated (filled bars) plots at two intertidal levels (low and high) and the control. Each bar represents mean (n=8) ± 1SE. Bars with the same letter above do not differ significantly (Tukey post hoc, $p<0.05$). There was no cleared control treatment in 2009 (nd).

Intertidal elevation had a significant effect on the overall growth rate of *Carex* in both years (Table 3.1, Figure 3.3 a, b); transplanted and control individuals grew more rapidly in the high intertidal zone than in the low marsh zone in 2010 (Figure 3.2 a, b). The presence of neighboring vegetation had a significant effect on the growth rate of *Salicornia* in both years (Table 3.1, Figure 3.3 c, d). The interaction between intertidal elevation and neighboring vegetation was also significant in both years because the presence of neighboring vegetation had an impact on growth in the low intertidal (low and control), but not in the high intertidal (Figure 3.3 c, d). The growth rate of *Distichlis* was significantly affected by intertidal elevation in both years (Table 3.1). In both years, control plants grew more quickly than some of the transplanted individuals (Figure 3.3 e, f). Low marsh transplants grew more rapidly than high transplants in 2010, but not in 2009 when the stress of transplanting seemed to have had a greater impact (Figure 3.3 e, f).

The effect of neighboring vegetation (RNE) differed among species and intertidal elevations (Table 3.1, Figure 3.4). In the high intertidal, neighboring vegetation significantly impacted the biomass of transplanted *Carex* in 2010, but not 2009 (Figure 3.4 a, b). Control individuals were not significantly affected by neighboring vegetation, possibly due to the fact that only aboveground competition was eliminated. Low marsh vegetation significantly competed with small *Salicornia* (both transplanted and control) in both years (Figure 3.4 c, d). Neighboring vegetation did not significantly impact the biomass of *Distichlis* in either year or at either intertidal elevation (Figure 3.4 e, f).

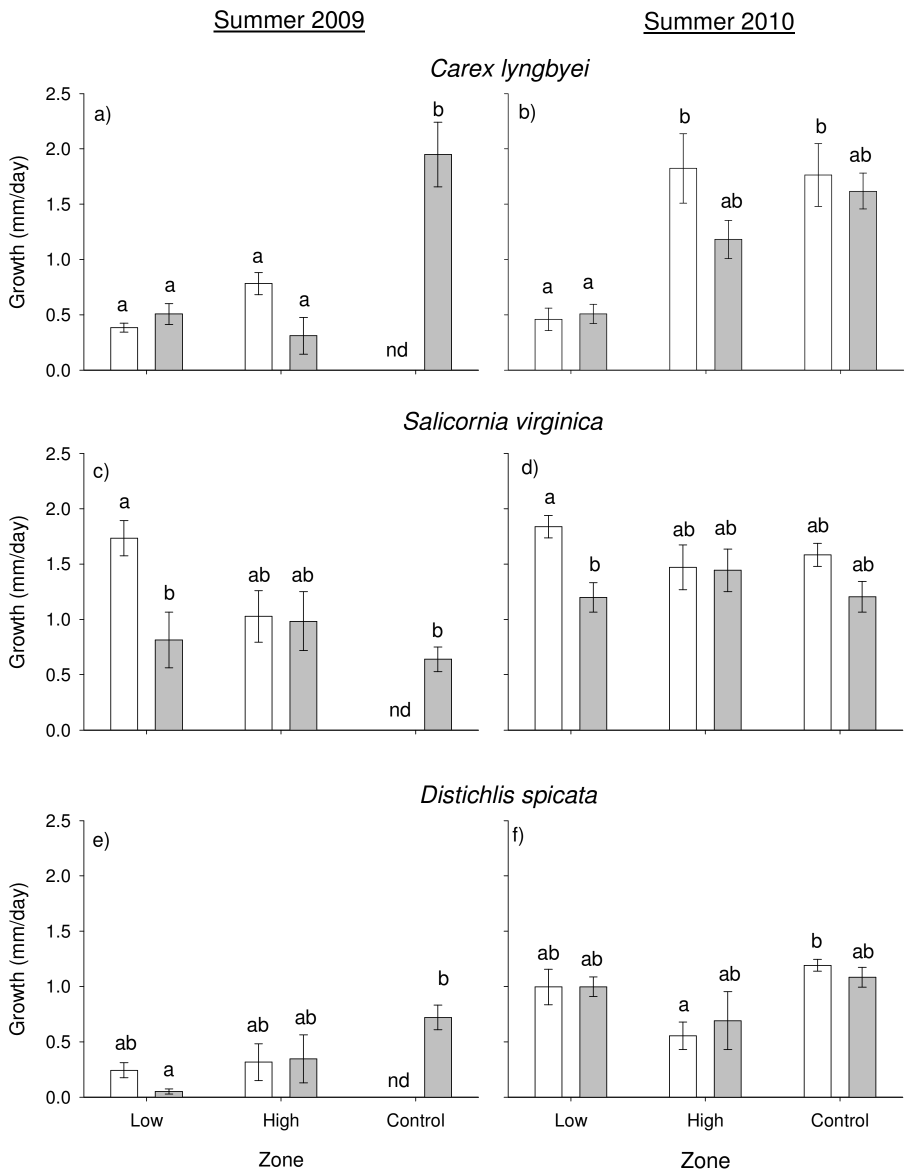

Figure 3.3. Growth (mm/day) of the three transplanted species (*Carex*: a, b; *Salicornia*: c, d; *Distichlis:* e, f) over the summer growing season for both years in cleared (empty bars) and vegetated (filled bars) plots at two intertidal levels (low and high) and the control. Each bar represents mean (n=8) ± 1SE. Bars with the same letter above do not differ significantly (Tukey post hoc, $p<0.05$). There was no cleared control treatment in 2009 (nd).

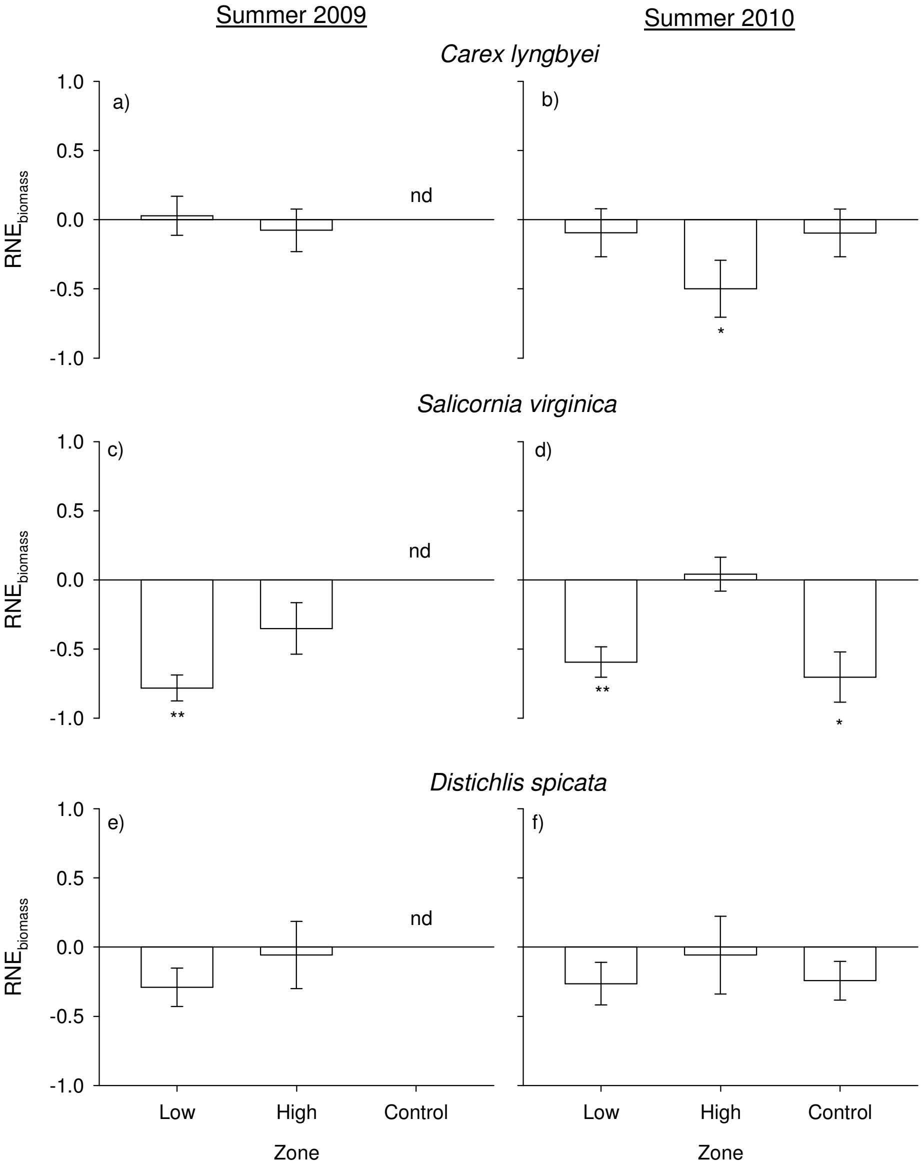

Figure 3.4. Relative Neighbor Effect (RNE) for dry biomass (g) of three species (*Carex*: a, b; *Salicornia*: c, d; *Distichlis:* e, f) at two intertidal levels (low, high) and the control. Each bar represents mean (n=8) ± 1SE. * indicates that mean differs significantly from zero (one sample t-test) $p<0.05$, ** $p<0.001$. There was no cleared control treatment in 2009, so RNE could not be calculated (nd).

Discussion

Comparisons of the biomass and growth rates among the three salt marsh species did not provide conclusive evidence in support of the hypothesis that competitive exclusion maintains the low marsh distribution of *Salicornia* and *Distichlis* (Figure 3.2-3.4). Neither species exhibited significant signs of competitive release when transplanted into cleared areas within the high marsh (Figure 3.2, 3.3). It is therefore unlikely that either species is competitively excluded from high marsh elevations. The only instances of significant competition occurred for *Salicornia* within its natural (low) marsh zone (Figure 3.4), which indicates that there may be strong biotic as well as abiotic stress in the low intertidal. The high marsh dominant species (*Carex*) exhibited slightly decreased biomass (Figure 3.2) and decreased growth (Figure 3.3) in the low marsh, which indicates that this species was physiologically stressed at lower intertidal elevations.

Transplanted *Carex* plants exhibited a strong signs of stress in response to transplantation in 2009 when they exhibited reduced biomass and growth rates (Table 3.1, Figures 3.2a, 3.3a) in comparison to the control individuals. At the end of the 2010 season, the biomass of *Carex* did not differ between transplant and control treatments. However, generally lower biomass of the low marsh transplants irrespective of the presence of neighboring vegetation indicated that some abiotic factor negatively impacted growth. Decreased growth of *Carex* was observed although the conditions in the low marsh were not overly harsh to kill the *Carex* transplants outright. *Carex lyngbyei* is known to grow in both saline and oligohaline conditions, but biomass and shoot height were lower under more saline conditions than within marshes with more fresh water input (Smythe and Hutchinson 1989). Although the low marsh community at the Metcalf study site generally experiences more stressful conditions (Chapter II), the additional precipitation over the growing season in 2010 may have ameliorated some of this stress. Summer 2010 (May through August) was significantly colder (t-test: t_{246}=5.621, p<0.001) and wetter (total precipitation: t_{246}= -2.669, p=0.008; cumulative precipitation: t_{246}= -2.835, p=0.005) than the summer of 2009 (National Estuarine Research Reserve; System-Wide Monitoring Program/ Centralized Data Management Office). It is possible that increased fresh water input and lower summer temperatures may have alleviated some of the stress associated with transplantation and tidal inundation.

The decreased growth rate of transplanted *Carex* in 2010 in the low marsh compared to high marsh is indicative of abiotic stress. Competition was significant between the transplanted *Carex* and neighboring vegetation in 2010 (Figure 3.4b). The interaction between control *Carex* individuals and the neighboring vegetation was less negative, possibly indicative of strong below ground competition, which was removed for the transplants, but not the controls. In a previous study with *Carex* species, a congener of *C. lyngbyei* exhibited the same amount of growth in the presence of neighboring roots alone and with both roots and shoots of neighbors (Gerry and Wilson 1995, see also Peltzer et al. 1998). The small size of the initial transplanted ramet may also have contributed to the strong competitive interaction with neighboring vegetation as competitive ability depends on size and therefore ability to acquire nutrients and light (Scholten et al. 1987).

In this study, *Salicornia* did not grow well in the high intertidal zone although in California salt marshes it has been observed previously to compete strongly with other high marsh species (Ungar et al. 1979, Pennings and Callaway 1992). Transplanted

Salicornia did not exhibit competitive release in terms of biomass or growth rate when transplanted, into cleared plots in the high intertidal; both overall biomass (Figure 3.2 c, d) and growth rate (Figure 3.3 c, d) were lower in the high intertidal transplants than in the low, cleared plots. These data suggest that although significant competition occurred between small *Salicornia* and neighboring vegetation in the low marsh (Figure 3.4), some factor other than competition with *Carex* prevented the spread of *Salicornia* toward the upland boundary of the marsh. *Salicornia* often occupies the most saline marsh zone and is capable of high yields even in saline sediments (Cooper 1982, Seliskar 1985, Boyer et al. 2001), so the relatively high yields from the low marsh were not unexpected, particularly in the cleared plots (Luo et al. 2010). The limited growth in the high marsh was unusual. The high marsh at the Metcalf study site was occasionally subjected to standing water after spring rainstorms (personal observation). Although *Salicornia* has the capability of increasing aerenchymatous tissue (Seliskar 1985) this species has limited growth under reducing and anoxic conditions like those created by standing water (Schat et al. 1987).

Transplanted *Distichlis* ramets were predicted to show the same pattern of competitive release that was anticipated for *Salicornia*, and though both species exhibited similar patterns of growth and biomass, neither followed the predicted pattern of competitive release in the cleared high marsh transplants. *Distichlis* has been observed to exhibit greater growth and increased biomass in low marsh (as compared to high marsh) transplants (Hansen et al. 1976, Seliskar 1985). However, grasses show varying degrees of competitive dominance (Silvertown et al. 1994, Keddy et al. 2000, Keddy et al. 2002, Hunter et al. 2008), and often illustrate a strong tradeoff between competitive ability and salinity tolerance (Kemp and Cunningham 1981, Kenkel et al. 1991). As with *Carex*, the transplanted *Distichlis* in 2009 exhibited significant stress of transplantation; the control treatment group exhibited significantly greater biomass (Figure 3.2e) and rapid growth (Figure 3.3e) in comparison with the transplants. Similar patterns of growth and biomass were apparent in 2010; the cleared control treatment exhibited higher biomass and more rapid growth than transplanted individuals. This gives some indication that aboveground competition may be important for this species in the low marsh (Figure 3.2f, 3.3f). Additionally, intermixed with the high marsh neighboring vegetation, transplanted *Distichlis* exhibited growth rates similar to transplanted and control individuals in vegetated plots in the low marsh. Growth rates in all vegetated treatments were lower than growth rates in the cleared low marsh plots. This suggests that though *Distichlis* was able to grow in the high marsh, below ground competition was limiting growth.

From these data, competitive release in cleared, high marsh plots would be predicted, but there was significantly less biomass and growth by transplanted *Distichlis* in the cleared plots in the high marsh, possibly due to biotic interactions other than competition, such as herbivory. Many of the high marsh transplants were consumed, either partially or wholly, over this study. Herbivory can have a significant impact on competitive plant interactions (Taylor et al. 1997, Rand 2003). The herbivore was not observed; both the Oregon meadow mouse (*Microtus oregoni*) and Canada geese (*Branta canadensis*) have been observed in Metcalf (Hoffnagle 1976; personal observation) and geese, at least, are known to readily consume marsh vegetation (Mulder and Ruess 1998, Esselink et al. 2000).

The relatively low biomass of *Distichlis* transplanted to the high intertidal may also be associated with changes in degree of mycorrhizal association. Mycorrhizal infection can be beneficial as the increased surface area of the hyphae can increase nutrient absorption (Allen and Cunningham 1983, Cooke et al. 1993) or provide protection from pathogens (Zeng 2006). Although the impact of infection in *Distichlis* is unknown, 9% of coastal *Distichlis spicata* are infected (Allen and Cunningham 1983) and some marsh species exhibit decreased growth after removal of their mycorrhizal symbionts (Daleo et al. 2008).

Strong competition was evident within the Metcalf study site (Figure 3.4) for both *Salicornia* and *Carex*, and competition occurred regardless of the tidal elevation. In some studies of East Coast marshes, the overall importance of competition was unrelated to salinity stress; competition influenced the mixture of species within a community regardless of the salinity (Scholten et al. 1987, Wilson and Tilman 1991, Keddy et al. 1994, La Peyre et al. 2001, Keddy et al. 2002, Sanderson et al. 2008). Neither *Salicornia* nor *Distichlis* exhibited any improved growth when transplanted into cleared areas of the high marsh, which suggests that competition with *Carex lyngbyei* is not the primary factor limiting the expansion of these species into the high marsh at the Metcalf study site. Transplanted *Carex* exhibited lower biomass in the low marsh, which could indicate physiological stress, (Dormann et al. 2000). However, in Metcalf marsh the data illustrate a trend rather than a significant difference. The growth rate of this high marsh sedge was significantly lower in the low marsh, which indicates that though *Carex* may survive short term in the low marsh, long term persistence may not be possible.

Physiological limits on the spatial distribution of *Carex* were expected and somewhat supported by the current study. The distribution of the low marsh species, *Salicornia* and *Distichlis*, were not, however, limited by competition, as was predicted from previous studies on other low marsh species. These data indicated that these two marsh species are limited to the low marsh possibly by different biotic factors (e.g. herbivory) or by physiological constraints, which prevented spread of the species into the high marsh.

Bridge II

Chapter III described the competitive interactions of isolated ramets of dominant species within their usual distributional zones. The observed interactions would be typical of species that spread vegetatively. Though many of the species within salt marshes depend primarily on vegetative propagation, some also germinate from seeds. The composition of seed banks in salt marshes is variable and heterogeneous. Chapter IV describes the seed density, viability and natural emergence of the seed bank in six marshes along the South Slough.

CHAPTER IV

COMPOSITION AND VIABILITY OF SALT MARSH SEED BANKS ALONG AN ESTUARINE SALINITY GRADIENT

Introduction

Seeds are an important aspect of any plant community as they represent the ability of the community to persist. Seeds remain viable in the sediment for variable periods of time. Those that persist for less than one year contribute to the transient seed bank while seeds that remain viable for more than one year contribute to the persistent seed bank (Thompson and Grime 1979, Fenner 1995, Wolters and Bakker 2002). Soil seed banks allow for dispersal of seed through time rather than through space (Fenner 1995). They provide a record of past vegetation patterns (Leck and Simpson 1987) as well as counteract environmental heterogeneity (Ungar 1995, Fenner and Thompson 2005). Seed banks are often less sensitive to environmental fluctuations than emergent communities and therefore represent a way for a community to recover from disturbance (Bonis and Lepart 1994, Ungar 1995, Amiaud and Touzard 2004, Wang et al. 2009).

The relationship between the seed bank and the aboveground plant community is highly variable (Leck and Graveline 1979, Moore 1980, Benoit et al. 1989, Leck and Simpson 1995, Jensen 1998, Kotorova and Leps 1999). The disparity between the aboveground community and the seed bank is often associated with the age of the community. Ecosystems dominated by annual species tend to have seed banks with similar composition to the aboveground community, while ecosystems dominated by perennials tend to have little similarity to the composition of the seed bank, which usually reflects the early successional species (Moore 1980, Bonis and Lepart 1994, Amiaud and

Touzard 2004). Although seed banks are most advantageous to a community in areas dominated by annual plants that experience frequent but unpredictable disturbances (Fenner and Thompson 2005), previous studies have shown the importance of seed banks in recovery of salt marshes where tidal influence increases the frequency of disturbance (Hopkins and Parker 1984, Welling et al. 1988, Hopfensperger et al. 2009).

Seeds that persist in salt marsh seed banks are able to tolerate the stress associated with periodic tidal inundation and associated increased salinity and anoxia (Hopkins and Parker 1984, Bakker et al 1985, Hutchings and Russell 1989, Liu et al. 2006). Flooding and high salinity reduce germination and survival (Baldwin et al. 1996, Egan and Ungar 1999, Baldwin et al. 2001, Keiffer and Ungar 2002), but many halophytic species have seeds with induced dormancy, which allows the seeds to survive and germinate when conditions become more tolerable (Hopkins and Parker 1984, Ungar 1979, Ungar 1995).

Although studies of salt marsh seed banks are not uncommon, there has been little consistency in observed relationships between the aboveground emergent vegetation patterns and the composition of the seed bank (Milton 1939, Leck and Graveline 1979, Ungar and Riehl 1980, Jefferies et al. 1981, Hopkins and Parker 1984, Hutchings and Russell 1989, Ungar 1995, Yuan et al. 2007). Differences between the composition of the seed bank and emergent plant community may be due in part to variation of the life history strategies of dominant species (Leck and Simpson 1995). Salt marsh seed banks are patchily distributed with higher seed densities common along the strand line (Leck and Graveline 1979, Kotorova and Leps 1999, Wolters and Bakker 2002) as wetland seeds disperse readily by floating on the water (Randwell 1972, Middleton 2000, Luan et al. 2007, Chang et al. 2008). The disparate distribution of seeds in the sediment also translates to patchy seed distribution and heterogeneity between and among different sites (Leck and Simpson 1987, Jensen 1998, Fenner and Thompson 2005). Spatial patterns of seed dispersal and deposition can have an impact on the regenerative processes (Grime and Hillier 2000) and ability of species to maintain populations (Bonis and Lepart 1994). Although intertidal marshes with both fresh and salt water inundation have been examined, few studies have evaluated differences among marshes within the same water drainage system and these only secondarily focused on the seed bank (Crain et al. 2008, Sharpe and Baldwin 2009).

The salt marshes along South Slough, Coos Bay, Oregon present an ideal environment to examine differences in seed bank composition along a relatively short estuarine salinity gradient. Six marshes with differing degrees of marine influence (marine, mesohaline and riverine) were evaluated (Rumrill 2006). Three major plant community types occur within these six salt marshes (*Carex* community, *Deschampsia* community and *Distichlis*/*Salicornia* community; see Chapter II). The primary purpose of this study was to evaluate the composition of the seed bank within these three major community types in salt marshes along an estuarine salinity gradient and to explore differences within a community type in marshes along that gradient. Given the readily transportable nature of many salt marsh seeds, I hypothesized that the composition of the seed banks within marshes in close proximity to one another will be most similar and that the composition will differ depending on the position of a marsh along the gradient (Peterson and Baldwin 2004).

Secondarily, this study examined the relationship between the seed banks and the existing marsh communities. Specifically, I hypothesized that the similarity between the seed bank and the existing emergent community will be relatively low as most of the marshes are dominated by perennial species, which generally contribute little to seed banks (Leck and Simpson 1987, Fenner 2005). The major community types within these South Slough marshes are dominated by perennial species (Chapter II), so low similarity was hypothesized for all community types within the study marshes.

Thirdly, this study examined the question of seed viability within these salt marsh seed banks. Viability was expected to differ between species and be generally higher at riverine marshes where high salinities are less prevalent (see Chapter II and Hopkins and Parker 1984, Bakker et al. 1985, Hutchings and Russell 1989, Baldwin et al. 1996, Baldwin et al. 2001). The importance of germination from the seed bank for recovery of small scale disturbance was examined in three of the study marshes. Salt marshes are frequently disturbed and are characterized as stressful environments where the presence of the seed bank can directly influence the ability of the marsh to recover from natural and anthropogenic disturbance (Allison 1995, Huiskes et al. 1995, Kalamees and Zobel 2002, Bertness et al. 2004, Hopfensperger and Baldwin 2009).

Methods

Site Descriptions

This study was conducted in six fringing or pocket salt marshes along South Slough, in Coos Bay, Oregon (Chapter II, Figure 2.1, Appendix A). The marshes were chosen based on their location within the slough, their history of minimal human impact and their accessibility. Two study marshes are categorized as marine (salinity range of 20-31 g/kg; Metcalf and Collver Point), two as mesohaline (salinity range of 15-28 g/kg; Valino Island and Hidden Creek) and two as riverine (salinity range of 0-21 g/kg; Danger

Point and Tom's Creek). These designations were based on the salinity regime of the estuarine water column (Rumrill 2006). Metcalf marsh, the most marine of the study marshes (Chapter II, Figure 2.1) is a small pocket marsh characterized primarily by a low marsh community dominated by *Distichlis spicata* and *Salicornia virginica* in addition to a few other species including *Jaumea carnosa* and *Triglochin maritima*. The *Distichlis/Salicornia* community type (Chapter II) also dominates the second of the marine marshes, Collver Point. The high intertidal marsh communities dominated by *Carex lyngbyei* (*Carex* community type) and *Deschampsia caespitosa* (*Deschampsia* community type) are also present in these two low estuarine marshes, but these two communities account for a much smaller area within these marshes than in the upper estuarine marshes and are present only along the upland boundary. At Collver Point, the *Carex* community dominates areas near fresh water input from the upland boundary and is primarily found in monotypic stands. The lowest mesohaline marsh in South Slough is Valino Island (Chapter II, Figure 2.1), which is small and fringing with limited patches characterized by the *Distichlis/Salicornia* and *Carex* community types. Most of the high marsh is dominated by the *Deschampsia* community type, which is characterized by particularly high species richness (Chapter II). The second mesohaline marsh, Hidden Creek, is a pocket marsh dominated primarily by the *Deschampsia* community type. The *Carex* community type is also present. The *Distichlis/Salicornia* community type is present only along the large tidal channel that bisects the marsh. The final two marshes examined in this study, Danger Point and Tom's Creek, occur toward the riverine end of the slough. Both are relatively high marshes dominated by large patches of the *Deschampsia* and *Carex* community types and the introduced grass *Agrostis stolonifera,* though many other species are present. Although Tom's Creek was diked, the area was never used for agriculture and has experienced open tidal circulation for at least 25 years (Cornu and Sadro 2002). The *Distichlis/Salicornia* community type is absent from these marshes though both species occur occasionally.

Sample Collection

Sediment samples were collected from patches dominated by the three major community types (*Carex, Deschampsia* and *Distichlis/Salicornia*) within four of the six marshes; the *Distichlis/Salicornia* community type is absent from the two riverine marshes. Collections were made after the growing season and subsequent seed fall in two consecutive years (February 2009 and December 2009). This timing made it possible to collect seeds from both the transient and persistent seed bank, though these were not separated. Sediment samples were taken from a total of seven haphazardly selected sites within each community type for each marsh. At the riverine marshes, where the *Distichlis/Salicornia* community type is absent, only 14 samples were collected, seven each from *Carex* and *Deschampsia* community types. Different sites were sampled during each sampling period (February 2009 and December 2009); a total of 224 samples were collected. At each sampling site, three sediment cores were taken to a depth of three centimeters using a 10 cm diameter PVC pipe (Figure 4.1). Most seeds occur within the top 3 cm of sediment (Thompson and Grime 1979, Ungar and Woodell 1993, Bonis and Lepart 1994, Ladd and Facelli 2005, Coteff and van Auken 2006) and small diameter cores provide a representative sample of the seed bank (Bigwood and Inouye 1988, Gross 1990, Brock et al. 1994). Each cylindrical core was split in half lengthwise and half of each core was placed into two separate, but matching composite samples, each to be evaluated in a different manner. Samples were placed in plastic bags for transport and were maintained at a constant temperature of 4 to 6°C prior to processing for either of the following assessment methods.

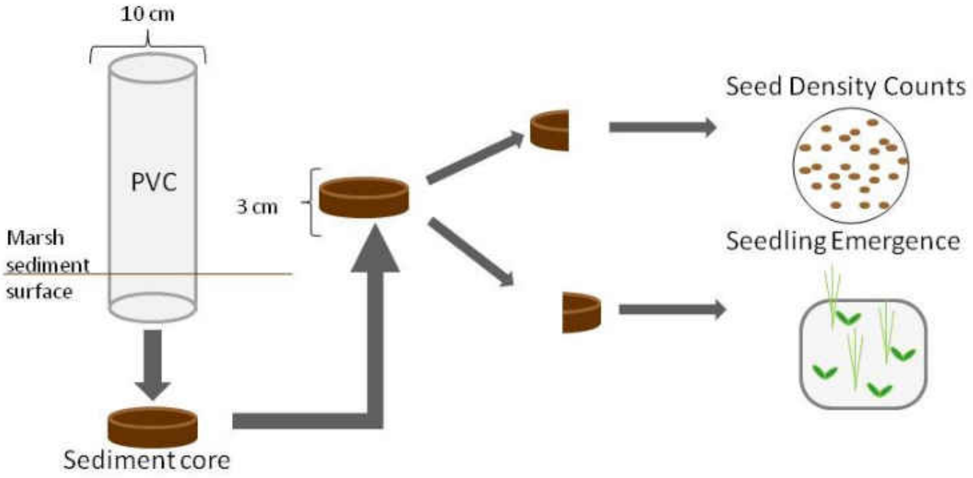

Figure 4.1. Diagrammatic illustration of the collection method of the seed bank samples from salt marshes within South Slough.

Seed Density

One set of seed bank samples was processed manually to enumerate seed counts. Each half core was wet-sieved and all material captured on the 1 mm sieve was collected and air dried to ease storage. Although many seeds are smaller than one millimeter, previous work indicated that smaller mesh sizes did not capture appreciably more seed (less than 6%) and all species were accounted for within the larger mesh sample (Keammerer unpub. data). Seeds were manually separated from each sample under light microscopy using a pair of fine forceps. Although seed counts often overestimate the seed bank due to counting both viable and non-viable seeds, effort was made to count only undamaged seeds (Le Peyre et al. 2005). Separated seeds were identified to lowest possible taxonomic level and counted. For identification, seeds were compared with known field collected seed. Samples from the two sampling periods (February and December) were combined for analyses. Manual seed density counts ranged from 3 to 650 seeds per sample and were scaled to seeds per m^2 for analyses.

Total seed densities for each marsh were log transformed and compared within the three community types using separate one-way ANOVAs. Differences between marshes were analyzed using post hoc Tukey HSD tests. Additionally, the relative seed density of each species in a sample was calculated as number of seeds of each species / total seeds in the sample. Therefore, the relative seed density for a given species was expressed as a proportion of the whole sample. Relative seed densities of each species were arcsine square root transformed and compared with a two-way ANOVA with marsh and community type as fixed factors (SPSS 19 for Windows).

For each community type within each marsh, mean relative seed density of each species was calculated. Variation in the composition of the seed bank among marshes and community types was evaluated using nonmetric multidimensional scaling (NMS) which utilizes ranked distances between sites in species space (Kruskal 1964, Mather 1976, Clark 1993, McCune and Grace 2002). Prior to analysis, mean relative seed density data were arcsine square root transformed. All analyses were performed using PCORD (Version 4; MjM Software Design, Gleneden Beach, OR). A two-dimensional configuration was chosen as increased dimensions did not significantly decrease stress (McCune et al. 1997). For each NMS analysis, a Sorensen (Bray-Curtis) distance measure was used with a 0.00001 stability criterion. Final runs for each species matrix were derived with 100 iterations and a randomly selected starting configuration (McCune and Grace 2002). Similar patterns emerge when all samples were used in the analysis, so for ease of interpretability mean relative counts were used.

The composition of the seed banks were compared to the emergent marsh communities based on percent cover of species within each community type collected during summer 2008 (Chapter II). Comparison with the seed bank was done using a cluster analysis based on mean relative vegetation cover and the mean relative seed density for each community type. The analysis was conducted using the relative Euclidian distance measure and Ward's method using PCORD. Prior to analysis, uncommon species (occurrence in fewer than 5% of the 224 samples) were removed (McCune and Grace 2002, Sharpe and Baldwin 2009). Additionally, similarity between the mean relative cover of the emergent communities and the mean relative seed densities were evaluated using Jaccard's index, which measures the similarity between communities based on presence/absence and is calculated as the number of shared species divided by the combined total of species in both the seed bank and emergent community (Looney and Gibson 1995).

Laboratory and Field Emergence

The second set of seed bank samples was evaluated through emergence growth studies. Large woody debris was removed from the samples and the marsh sediment was spread thinly over a bed of saturated potting soil [*Sphagnum* moss combined with earthworm castings (Sun Gro Horticulture Inc., Black Gold®)]. Each sample was placed in a separate potting tray (10 cm^2). The 112 sample trays were placed outside in early March 2009 and 2010 to allow germination under natural weather conditions (Looney and Gibson 1995). Sample trays were watered daily with fresh water to induce germination (Ungar 2001). Sample trays were checked weekly until germination had ceased, which occurred by early July of both years. Seedlings were counted and identified to lowest possible taxonomic division. Prior to analysis, emergence from both sampling periods was combined. Numbers of emerged seedlings ranged from 2 to 35 per sample and were scaled to seedlings per m^2 for analyses. Differences in total laboratory seedling emergence were evaluated between marshes within each community type with separate one-way ANOVAs.

In addition to laboratory emergence of collected seed bank samples, emergence of seedlings from the seed bank was evaluated in the field within three of the six study marshes (Metcalf, Hidden Creek and Tom's Creek) during the spring and summer of 2010. Five small clearings were made (25 cm x 25 cm) within each of the community types within each marsh in February 2010. These were monitored weekly through March and bi-weekly April through August. Emerging seedlings were counted and identified to lowest possible taxonomic level. Total seedling emergence was defined as the peak number of seedlings for a given species. Numbers of emerged seedlings ranged from 2 to 40 per site and were scaled to seedlings per m^2 for analyses. Differences in total field seedling emergence were evaluated between marshes within each community type with separate one-way ANOVAs.

For each seed bank sample, the viability of seeds within the seed bank was estimated by comparing the seedling emergence to the seed density counts. Mean viability was calculated for each species within each community type in all study marshes. A non-parametric Kruskal-Wallis test was used to evaluate the differences in viability among marshes and community types.

Results

Seed Density

Seeds of five species (*Carex lyngbyei, Distichlis spicata, Deschampsia caespitosa, Salicornia virginica* and *Triglochin maritima*) accounted for more than 75% of all seeds in the seed bank of marshes within South Slough (Figure 4.2). The total number of seeds within a community type varied significantly by marsh (ANOVA *Carex* type: $F_{5,78}=7.24$, $p<0.001$, *Deschampsia* type: $F_{5,78}=6.52$, $p<0.001$, *Distichlis*/*Salicornia* type: $F_{3,52}=4.70$, $p=0.006$). Within the *Carex* community type, samples taken from Valino Island had significantly fewer total seeds per square meter than any of the other marshes (Tukey post hoc $p<0.05$; Figure 4.2a). A large number of seeds of *Agrostis stolonifera* within this community type in Tom's Creek contributed to the relatively large proportion of 'other species' seeds within that community (Figure 4.2a, Appendix D).

Within the *Deschampsia* community type, samples taken from Tom's Creek had higher total seed density than samples taken from Danger Point, Hidden Creek and Collver Point (Figure 4.2b). The samples from within the *Deschampsia* community at Metcalf and Valino Island did not differ significantly from the other marshes or from each other (Figure 4.2b). The majority of seeds collected from this community type on Valino Island were *Juncus balticus,* which contributes to the large proportion of 'other species' seeds in that community (Figure 4.2b, Appendix D).

Samples from the *Distichlis*/*Salicornia* community at Metcalf had significantly higher seed density than samples taken within that community at any other marsh (Figure 4.2c). Seed density of each species varied significantly both by marsh and community type (Table 4.1). Of the nineteen identifiable species that appeared in more than 5% of all

224 samples, the seed density of 17 differed significantly by marsh and 13 differed significantly by community type (Table 4.1). In most cases, the patterns of seed density for a species were not consistent among marshes and community types, resulting in significant interactions between the factors.

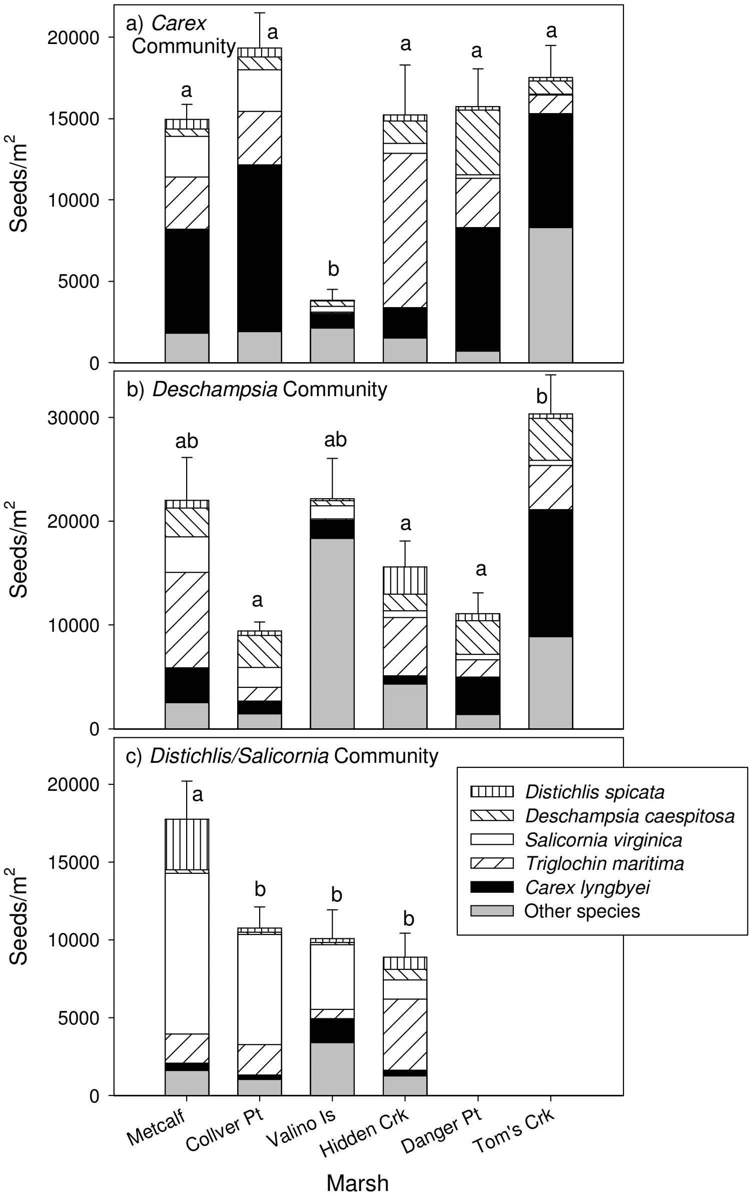

Figure 4.2. Mean total seeds per m^2 from marsh communities dominated by a) *Carex lyngbyei* b) *Deschampsia caespitosa* and c) *Distichlis spicata/Salicornia virginica* in each of six marshes. Error bar represents standard error of the total mean seeds. Within each community type, bars with the same letter above are not significantly different (Tukey post hoc $p<0.05$). The five species accounting for 75.9% of all seeds are shown. Note: the scales of the y-axes vary.

Seed Bank Composition

The NMS ordination of mean relative seed density resulted in a two-dimensional distribution with a stress of 9.18 and final instability of 0.00001 after 90 iterations (Figure 4.3). Within the distribution, seed bank samples taken from the same marsh generally cluster together. With the exception of the two marine marshes (Metcalf and Collver Pt.), the seed banks of the *Carex* and *Deschampsia* communities within a given marsh were more closely associated to one another than to the seed banks of other community types from other marshes; the seed banks of these two communities grouped by marsh. The low marsh *Distichlis/Salicornia* community seed bank samples did not, however, group with other seed bank samples from the same marsh, but tended to group together (Figure 4.3).

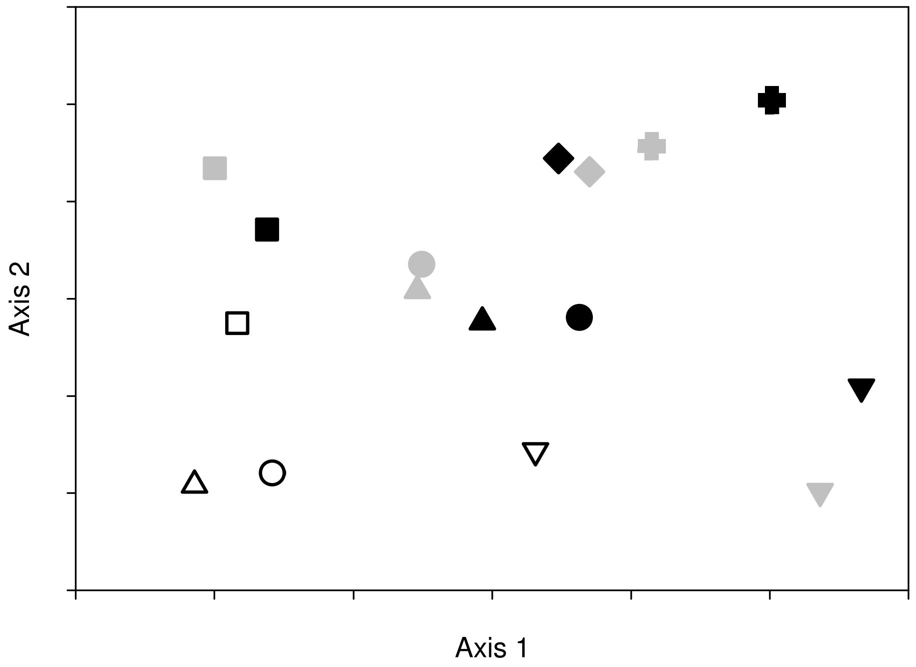

Figure 4.3. NMS ordination of salt marsh seed bank communities from six marshes based on the mean relative seed density for each community: *Carex* (black filled symbols), *Deschampsia* (gray filled symbols) and *Distichlis/Salicornia* (open symbols). Marshes: Metcalf (▲, ▲, △), Collver Pt. (●, ●, ○), Valino Is. (▼, ▼, ▽), Hidden Creek (■, ■, □), Danger Pt. (◆, ◆), Tom's Creek (✚, ✚). The distribution accounts for 90.9% of the variation in the community: Axis 1 (54.2%) and Axis 2 (36.7%) with a final stress of 9.18.

Table 4.1. Two-way ANOVA results for effects of marsh (df = 5), community type (df = 2) and their interaction (M x C; df = 8) on seed density for identified species present in more than 5% of all 224 seed bank samples. Marshes and community types are listed in order of smallest mean number of seeds (left) to largest mean number of seeds (right); a shared line (under or over) indicates no significant difference (post hoc: Tukey HSD, p<0.05). When there were not significant differences among marshes or community types, lines were omitted. Marshes: Metcalf (M), Collver Pt. (C), Valino Is. (V), Hidden Creek (H), Danger Pt. (D) and Tom's Creek (T). Community types: *Carex lyngbyei* (C), *Deschampsia caespitosa* (D), and *Distichlis spicata/Salicornia virginica* (DS).

Species	Marsh	Community Type	M x C
Agrostis stolonifera	M V C H D T **	DS C D	*
Atriplex patula	T V C D H M **	C DS D *	NS
Carex lyngbyei	H M C V D T **	DS D C **	**
Carex obnupta	H C D M V T *	DS C D *	*
Cuscuta salina	D T H V C M **	D C DS *	NS
Deschampsia caespitosa	V M C T H D **	DS C D **	**
Distichlis spicata	V D T C H M **	C D DS *	*
Glaux maritima	H M D C T V **	C DS D *	*
Grindelia integrifolia	V C M D H T	DS C D **	*
Jaumea carnosa	T V D C M H **	D C DS	NS
Juncus arcticus ssp. *balticus*	H M C D T V **	DS C D **	**
Juncus gerardii	D M T C V H	DS C D	NS
Plantago maritima	D T M V C H **	D C DS	NS
Rumex maritimus	T M C D V H **	DS C D **	**
Salicornia virginica	T D V H M C **	C D DS **	*
Spergularia marina	D H T C V M **	C D DS	NS
Triglochin concinna	H M C D V T **	DS C D **	**
Triglochin maritima	V T C M D H **	DS C D	**
Trifolium wormskjoldii	V C D M H T *	DS C D *	*

* p<0.05, **p<0.001

Seed Bank and Emergent Marsh Community

The compositions of the emergent plant communities and the seed banks were not closely associated. The similarities between the seed banks and the marsh communities were variable by marsh and community type. Similarities ranged from 28.6% (*Carex* community type at Tom's Creek) to 53.3% (*Distichlis/Salicornia* community type at Metcalf) and the mean similarity between the emergent community and the seed bank composition was 39.6% (Table 4.2).

Table 4.2. Percent similarity (Jaccard's similarity coefficient) between emergent marsh community and seed bank composition at each marsh and within each community type

Marsh	Community type	Similarity (%)
Metcalf	*Carex lyngbyei*	52.6
	Deschampsia caespitosa	47.6
	Distichlis spicata/Salicornia virginica	53.3
Collver Point	*Carex lyngbyei*	31.8
	Deschampsia caespitosa	34.8
	Distichlis spicata/Salicornia virginica	33.3
Valino Island	*Carex lyngbyei*	30.0
	Deschampsia caespitosa	36.4
	Distichlis spicata/Salicornia virginica	36.0
Hidden Creek	*Carex lyngbyei*	41.7
	Deschampsia caespitosa	50.0
	Distichlis spicata/Salicornia virginica	46.7
Danger Point	*Carex lyngbyei*	31.8
	Deschampsia caespitosa	42.9
Tom's Creek	*Carex lyngbyei*	28.6
	Deschampsia caespitosa	36.4

Cluster analysis returned nine groups using 75% of the community information (Figure 4.4). In only one case (group B) did the cover of the emergent community and the seed density from the same community group together, though the emergent cover and seed bank composition of the low marsh *Distichlis*/*Salicornia* community are closely related (groups H and I; Figure 4.4). The emergent cover clustered by community type (groups A, F, G and H; Figure 4.4). The composition of the seed bank generally clustered by marsh (groups D, E; Figure 4.4) with the exception of the low marsh (*Distichlis/Salicornia*) community (group I; Figure 4.4). The high marsh communities, *Carex* and *Deschampsia*, exhibited more similarity to one another across marshes (group C), but the finer divisions of the dendrogram generally subdivided by marsh (not shown).

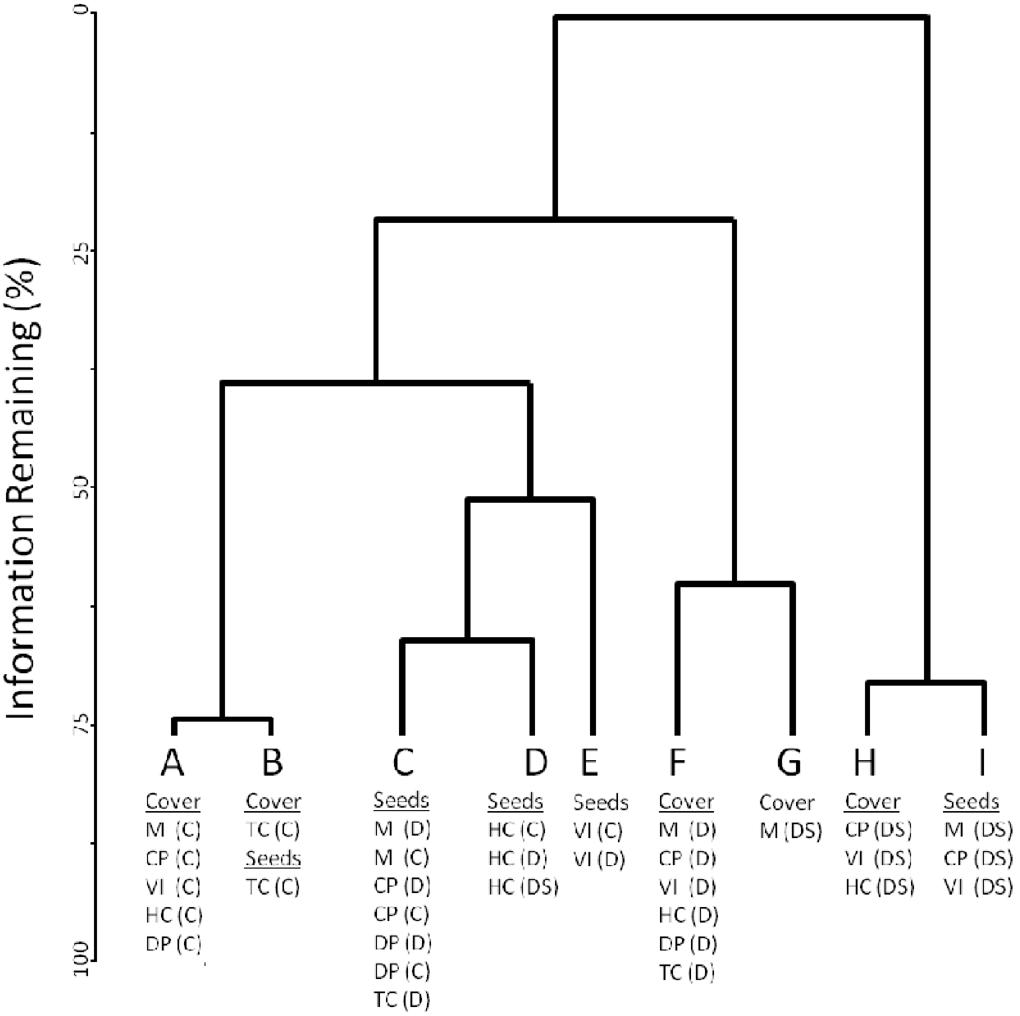

Figure 4.4. Dendrogram representing the cluster analysis of the mean relative cover and mean relative seed density for each of the three community types: *Carex* type (C), *Deschampsia* type (D), and *Distichlis/Salicornia* type (DS) in all six marshes: Metcalf (M), Collver Point (CP), Valino Island (VI), Hidden Creek (HC), Danger Point (DP) and Tom's Creek (TC). Cluster analysis: relative Euclidean distance and Ward's method. Samples within each group are listed below the group designation (A-I) on the dendrogram.

Seedling Emergence

More seedlings emerged from collected samples than from cleared areas in the marshes (Figure 4.5, Appendix E). Within the *Carex* community, more seedlings emerged from samples collected at Tom's Creek than from those collected at Valino Island (ANOVA $F_{5,78}$=3.22, p=0.01, Figure 4.4a), but seedling density did not differ among the other marshes. The density of seedlings emerging from cleared areas in the field did not differ between marshes within the *Carex* community (ANOVA $F_{2,12}$=1.33, p=0.3; Figure 4.5a). Seedling density did not differ among marshes in samples collected from the *Deschampsia* community type ($F_{5,78}$=1.65, p=0.16; Figure 4.5b), but significantly more seedlings emerged in field cleared areas in Metcalf than either Hidden Creek or Tom's Creek ($F_{2,12}$=6.97, p=0.01, Figure 4.5b). Seedling density within the *Distichlis/Salicornia* community type did not differ among marshes for collected samples ($F_{3,52}$= 0.18, p=0.18) or field cleared areas ($F_{1,10}$=1.69, p=0.22; Figure 4.4c).

Viability of seeds (percent germination) within the seed bank was assessed for 13 species that were present both in the manual counts of seed density and in the paired laboratory emergence samples (Appendix F). Viability was highly variable among species, and seven of 13 exhibited significant differences between marshes and community types (*Agrostis stolonifera*, χ^2=57.2, p < 0.001; *Atriplex patula*, χ^2=50.4, p < 0.001; *Distichlis spicata* χ^2=35.2, p = 0.002; *Deschampsia caespitosa* χ^2=64.3, p < 0.001; *Jaumea carnosa* χ^2=32.3, p = 0.006; *Glaux maritima* χ^2=37.4, p = 0.001 and *Salicornia virginica* χ^2=66.1, p < 0.001; Figure 4.6). Both *A. stolonifera* and *G. maritima* exhibited higher viability in terms of percent germination in riverine marsh samples (Figure 4.6 a, b), while *A. patula* and *S. virginica* exhibited lower viability in riverine marsh samples (Figure 4.6c, d). Seeds of *D. caespitosa* germinated from thirteen of the sixteen collected samples (Figure 4.6e) while *D. spicata* only germinated from eight (Figure 4.6f).

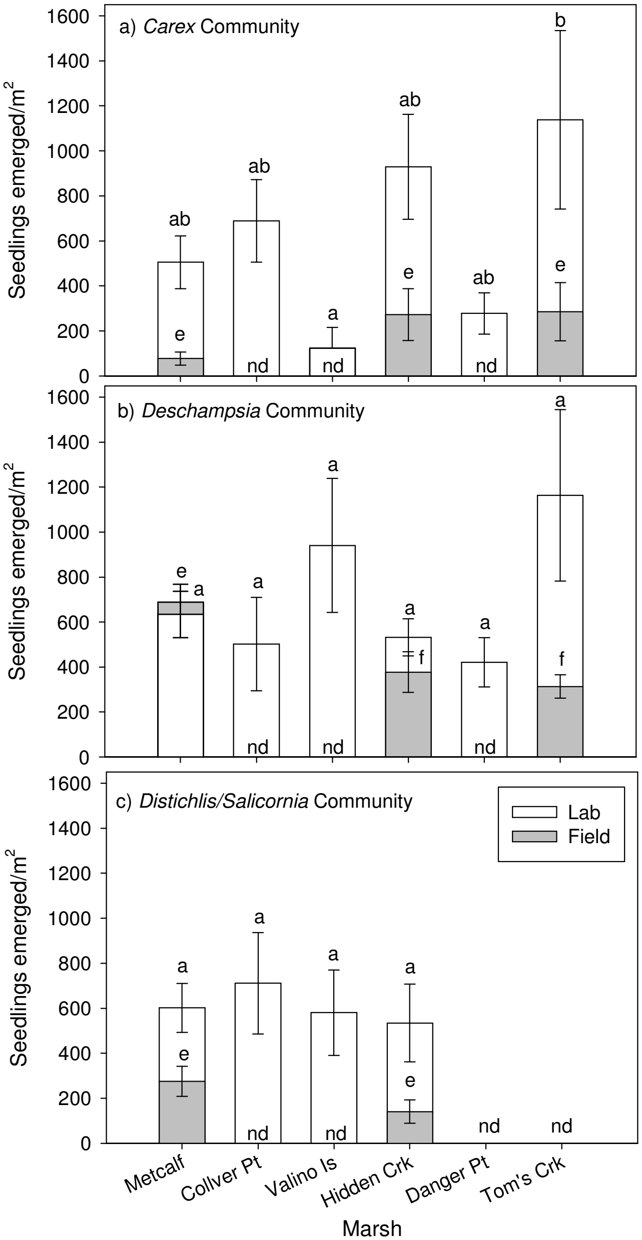

Figure 4.5. Mean number of total seedlings emerged per m^2 for either collected samples (lab emergence, open bars) or observed field emergence (filled bars) in the three major community types (*Carex*, *Deschampsia* and *Distichlis/Salicornia*) in six marshes. Error bars are standard error of the mean. Bars with the same letter above do not differ significantly (Tukey post hoc, $p<0.05$); lab and field emergence were tested separately. No field emergence data were collected at Collver Pt, Valino Is or Danger Pt (nd); the *Distichlis/Salicornia* community type was absent from Danger Pt and Tom's Creek.

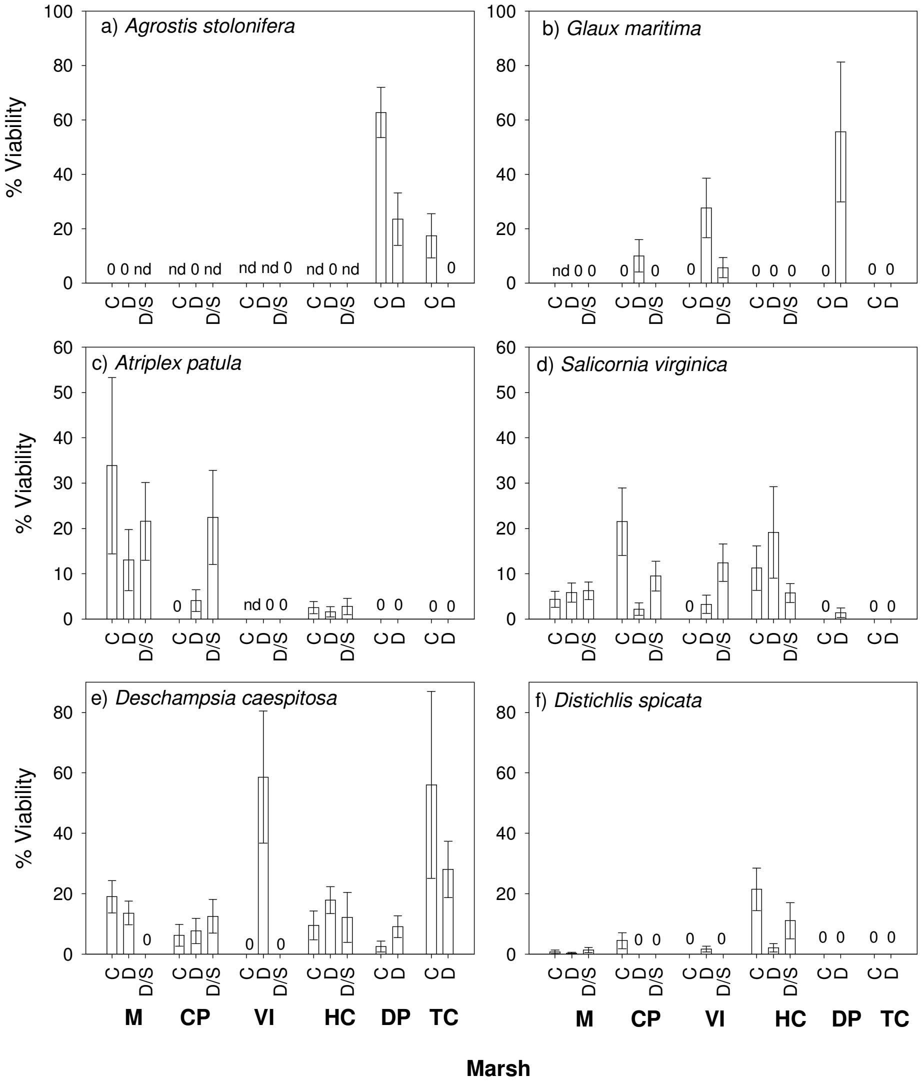

Figure 4.6. Percent viability of seeds of six species within the seed banks of six marshes in three community types based on collected samples. Marshes: Metcalf (M), Collver Pt (CP), Valino Island (VI), Hidden Creek (HC), Danger Pt (DP) and Tom's Creek (TC). Community types: *Carex lyngbyei* (C), *Deschampsia caespitosa* (D), and *Distichlis spicata/Salicornia virginica* (D/S). Error bars represent standard error of the mean. nd: indicates no seeds present in the sample. 0: seeds present but no germination (no viability). Note: the *Distichlis*/*Salicornia* community type was absent from Danger Pt and Tom's Creek.

Discussion

The seed banks within the salt marshes of the South Slough were dominated by seed from relatively few species (Figure 4.2, Table 4.1, Appendix D). There were significant differences in number of seeds per m^2 among marshes within a given community type (Figure 4.2). The most riverine marsh (Tom's Creek) had the highest overall seed density primarily due to the high numbers of *Agrostis stolonifera* seeds present (Appendix D). Accumulation of large numbers of seeds in the seed bank is common for species within that genus (Thompson and Grime 1979), but the seeds need light to germinate and so only contribute to changes in emergent vegetation if areas are cleared (Appendix E, Leggett 1945, Jerling 1983). The *Deschampsia* community type exhibited the highest density of seeds among all community types due partially to the high seed density at Valino Island within this community type (Figure 4.2, Appendix D). The density of *Juncus balticus* seeds within this community was high (13,386 ± 3673 seeds/ m^2; Appendix D). These seeds are numerous, but they do not disperse far from the parent plants. Limited dispersal is commonly cited as the explanation for patchy seed distributions (Thompson and Grime 1979, Fenner 1995, Rand 2000, Crain et al. 2008). Seed bank density is highly variable and site differences are common (Fenner 1995, Chang et al. 2001, Landman et al. 2007, Elsey-Quirk et al. 2009 a, b). The seed densities found in the seed banks of the South Slough study marshes was relatively high compared to other studies on salt marshes (Ungar and Woodell 1993, Maranon 1998, Rand 2000, La Peyre et al. 2005).

Dominance of seed banks by only a few species is also relatively common (Milton 1939, Parker and Leck 1985, Shumway and Bertness 1992, Ungar and Woodell

1996, Maranon 1998, Leck 2003), but unlike the majority of salt marsh seed bank studies, in South Slough marshes most of the seeds were from perennial species (97%) rather than the usual seed bank dominance by annual species (Leck and Simpson 1987, Ungar and Woodell 1996). This is probably due to the fact that few annual species are present in these marshes and though most perennial species produce fewer seeds, over time these seeds can build up in the seed bank. In the salt marshes in South Slough, the most common species in the seed bank were found in most of the community types, indicating that some dispersal of seed occurs within the marsh (Figure 4.2, Appendix D). Variability in seed production by different species may contribute to differences in species contribution to the seed bank (Leck 2003).

Within marshes of South Slough, the composition of seeds within the seed bank samples was more similar within a marsh than within a community type (Figure 4.3). The emergent cover clustered by community type (groups A, F, G, and H; Figure 4.4) while seed bank composition generally clustered by marsh (groups D, E). Seed banks of the two high marsh communities (*Carex* and *Deschampsia*) were very similar in the two riverine marshes that lacked the *Distichlis/Salicornia* community type. Within marshes with all three community types, greater similarity occurred between seed bank samples collected from the two high marsh communities (*Carex* and *Deschampsia*) than with the seed bank samples from the *Distichlis/Salicornia* community (Figure 4.3). In the marshes of South Slough, the seed banks within the low marsh community type (*Distichlis*/*Salicornia* community) were the most similar of any of the community types (Figure 4.3).

Huiskes et al. (1995) found that more seeds were swept out of marshes on ebb tides than were brought in on flood tides, and most of those seeds transported out of the marsh originated in the low intertidal. Therefore, the similarity between the low marsh seed bank community composition of different marshes may be partially due to input from other marshes (group I; Figure 4.4). It is also possible that the low marsh emergent communities are more similar to one another due to the presence of relatively fewer species able to tolerate the conditions, and therefore a smaller number of species contribute to the seed bank (see Chapter II). The composition of the seed bank from samples in the higher marsh communities was more similar within a marsh due possibly to the tidal transport of seeds from the mid-marsh to the high tide strand line (Randwell 1972, Huiskes et al. 1995, Ungar 1995, Rand 2000, Hopfensperger and Baldwin 2009).

Despite the variable seed distribution observed in salt marshes, many salt marsh species have seeds that disperse readily on water (Leck and Graveline 1979, Hopkins and Parker 1984, Bakker et al. 1985, Baldwin et al. 1996, Rand 2000, Neff and Baldwin 2005) by the wind (Neff and Baldwin 2005) or on the feathers and feet of waterfowl (Vivian-Smith and Stiles 1994). Although transportation by water is not generally a common method of dispersal in most plant communities (Fenner and Thompson 2005), tidal flux is the primary method of transport for salt marsh seeds (Bakker et al. 1985, Huiskies et al. 1995, Hopfensperger and Baldwin 2009). Some salt marsh species are able to float for long periods seemingly due to modifications in structure (e.g. *Triglochin maritima*, Davy and Bishop 1991), but even seeds without specially modified structures can be moved by tidal currents (Chang et al. 2008). The seeds of many species can remain viable after days or weeks of continual salt water exposure (Randwell 1972, Koutstaal et al. 1987). The results of the current study, however, indicate that in the small fringing and pocket marshes typical of Oregon estuaries, seeds do not mix appreciably between marshes except in the lowest intertidal marsh communities.

The cluster analysis results indicate that the emergent community was defined by the community type while the seed bank composition was defined by the marsh. While the seed bank communities did not cluster by community type, the emergent vegetation did (Figure 4.4 see also Chapter II and Egan and Ungar 2000). The similarities between the seed banks and the emergent marsh communities were variable by community type and marsh (Table 4.2). In perennial dominated marsh habitats, similarities between emergent vegetation and seed bank composition are usually less than 30% (Hutchings and Russell 1989, Ungar and Woodell 1993), though for low marsh communities, similarities close to 60% are not uncommon (Egan and Ungar 2000). The composition of seed banks of the low intertidal community (*Distichlis*/*Salicornia*) in South Slough marshes had the highest mean similarity (42.3%) with the composition of the emergent community (Table 4.2, Figure 4.4). The low *Salicornia* dominated zones in other marshes are highly variable, but generally have high similarities between the emergent and seed bank communities due partially to the abundance of *Salicornia* seed in the seed bank (Ungar and Woodell 1993, Egan and Ungar 2000, Ungar 2001). Congeners of *S. virginica* have very low dispersal abilities, seeds fall and remain close to parent plants (Ellison 1987) so high cover by *Salicornia* and high density of *Salicornia* seed are commonly highly correlated. In contrast, *D. spicata* does not contribute greatly to the seed bank (Appendix C, but see also Smith and Kadlec 1983).

The composition of the seed banks from the *Carex* and *Deschampsia* community types generally had slightly lower similarity to the emergent community (36.1% and

41.3% respectively) when compared to the similarity of the *Distichlis/Salicornia* seed bank and emergent marsh community (42.3% ; Table 4.2). Additionally, the riverine marshes (Tom's Creek and Danger Pt.) had the lowest similarity between the emergent communities and the seed bank composition (34.9%) compared to the mesohaline (Valino Is and Hidden Creek; 40.1%) and marine marshes (Metcalf and Collver Pt.; 42.3%). Although the riverine marshes are still technically salt marshes, the inundating water has a lower overall salinity and freshwater tidal marshes often have low similarities between aboveground vegetation and seed bank communities (Wilson et al. 1993, Erfanzadeh et al. 2010). The overall intermediate similarity (28.6%- 53.3%) between the emergent community and the seed bank is uncommon in perennial dominated areas, but not entirely unprecedented (Looney and Gibson 1995, Rand 2000, Leck 2003, Hopfensperger et al. 2009). As noted earlier, high similarities between aboveground vegetation and seed bank are found in areas dominated by annual plants; in the South Slough marshes, however, perennials dominate. The relatively high similarity may relate more to the reduced potential of seeds to germinate; that is, the seeds fall and remain in the seed bank because there is not enough open space or continual disturbance to allow germination (Jutila 2003, see Chapter V).

More seeds were able to germinate from the seed bank when samples were removed from the field and exposed to more favorable conditions than in cleared areas in the marshes (Figure 4.5, Appendix E). There was no clear pattern associated with the estuarine salinity gradient for the emergence of seedlings from either laboratory or field germinated samples. Samples collected from the *Carex* community type at Tom's Creek exhibited higher emergence than samples from Valino Island (Figure 4.4a). This is consistent with the negative impact of salinity on germination (Davy and Bishop 1991, Shumway and Bertness 1992). However, significantly lower seedling emergence occurred from the samples taken within the *Carex* community at Danger Pt. despite the relatively high seed density within those samples; only three species (*Agrostis stolonifera, Deschampsia caespitosa, Triglochin maritima*) were able to germinate successfully (Figure 4.6, Appendix F). The *Carex* community at Danger Pt. is the lowest marsh community and is frequently inundated with sea water and therefore is subjected to more saline and waterlogged conditions (see Chapter II). Low seed viability at this site may result from the inability of many of the high marsh species prevalent at Danger Pt. to cope with these conditions. Salinity stress and waterlogging both decrease seed viability (Hutchinson and Smythe 1986, Davy and Bishop 1991). The relatively large number of seeds emerging from cleared areas in Metcalf within the *Deschampsia* community (Figure 4.5b) may be due, in part, to fresh water input along the upland boundary of that marsh (personal observation). Fresh water induces germination in many salt marsh species (Davy and Bishop 1991, Shumway and Bertness 1992, Kieffer and Ungar 2002) so conditions in these areas may have been more conducive to germination in the field than the conditions at many of the other site. These conditions may have been closer to the conditions represented by laboratory emergence with fresh water addition. Germination from cleared areas in the field is commonly less than that observed in laboratory or greenhouse emergence studies (Milton 1939, Hopkins and Parker 1984, Parker and Leck 1985, Goldberg 1987, Jutila 2003, Elsey-Quirk et al. 2009b).

The viability of seeds within the seed bank was highly variable (Figure 4.6, Appendix F). For some species (e.g. *Agrostis stolonifera* and *Glaux maritima*; Figure

4.5) seeds had greater viability in samples collected from riverine marshes where salinity stress would be less and therefore less likely to adversely affect the seeds (Ungar 1979, Shumway and Bertness 1992, Necajeva and Ievinish 2008). *Atriplex patula,* however, exhibited the opposite pattern of viability with no germination from samples from the riverine marshes and higher viability in samples from the marine marshes (Figure 4.6c). Low germination of these seeds in riverine sediments may be due to the fact that there were few adults of these species within those marshes (Chapter II) so seed supply was limited and seeds of that species may have travelled there from considerable distances in salt water. Additionally, viability was tested through emergence, but many seeds have specific germination requirements that may not have been fulfilled (Ungar 1979, Jerling 1983, Hutchinson and Smythe 1986, Davy and Bishop 1991). If these requirements were not met, or met only partially, viability measured in this study would be an underestimate of all viable seeds in the seed bank.

Although seeds emerged from cleared areas within the marshes, these areas were more readily invaded vegetatively by neighboring plants. These invading plants seemed to compete with the emerging seedlings and may have limited seedling persistence. Although anecdotal, this suggests that species recovery from small disturbances is likely to occur through vegetative propagation rather than emergence from the seed bank (Shumway and Bertness 1992, Allison 1995, Brewer and Bertness 1996, Noe and Zedler 2000, Crain et al. 2008). As in other marshes, natural seedling recruitment in the South Slough marshes seems rare and recovery more often occurs through lateral spread of existing vegetation (Shumway and Bertness 1992). The seed banks of marshes along the South Slough estuary had high numbers of seeds and though not all were viable, a large numbers were able to germinate in the field (Figure 4.5, shaded bars). In the event of large scale disturbance where lateral vegetative recovery is not possible, this data suggests that seedling recruitment can help maintain the structure of the marsh vegetation. In these marshes, abundant seed was produced, though not all species contributed evenly to the seed bank. Most seeds were from plant species which account for most of cover in the marshes. The large numbers of seeds which seemingly remain near the parent plants confirms that when disturbance occurs, seeds are situated in areas of the marsh conducive to growth of that species and therefore the seed bank contributes to the maintenance of the population and marsh community.

Bridge III

Chapter IV detailed the composition and viability of six salt marshes along the South Slough. In combination with Chapter II, Chapter IV described the community both above and below ground within six marshes along an estuarine gradient, from marine-dominated to riverine-dominated environments. Presence in the seed bank does not necessarily indicate presence in the marsh, as seeds must germinate and survive in order to become part of the marsh community structure. The interactions between germinating seedlings and the existing neighboring vegetation in the emergent marsh can be both positive (facilitative) and negative (competitive). Chapter V examines the interactions between seedlings of five salt marsh species and the emergent marsh communities at three marshes within the South Slough.

CHAPTER V

INTERACTIONS BETWEEN SEEDLINGS AND EXISTING SALT MARSH VEGETATION ALONG AN ESTUARINE GRADIENT

Note

This work was developed with advice from S. D. Hacker (co-author). The original experimental design was suggested by S. D. Hacker. Alterations to the initial method, experimental installation, field work, data collection and analyses were performed by H. Keammerer. The following chapter was written with input and suggestions from S. D. Hacker.

Introduction

One objective in plant community ecology is exploration of the relative roles of biotic and abiotic factors in structuring communities (Booker 2006, Seifan et al. 2010). The abiotic environment is critical in dictating overall community structure, especially in areas with high levels of stress such as alpine, desert, and salt marsh communities (Callaway et al. 2002, Cavieres et al. 2006, Holzapfel and Mahall 1999, Bertness and Ewanchuck 2002). Though mediated by the environment, species interactions can play an important role in determining the inclusion of species within communities. Interactions between individuals can be either positive (facilitation) or negative (competition). Bertness and Callaway (1994) hypothesized that positive interactions should increase in areas with high levels of abiotic stress, where neighboring vegetation can have an ameliorating effect on the environment. Similarly, Grime (1973) and Thompson and Grime (1988) suggest that competition should be strongest in productive habitats

Differing interactions between species are expected along gradients where there are trade-offs between stress tolerance and growth (Wilson 2007, Van der Putten 2009). The Stress Gradient Hypothesis (SGH) suggests that in areas of increased abiotic stress (e.g., high temperature, high altitude, low precipitation, high salinity) there is an increase in the intensity and number of positive interactions that occur in the plant communities (Bertness and Callaway 1994). Evidence supporting SGH has been observed in freshwater marshes (Taylor et al. 1997, Luo et al. 2010), alpine vegetation worldwide (Callaway 1998, Olofsson 2004, Choler et al. 2001, Callaway et al. 2002, le Roux and McGeoch 2010), deserts (Fuentes et al. 1984), and salt marshes (Hacker and Bertness 1995, 1999, Pennings et al. 2003) as well as along nutrient (Wilson and Keddy 1986) and grazing gradients (Graff et al. 2007). Although evidence supporting this hypothesis is common, there are a number of cases in which greater intensity or occurrence of positive interactions did not occur with increased abiotic stress, but rather many studies find both competitive and facilitative interactions under environmentally stressful situations (Walker and Chapin 1986, Holzapfel and Mahall 1999, Pugnaire and Luque 2001, Liancourt et al. 2005). Some authors suggest that the observed differences in overall interaction direction are due to decreased facilitation rather than increased competition in the community when environments are mild (Pugnaire and Luque 2001). Since positive and negative effects act simultaneously, observed differences describe the balance of both types of interactions rather than the presence of one in the absence of the other (Holzapfel and Mahall 1999, Holmgren et al. 1997). The context of the observed interaction is also important as changes in both the abiotic (stress and disturbance) and biotic (composition of the community) will impact species differently. Strength and direction of the interactions are determined not only by the environment, but by the species in question, as each species interacts with the environment in a slightly different way. In addition, not all individuals within a species will react to the same environment (abiotic and biotic) in the same way (Hacker 2009).

Salt marshes are ideal ecosystems in which to examine the relationship between positive and negative interactions because they are usually easily manipulated and they have strong environmental gradients (Pennings et al. 2003). Abiotic stress increases with increased inundation and salt stress, so plants growing at lower elevations in salt marshes must be able to tolerate these conditions as they are more frequently inundated by salt water (Pennings and Callaway 1992). Positive plant interactions have been observed in marshes along the East Coast of North America (Hacker and Bertness 1995, 1999), but with little consistency over large spatial scales (Bertness and Ewanchuk 2002, Pennings et al. 2003). The relative importance of facilitation and competition in marshes along the West Coast of North America has not been studied.

Two environmental gradients are important in salt marshes: (1) tidal height with decreasing abiotic stress from the lower intertidal (high abiotic stress) to the higher intertidal elevations (low abiotic stress), and (2) location in the estuary with physical stress decreasing from marine to more riverine locations. Thus, areas in the low intertidal and/or at the mouth of the estuary are more stressful to plants than those in the high intertidal or more riverine marshes and one might assume positive interactions would dominate at these locations. In this study, we examined the Stress Gradient Hypothesis with seed addition manipulations in salt marshes along an intertidal and estuarine gradient in Oregon. Recruitment can be limited by the presence of neighboring vegetation

(Suding and Goldberg 1999, Goldberg 1987, Callaway and Walker 1997) and seedlings can be more sensitive than later life history stages and therefore may be more dependent on facilitative interactions (Callaway et al. 1996, Foster and Gross 1997, Foster 1999, Howard and Goldberg 2001). Seed additions were made to vegetated and cleared plots at three intertidal levels in each of three marshes to evaluate the role of competition and facilitation in the germination and survival of five species. We predicted that areas of higher stress should show increased germination and survival in plots with un-manipulated vegetation while in areas of lower stress, seeds should germinate more readily and show improved survival in plots without neighboring vegetation.

Methods

Site and Species Descriptions

This study was conducted in three marshes along an estuarine gradient in the South Slough National Estuarine Research Reserve located in a southern branch near the oceanic mouth of Coos Bay estuary on the southern Oregon Coast (Chapter II, Figure 2.1, Appendix A). The site with the greatest marine influence, Metcalf marsh (N 43° 20´07˝, W 124° 19´ 41˝), is located 4.4 kilometers from the mouth of Coos Bay estuary (Chapter II, Figure 2.1) with inundating seawater ranging in salinity from 20 to 31 g/kg. It is characterized by *Salicornia virginica* L. and *Distichlis spicata* (L.) Greene with small patches of *Triglochin maritima* L. and *Jaumea carnosa* (Less.) A. Gray in the lower elevations and by intermittent patches of *Carex lyngbyei* Hornem. and *Deschampsia caespitosa* (L.) P. Beauv along the upland boundary (Table 5.1). The low marsh is characterized by higher pore water salinity and longer periods of inundation than the high marsh (Table 5.1, see also Chapter II).

Table 5.1. Average abiotic conditions and existing community richness and biomass of sites and intertidal zones of transplant locations (Chapter II). Pore water salinity and redox potential are presented as the minimum and maximum values taken from July 2008, July 2009 and January 2010 (minimum; maximum). Species abbreviations are the following: *Agrostis stolonifera* (AGST), *Argentina egedii* ssp. *egedii* (AREG), *Atriplex patula* (ATAP), *Carex lyngbyei* (CALY), *Carex obnupta* (CAOB), *Cuscuta salina* (CUSA), *Deschampsia caespitosa* (DECA), *Distichlis spicata* (DISP), *Glaux maritima* (GLMA), *Grindelia integrifolia* (GRIN), *Hordeum brachyantherum* (HOBR), *Hordeum jubatum* (HOJU), *Jaumea carnosa* (JACA), *Juncus arcticus* ssp. *balticus* (JUBA), *Plantago maritima* (PLMA), *Salicornia virginica* (SAVI), *Spergularia marina* (SPMA), *Triglochin maritima* (TRMA), *Trifolium wormskjoldii* (TRWO).

Site	Marine (Metcalf marsh)			Mesohaline (Hidden Creek)			Riverine (Tom's Creek)		
Intertidal zone	Low	Mid	High	Low	Mid	High	Low	Mid	High
Inundation (days/mo)	13.6	8.8	4.2	23.0	15.1	1.7	16.0	4.8	0.3
Pore water salinity (g/kg)	20; 35	13; 24	2; 11	18; 30	20; 27	10; 22	17; 21	10; 18	10; 25
Redox potential (mV)	-206; 80	-130; 61	-47; 108	-234; 69	-29; 54	34; 107	-468; 47	-109; 94	-25; 187
Species richness	5	7	10	5	9	10	3	6	11
Total biomass (dry g/m^2)	505	523	505	568	568	791	767	1226	1373
Species biomass (percent total biomass)									
AGST	--	--	--	--	9	--	--	45	25
AREG	--	--	--	--	--	--	--	--	<1
ATAP	<1	2	<1	--	<1	--	--	--	--
CALY	--	26	--	--	17	<1	<1	10	20
CAOB	--	--	--	--	--	--	96	--	--
CUSA	<1	--	<1	--	<1	--	--	--	--
DECA	--	<1	41	--	2	50	--	19	24
DISP	46	30	5	24	2	18	--	--	1
GLMA	--	--	--	--	2	2	--	--	--
GRIN	--	--	<1	--	--	--	--	--	16
HOBR	--	--	--	--	--	3	--	--	--
HOJU	--	--	<1	--	--	--	--	--	--
JACA	--	<1	10	66	37	22	--	7	<1
JUBA	--	--	8	--	--	--	--	7	7
PLMA	--	--	--	--	3	<1	--	--	--
SAVI	39	3	5	9	--	1	--	--	2
SPMA	--	--	--	<1	--	--	--	--	--
TRMA	14	39	31	<1	28	4	3	12	4
TRWO	--	--	--	--	--	--	--	--	<1

The mesohaline site, Hidden Creek marsh (N 43° 17´33˝, W 124° 19´ 27˝), is located 9.2 kilometers from the mouth of the Coos Bay estuary (Figure 5.1) with inundating water salinities ranging from 15 to 28 g/kg. This pocket marsh is dominated primarily by *Deschampsia*, with *Jaumea*, *Triglochin* and *Agrostis stolonifera* L. *Carex lyngbyei* is present in small patches throughout the mid marsh elevations and near freshwater inputs (Table 5.1). The pore water salinities are similar in the low and mid marsh and lowest in the high marsh (Table 5.1). The inundation stress is considerably higher in the low areas of this marsh. The most riverine site, Tom's Creek marsh (N 43° 16´45˝, W 124° 19´ 06˝), is 11.2 kilometers from the mouth of Coos Bay estuary (Figure 5.1) where the salinity of the inundating water ranges from 0 to 21 g/kg. This high marsh is dominated primarily by large patches of *Deschampsia* mixed with *Agrostis stolonifera* and *Carex lyngbyei*. The low portions of the marsh, along tidal channels and at the edge of the slough proper, are dominated by *Carex obnupta* L.H. Bailey. Although the high marsh at Tom's Creek has the highest salinity within the marsh due to the combination of evapotranspiration and infrequent flooding, it also has the least reducing environment within the sediment and the fewest hours of inundation.

We used five salt marsh species in this study: *Salicornia virginica, Distichlis spicata, Triglochin maritima,* and *Plantago maritima* (Lam.) A. Gray are perennial species while *Atriplex patula* L. is an annual species. Seeds of these species were collected from three study marshes in the fall of 2009 and each species seeds were combined in equal portions from each site before viability testing or out-planting. To ensure that the seeds were viable before use in the experiments, they were tested at the Seed Laboratory at Oregon State University using Tetrazolium staining techniques

(Moore 1972). Seed viability varied from intermediate (*Salicornia virginica:* 66%; *Distichlis spicata:* 89%), to high (*Triglochin maritima:* 85%; *Plantago maritima*: 89%; *Atriplex patula:* 91%).

Experimental Design

In each marsh described above, nine paired plots were established and seeds of a single species were added to a total of 270 plots at three intertidal levels (low, mid and high). For each of the paired plots, one was cleared of the existing vegetation and litter using hand clippers ('cleared') and in the other was left undisturbed ('vegetated'). Twenty-five seeds of the five species (one species per plot) were added to each plot. To prevent seed loss, seeds were caged with woven wire mesh (hardware cloth: 8 cm x 60 cm; 6.4mm mesh), which was shaped into circular 'corrals' (20 cm diameter). Initial seed loss was prevented by a layer of transparent fabric (organza; 30 cm x 30 cm) placed under the hardware cloth 'corral' and kept tented off the substrate by the placement of a wooden stick inserted into the center of the plot. This allowed space for germination, but prevented the seeds from floating out of the plots during high tide. Cleared plots were maintained throughout the growing season. In plots with existing vegetation, percent cover of each non-target species was recorded at peak growth (mid-July 2010).

Seedlings began to germinate mid-February 2010 at which time the organza layer was removed. Subsequent germination was monitored weekly through March 2010 at which point the majority of germination was assumed to have occurred. Plot monitoring continued every other week to observe survivorship and mortality of seedlings through the end of the growing season (September 2010). Germination and survival were analyzed as percent out of 25 seeds.

Interaction Intensity

Interaction intensity can be measured as either absolute or relative impact of neighboring vegetation on the target individual, though using relative measures has been emphasized as it incorporates variability in environment (Wilson and Keddy 1986, Grace 1993, Wilson and Tilman 1995, Weiglet and Jolleffe 2003). Here, interaction intensity of existing vegetation with germinating seedlings was evaluated using the relative neighbor effect (RNE) based on both germination and survival of the seedlings (Markham and Chanway 1996, Goldberg et al. 1999). RNE was calculated for both germination and survival of the target species as:

$$\text{RNE}= (X_{\text{vegetated}}-X_{\text{cleared}})/\max\,(X_{\text{vegetated}} \text{ or } X_{\text{cleared}})$$

where X is either germination or survival, $X_{\text{vegetated}}$ is the abundance from plots with existing vegetation, and X_{cleared} is the abundance from plots where existing vegetation was removed. The denominator of the equation is based on the maximum value of either the vegetated or cleared plot; this creates a symmetric distribution of possible values around zero from -1 to 1 (Armas et al. 2004). Where plants show greater germination or survival in the presence of neighbors, the values of RNE are positive (facilitation) whereas less germination or decreased survival with neighboring vegetation yields negative RNE values (competition). RNE values close to zero indicate no effect of existing vegetation. The mean RNE, both based on germination ($\text{RNE}_{\text{germination}}$) and survival ($\text{RNE}_{\text{survival}}$), for each species was arcsine transformed and compared to zero using a one-sided t-test.

In addition, the percent germination and survival for each species were arcsine square root transformed to fit assumptions and were analyzed separately using a three-way ANOVA with marsh, intertidal height, and vegetation treatment (cleared or vegetated) as fixed factors. $RNE_{germination}$ and $RNE_{survival}$ were arcsine transformed and analyzed with separate two-way ANOVAs with marsh and intertidal height as fixed factors.

Results

Germination and survival of the five plant species varied significantly among marshes, intertidal heights, and between cleared and vegetated plots (Table 5.2, Figure 5.1). For all of the species except *Atriplex*, cleared plots had significantly more germinating seedlings than vegetated plots (Table 5.2, Figure 5.1). Germination and survival of *Triglochin* differed between marshes by intertidal height resulting in a significant marsh x height interaction (Table 5.2, Figure 5.1a). For *Triglochin*, high plots at the marine site (Metcalf) and low plots in the riverine site (Tom's Creek) had the most germination, but overall survival was highest at the mesohaline site (Hidden Creek) (Figure 5.1a). *Salicornia* showed significant variation in survival and germination with intertidal height, but the effect was inconsistent across marshes and vegetation treatment, resulting in a significant three-way interaction (Table 5.2, Figure 5.1b). For *Salicornia*, germination and survival were higher in the mid marsh at both the marine and mesohaline sites (Metcalf and Hidden Creek), but highest in the high intertidal at the riverine site (Tom's Creek). Though survival was generally higher in cleared plots, more *Salicornia* seedlings survived in the vegetated plots in the high intertidal at the marine site (Metcalf), confounding the effect of vegetation (Figure 5.1b). *Atriplex* was the only species for which germination in both cleared and vegetated plots was not statistically different (Table 5.2, Figure 5.1c).

Table 5.2. ANOVA (F-ratio) results for effects of marsh (M), height (H), and vegetation treatment (V) on germination, survival, RNE $_{\text{germination}}$ and RNE $_{\text{survival}}$ of five species.

sources of variation	d.f.	*Triglochin maritima*	*Salicornia virginica*	*Atriplex patula*	*Distichlis spicata*	*Plantago maritima*
Germination						
Marsh	2	1.58	2.96	7.84**	10.46**	4.71*
Height	2	3.17*	8.15**	36.26**	37.41**	29.23**
Vegetation	1	69.64**	77.56**	3.61	46.22**	26.05**
M x H	4	6.53**	2.15	9.38**	8.59**	1.06
M x V	2	2.23	0.07	0.42	1.27	2.28
H x V	2	1.18	7.13**	0.08	7.73	1.25
M x H x V	4	2.11	2.59*	0.96	1.84	2.27
error	144					
Survival						
Marsh	2	11.92**	1.51	10.53*	0.92	11.26**
Height	2	7.17**	9.23**	12.56**	2.27	3.74*
Vegetation	1	31.96**	31.02**	5.42*	8.82**	6.00*
M x H	4	3.01*	9.79**	3.26*	0.34	1.95
M x V	2	5.30*	2.14	9.38**	4.18*	1.76
H x V	2	0.50	4.95*	0.02	0.98	0.27
M x H x V	4	1.30	5.25**	0.39	0.75	0.74
error	144					
RNE(Germination)						
Marsh	2	1.69	4.25*	0.56	3.68*	1.58
Height	2	2.99	0.75	0.20	1.05	0.22
M x H	4	2.55*	3.79*	1.39	1.23	1.89
error	72					
RNE(Survival)						
Marsh	2	5.01*	1.23	1.21	9.23**	0.19
Height	2	0.32	3.65*	11.88**	10.51**	0.30
M x H	4	0.20	0.57	1.32	7.06**	0.48
error	72					

** $p<0.001$, * $p<0.05$

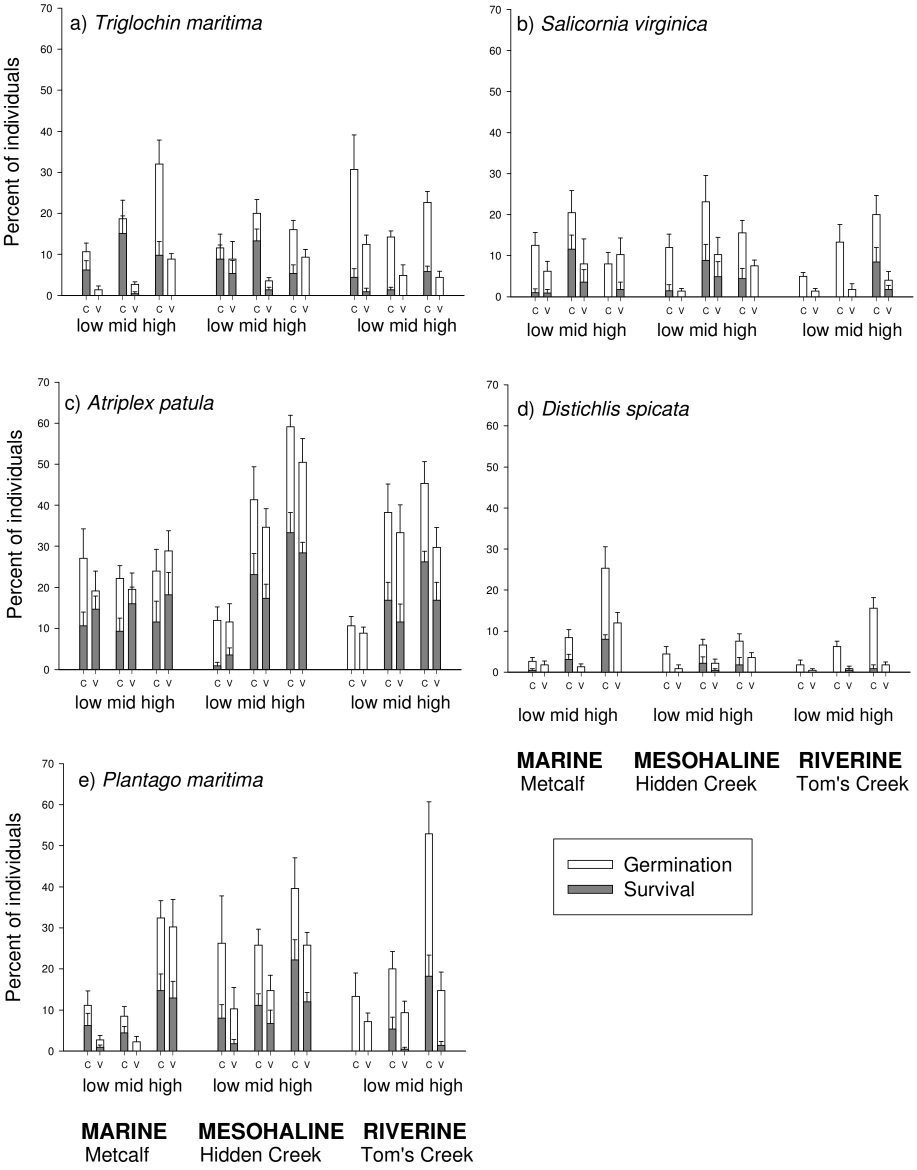

Figure 5.1. Percent germination and survival of 25 out-planted seeds of five species at three intertidal levels (low, mid, high) in three marshes along an estuarine gradient (Marine: Metcalf, Mesohaline: Hidden Creek, Riverine: Tom's Creek) in both cleared (C) and vegetated (V) plots. Each bar represents mean (n=9) + 1SE.

For *Atriplex*, germination was similar across all intertidal heights at the marine site (Metcalf), but differed by intertidal height at both the mesohaline and riverine sites (Hidden Creek and Tom's Creek), resulting in a significant interaction between marsh and intertidal height (Figure 5.1c). More *Atriplex* seedlings survived in vegetated plots both at Metcalf and the low marsh at Hidden Creek, which confounded the effect of vegetation, marsh and intertidal height for this species. *Distichlis* had the lowest germination rates of all the plant species with appreciable germination apparent only at the marine site (Metcalf) (Table 5.2, Figure 5.1d). *Plantago* seeds had better germination and survival in high intertidal plots without existing vegetation at all the sites although the mesohaline site (Hidden Creek) showed the best response (Table 5.2, Figure 5.1e).

Using germination as the response variable, we found that the species interactions of the five plant species with existing vegetation were negative or neutral (Figure 5.2, Table 5.2). We found that the highest proportion of strong negative species interactions tend to be at high intertidal heights and at riverine and mesohaline sites (Figure 5.3). For example, germinating seedlings of all species experienced the most significant competition with existing vegetation in the mid and high intertidal plots at the riverine site (Tom's Creek) (Figure 5.3).

As mentioned earlier, survival of seedlings was variable among sites with some species showing total mortality especially at the riverine site (Figure 5.1). Considering those species that survived, we found that the species interactions of the five plant species with existing vegetation were positive, negative, or neutral (Figure 5.4). However, the majority of $RNE_{survival}$ interactions were not significantly different from zero; thus the existing vegetation had no effect on the survival of most species (Figure 5.5). The only significant positive interaction occurred with *Atriplex* in the mesohaline and marine sites. Existing vegetation had a significant negative effect on the survival of some of the target seedlings particularly in the high intertidal of all three marshes.

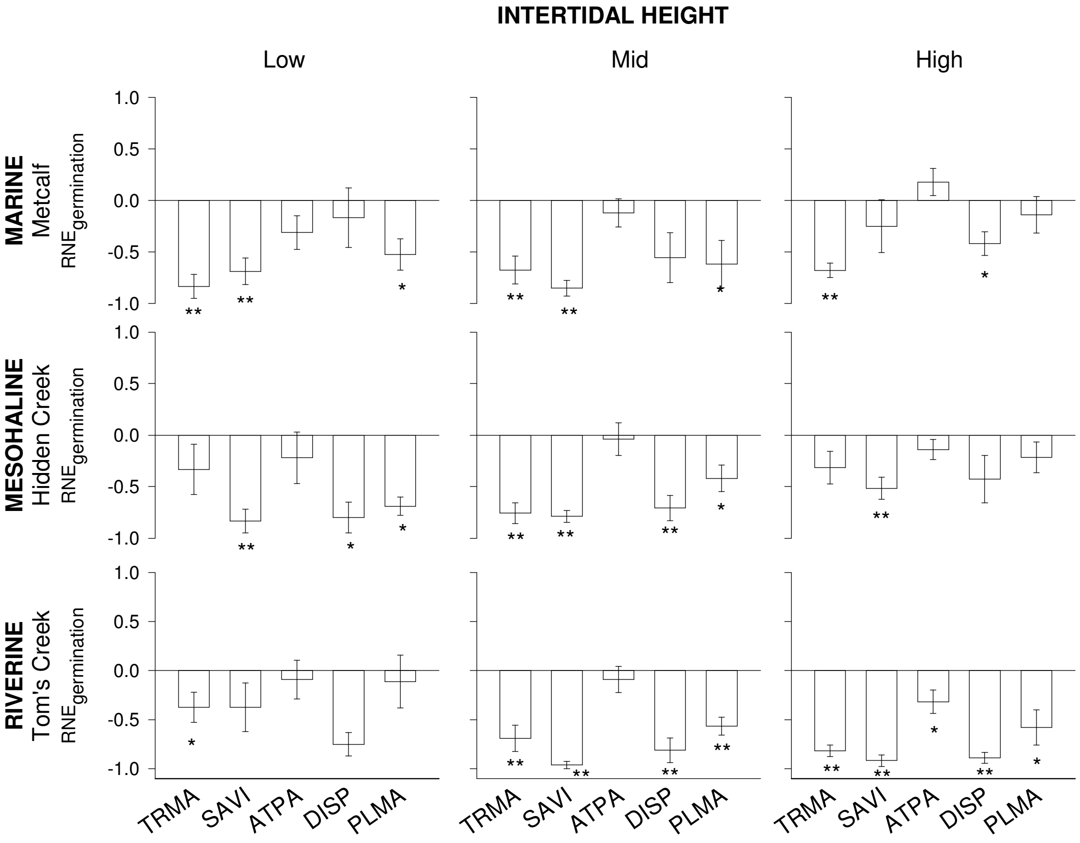

Figure 5.2. Relative Neighbor Effect (RNE) for seedling germination of five species at three intertidal levels (low, mid, high) in three marshes along an estuarine gradient (Marine: Metcalf, Mesohaline: Hidden Creek, Riverine: Tom's Creek). Each bar represents mean (n=9) ± 1SE. * indicates that mean differs significantly from zero (one sample t-test) $p<0.05$, **$p<0.001$. Species: TRMA*: Triglochin maritima;* SAVI*: Salicornia virginica;* ATPA*; Atriplex patula;* DISP*: Distichlis spicata;* PLMA*: Plantago maritima*.

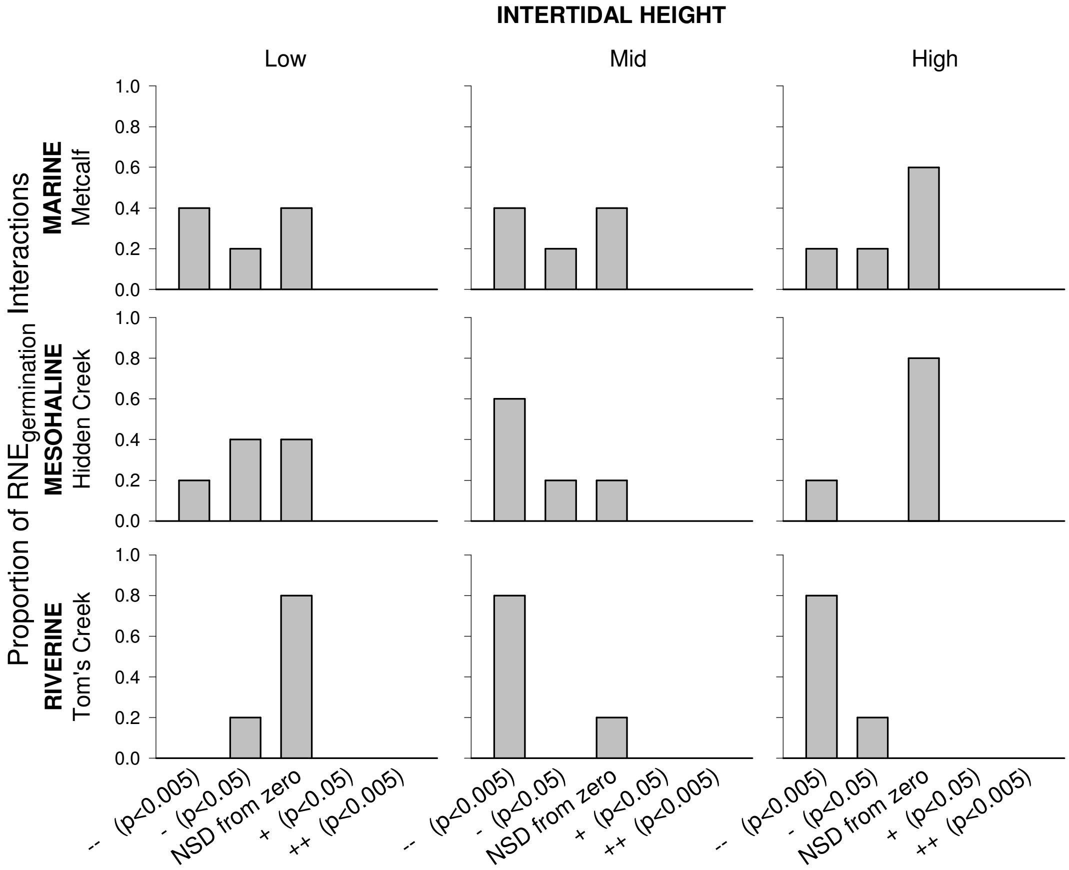

Figure 5.3. Proportion of interactions in which the Relative Neighbor Effect for germination ($RNE_{germination}$) is either positive or negative and not significantly different (NSD) from zero, different from zero at $p<0.05$, or different from zero at $p<0.005$ for all species in each intertidal level of each marsh.

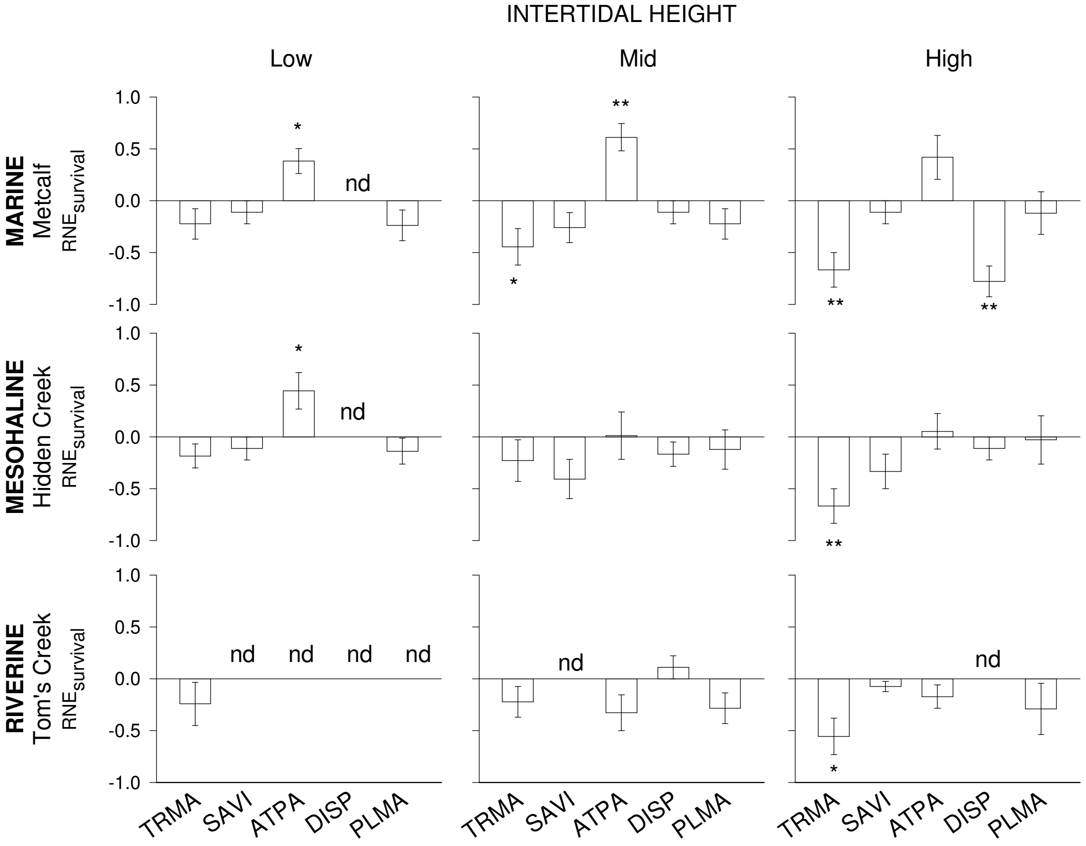

Figure 5.4. Relative Neighbor Effect (RNE) for seedling survival of five species at three intertidal levels (low, mid, high) in three marshes along an estuarine gradient (Marine: Metcalf, Mesohaline: Hidden Creek, Riverine: Tom's Creek). Each bar represents mean (n=9) ± 1SE. * indicates that mean differs significantly from zero (one sample t-test) $p<0.05$, $^{**}p<0.001$. nd: no data because no surviving individuals. Species: TRMA*: Triglochin maritima;* SAVI*: Salicornia virginica;* ATPA*; Atriplex patula;* DISP*: Distichlis spicata;* PLMA*: Plantago maritima.*

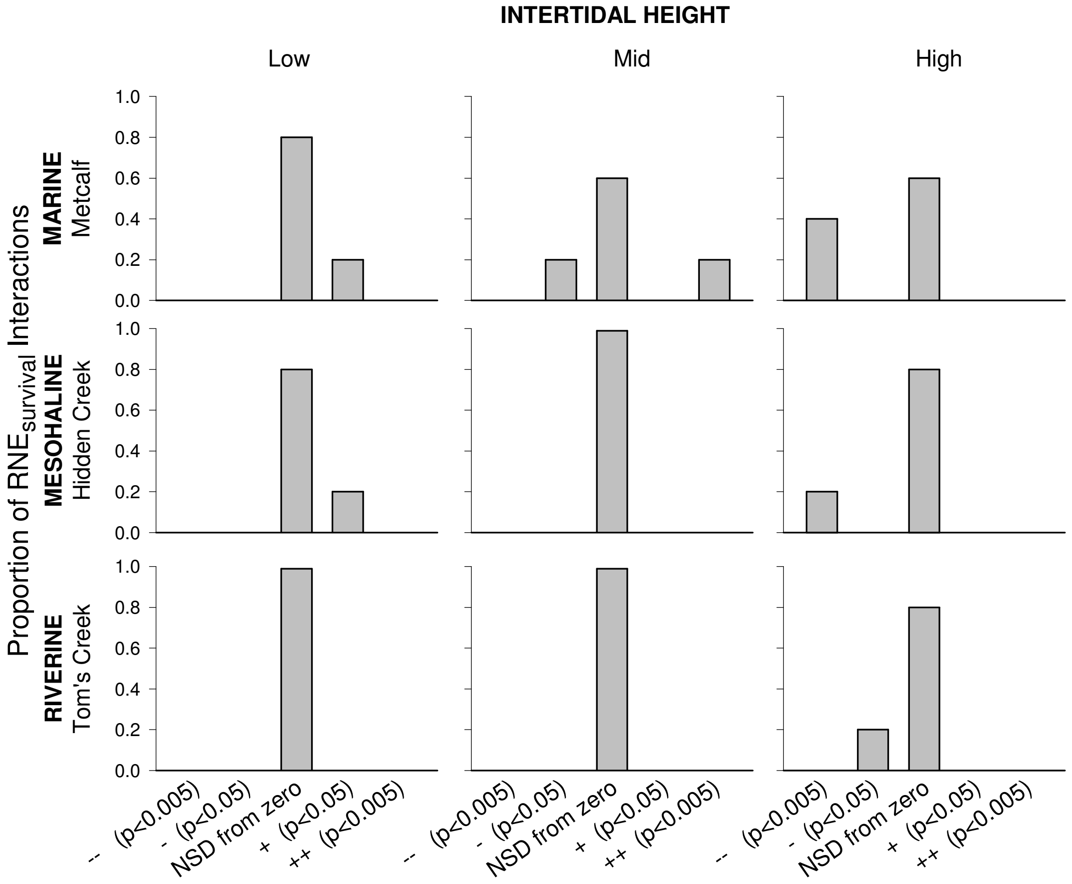

Figure 5.5. Proportion of interactions in which the Relative Neighbor Effect for survival (RNE$_{survival}$) is either positive or negative and not significantly different (NSD) from zero, different from zero at $p<0.05$, or different from zero at $p<0.005$ for all species in each intertidal level of each marsh.

Discussion

We found that many of the interactions measured across the intertidal and estuarine gradient within this Pacific coast estuarine system were negative or neutral (Figures 5.2-5.5). The direction of the interactions depended on life history stage to some extent, with neighboring plants having a neutral or negative effect on seed germination, but in most cases, a neutral or positive effect on seedling survival especially at lower intertidal locations (Figures 5.3, 5.5). This is in contrast to other salt marsh studies in New England (e.g., Bertness and Hacker 1994, Hacker and Bertness 1995, 1999) and other locations (e.g., Taylor et al. 1997, Dormann et al. 2000). These studies showed a greater prevalence of positive interactions across salt marsh intertidal gradients. The previous work (cited above), however, was primarily evaluated using transplants of adult individuals (Bertness and Hacker 1994, Hacker and Bertness 1995, 1999, Taylor et al. 1997, Dormann et al. 2000) and occasionally greenhouse germinated seedlings (Dormann et al. 2000). The life history stage examined in the current study (seedlings) may, therefore, contribute to the primarily negative and neutral interactions observed. In this study, we also found that the intensity of the interactions between species and their neighboring plant community varied greatly depending on the context in which they occurred (Figures 5.2-5.5). Factors including location within the estuary, intertidal height, and species identity all appear to be important in determining the strength of the interactions. Below we discuss these factors in more detail.

First, we found that species interactions were overall more negative in the riverine site, Tom's Creek, compared to the mesohaline and marine sites (Figures 5.2, 5.3). This is likely due to two related factors: more benign physical conditions and higher neighboring plant productivity (Table 5.1). Tom's Creek was characterized by overall high vegetation biomass and species richness compared to the other study sites (Table 5.1) as well as some of the least saline, waterlogged, and reduced sediments (Table 5.1). The intensity of negative interactions at the marine and mesohaline sites were more muted (Figures 5.2, 5.3), corresponding to lower overall biomass, higher salinity, more tidal inundation, and more reducing sediments (Table 5.1). But, nonetheless, we found that even at the most marine site, and thus potentially the most stressful marsh, negative interactions dominated at the germination stage (Figures 5.2, 5.3).

Second, we found that species interactions were overall more negative at high intertidal elevations compared to lower intertidal elevations especially at the riverine site (Figures 5.2-5.5). The high intertidal generally had much higher biomass and species richness, and more benign sediment chemistry (Table 5.1). Depending on the site, the high intertidal is dominated by tall grasses such as the pasture grass, *Agrostis stolonifera*, introduced from Western Europe, which creates a thick layer of litter and leaves with very little open space (Wu 1981), the native tufted hair grass, *Deschampsia caespitosa*, and the sedge, *Carex lyngbyei*. In contrast, the mid and low intertidal elevations had much lower biomass and species richness and more stressful sediment conditions (Table 5.1). The neighboring vegetation consisted mostly of salt tolerant and lower stature plants including *Distichlis spicata*, *Salicornia virginica*, and *Jaumea carnosa*. The interactions in these areas tended to be less negative, more neutral, or even positive dependent to some degree on whether germination or survival was considered (Figures 5.2-5.5).

Third, we found that species differed in how neighboring vegetation affected the germination of seeds and seedling survival. For some species, the absence of vegetation allowed for germination and establishment in areas of the marsh in which they do not usually occur. For example, *Salicornia* was able to germinate and persist in the absence of existing vegetation both in the mid and high intertidal at Hidden Creek as well as the high intertidal at Tom's Creek (Figure 5.1) though it is uncommon in both marshes (Table 5.1). The seed bank of the high intertidal at Tom's Creek contained comparatively few *Salicornia* seeds, which indicates that seed supply may limit the distribution of this species (Chapter IV, Appendix D). Additionally, *Triglochin* germinated well in the high marsh in Tom's Creek, though it is not commonly found there (Table 5.1). *Triglochin* is highly clonal and perennial (Davy and Bishop 1991) and likely spreads through the marsh primarily vegetatively. The seeds of this species are positively buoyant and salt tolerant (Necajeva and Ivenish 2008) and are found throughout the marsh (Keammerer, pers. obs.), so the adult population is likely not limited by seed supply. It seems likely therefore, that *Triglochin* is competitively excluded from this more benign high marsh as it was unable to survive in the presence of neighbors (Figure 5.1).

In contrast, *Plantago* had good germination and survival both in the presence and absence of neighbors in the high intertidal of Metcalf and Hidden Creek, which indicates that competition does not prevent the spread of this species to the high intertidal of the lower estuarine marshes (Figure 5.1). The seeds of this species are negatively buoyant, and so this species may have limited dispersal to higher intertidal heights (Rand 2000). However, in the riverine marsh, Tom's Creek, germination of this species was decreased by existing vegetation, which is consistent with previous work, which suggests that this species does not germinate well in the presence of neighbors (Dormann et al. 2000) or in shaded areas (Jerling and Liljelund 1984).

Another species whose distribution in the intertidal may be affected by species interactions is *Salicornia.* Despite the fact that *Salicornia* is found only occasionally in the high marsh (Table 5.1), it germinated and survived in the high marsh regions of both Hidden Creek and Tom's Creek in the absence of neighboring vegetation (Figure 5.1) suggesting that the distribution of this species is limited by competition with other species. However, *Salicornia* did not survive in the low and mid marsh of Tom's Creek, suggesting intolerance of that environment. *Salicornia* had improved germination in the presence of salt water (Shumway and Bertness 1992, Kahn and Weber 1986) suggesting that the low salinity of the low and mid areas of Tom's Creek may be inhibiting the expansion of this species into the marsh. Although *Salicornia* seeds are positively buoyant, the high marsh is rarely inundated, so seed supply may also limit expansion of this species.

Distichlis had the lowest germination regardless of marsh or intertidal height, but germinated more frequently in bare areas, a finding consistent with other studies (Bertness and Ewanchuk 2002). Like *Triglochin*, *Distichlis* seems to be competitively excluded from the high marsh in Metcalf, for though it germinated and survived best in this area, it is not commonly found there. However, exclusion of seedlings may not be the only possible explanation as *Distichlis* seedlings are uncommon even in close proximity to seed producing adults (Shumway and Bertness 1992), so it is likely that this species relies more heavily on vegetative propagation than seed production. Although natural small openings in marsh vegetation often had seedlings emerging from the seed bank, larger gaps (e.g., salt pans) were more commonly devoid of seedlings (Keammerer, pers. obs.).

In the present study, positive interactions with existing vegetation were seen only with *Atriplex*. This would seem to be consistent with the life history of this species; it is the only study species that is an annual (Bassett and Munro 1987) and thus must coexist with neighboring vegetation in order to persist from year to year. Positive associations for *Atriplex* have also been seen in salt marshes on the East Coast of North America where it grew better and was more able to recover from insect herbivory in the presence of neighbors (Bertness and Ewanchuk 2002, Rand 2004). Additionally, naturally germinating seedlings occur and survive more commonly in the high marsh where salt stress does not inhibit germination (Ungar 1996, Hacker and Bertness 1999, Rand 2000). The positive associations with neighboring vegetation allows *Atriplex* to persist lower in the marsh than it could normally have without neighbors suggesting that positive interactions extend the distribution of this plant both among intertidal elevations and among marshes (Figure 5.1d).

We found fewer positive interactions than expected based on other salt marsh studies (e.g., Bertness and Hacker 1994, Hacker and Bertness 1995, 1999, Pennings et al. 2003), we hypothesize two possible reasons for the overall lack of positive interactions in these marshes. The intensity and direction of interaction depended somewhat on the life history stage of the seedling, with competition being more important for seedling germination than their survival (Figures 5.2, 5.4). This may be due, in part, to the shading effect of existing vegetation. Despite relatively low neighboring plant biomass during germination, the cleared plots would receive increased light which increases germination (Leggatt 1945, Jerling 1983). Differences in interaction intensity and direction between different life history phases have been noted in other studies (Walker 1994). For instance, Goldberg and Novoplansky (1997) found an increase in competition with increased productivity of the community if survival was measured, but not growth. Contrarily, Ladd and Facelli (2005) found that competitive effects on biomass increased with productivity but more neutral effects were observed when survival was measured. We found that competitive effects were stronger at the germination stage while having less of an influence on survival.

Another possible factor that influences the strength and direction of interactions between plants is the climate, which may influence the results of the present study in two possible ways. Firstly, the relatively cool and moist climate present along the Pacific Northwest coast may decrease the likelihood of positive interactions even in the relatively harsh environment of the marsh. Without strong solar radiation and surface evaporation, the mid marsh may not reach hypersaline conditions that characterize salt marshes elsewhere (e.g., Bertness and Hacker 1994, Hacker and Bertness 1995, 1999). Additionally, interannual variation can be significant (Shevtsova et al. 1995). The summer during which this study was performed was cooler and moister than usual (National Climatic Data Center). In wet years or wet climates there is often an observable increase in competitive interactions between plants (Fuentes et al. 1984, de Jong and Klinkehamer 1998, Frost and McCougal 1989, Belsky 1994, Holzapfel and Mahall 1999, Bertness and Ewanchuk 2002, Pennings et al. 2003). In some cases, positive interactions are entirely absent in communities in wet years (Greenlee and Callaway 1996) or can be present only under wet conditions (Teilborger and Kadmon 2000).

Although previous studies have indicated that positive interactions between plant species are common in salt marshes (Bertness and Hacker 1994, Hacker and Bertness 1995, 1999), the current study indicates that these interactions are not consistent across all marshes. Additionally, the number and extent of negative or neutral interactions observed for seedling germination in the salt marshes of South Slough indicate that the role of positive interactions within marshes may be dependent on the life history stage of the studied species; adult transplants may interact differently than younger transplants (Dormann et al. 2000). Seed and seedling transplant studies are uncommon in the literature and more studies would be necessary to evaluate whether the negative interactions seen in the current study are present in other marshes or whether marshes in Oregon are uniquely dominated by negative interactions.

Establishment of new seedlings in the presence of existing vegetation can alter the structure of the marsh community and shift the distribution of species within the marsh. This study illustrates the role of species interactions in germination and establishment of species within the relatively unstudied marshes of the Oregon coast. Seedling interactions with the marsh community were largely negative. High productivity of the marsh community in the high intertidal zones increased the strength and ubiquity of negative interactions. Positive interactions occurred in areas with high pore water salinity and strongly reduced sediments. Though interactions between seedlings and the existing plant communities within marshes along an estuarine gradient were primarily negative, they were also highly context dependent.

CHAPTER VI

GENERAL CONCLUSION

The structure and composition of salt marshes in South Slough were defined, primarily, by four communities dominated by four common species, *Carex lyngbyei*, *Deschampsia caespitosa*, *Distichlis spicata* and *Salicornia virginica*. The distribution of smaller subgroups within these communities was affected primarily by the within-marsh intertidal gradient rather than by the position of the marsh along the estuarine salinity gradient. Changes in the magnitude of abiotic parameters particularly marsh pore water salinity, pH and sediment texture were primarily responsible for changes in the vegetation structure along the estuarine gradient. Position of the marsh along the estuary was not as significant a defining factor as the more local abiotic conditions, but communities dominated by the most salt tolerant species (*Distichlis spicata* and *Salicornia virginica*) were absent from the riverine marshes. In general, the abiotic conditions that vary along the within-marsh intertidal gradient were strongly associated with community type. Communities within the South Slough seem to develop based principally on the abiotic conditions, and therefore are likely to be dictated primarily by the physiological tolerances of each species.

As predicted, the high marsh dominant species, *Carex lyngbyei*, in a marine-dominated salt marsh, did not exhibit the same amount of growth or the same growth rate when transplanted into the low marsh, regardless of the presence of neighboring vegetation. This suggests that the lower edge of the *Carex* dominated zone was determined by the physiological tolerance of the species to the abiotic conditions rather than by competitive interactions with the low marsh dominant species (*Distichlis spicata* and *Salicornia virginica*). In contrast to previous studies, the low marsh dominant species did not exhibit improved growth in the high marsh in the absence of neighboring vegetation (Bertness and Ellison 1987, Bertness 1991a,b, Hacker and Bertness 1995, 1999). Neither *Salicornia* nor *Distichlis* exhibited the expected competitive release when transplanted into the high marsh indicating that competition with high marsh species does not limit the upper marsh distributional boundary for these species. There was, however, considerable inter and intra-specific competition between individuals of *Salicornia* and *Distichlis* and the emergent marsh community when ramets were transplanted within their normal zone of distribution.

In contrast to the composition of the emergent marsh communities, the composition of the seed bank was more similar within a given marsh than within areas dominated by the same community type from different marshes. Overall similarity with the emergent marsh communities was highest in the low marsh (*Distichlis/Salicornia*) community and within the low estuarine (marine-dominated) marshes. This may be due, in part, to greater export of seed from the low marsh into the estuary, but it would be necessary to collect seeds transported from the marsh in order to establish the connectivity of the low marsh seed bank with marshes further up the estuary. Most seed seems to be transported to the higher marsh communities, which were more similar within individual marshes, indicating some isolation from the other marshes despite close proximity. Seed density in sediment samples was relatively high, but the viability of the species was highly variably both by collection location and species. Seed and seedlings from collected sediment samples as well as naturally emerged seedlings from cleared marsh areas were primarily from the few dominant species within the marshes.

Competition was not limited to the transplanted ramets within the marine-dominated salt marsh. The interactions between seedlings and emergent marsh vegetation were primarily negative (competitive) or neutral, but this was partially dependent on the life history stage of the individual. In general, more of the interactions were negative or neutral for germination and neutral or positive (facilitative) for survival, particularly in the low intertidal. Interaction intensity was generally more positive in the low intertidal and within the lower region of the estuary.

Salt marsh communities in South Slough were relatively consistent within dominant vegetation types and ranges of abiotic factors. Seed banks had high seed density and were generally distinct between marshes, indicating that there is little mixing of higher marsh community seeds. Artificially cleared patches within marshes allowed for germination of seeds from the seed bank, but the majority of seedlings were of the dominant salt marsh species, suggesting that in the event of small scale disturbance, the overall structure of the marsh is likely to remain unchanged. However, though seedlings were able to germinate in cleared areas where adults of that species were absent, illustrating the ability of the marsh to shift species composition in the event of larger scale disturbance, the presence of the existing emergent marsh community negatively affected germination and seedling establishment. Competition was an important factor in the germination and establishment of seedlings, but had limited impact on the boundaries between intertidal zones dominated by different species.

Most of the previous work on structure and function in salt marsh communities has occurred along the East Coast of the United States, where broad, expansive marshes with clear patterns of zonation are present. In those marshes, the low boundaries of the zones of vegetation are dictated by the abiotic tolerances of the species while the upper boundaries are defined by competitive interactions with the higher marsh dominants. Some species are able to increase their range within a marsh by the ameliorating effect of other species. These positive interactions are common, particularly in the lower marsh elevations where salt stress is more pervasive.

The results of this study, however, indicate that the salt marshes within estuaries along the Pacific Coast do not function in the same way, as was assumed. Although high marsh species are limited by abiotic stress, the low marsh species do not seem to be competitively excluded from the high marsh regions. Rather, something physiological (stress of anoxia) and perhaps biotic (herbivory) are limiting the expansion of the low marsh species into the higher marsh elevations. Additionally, though some of the species (*Distichlis spicata* and *Salicornia virginica*) in the South Slough marshes are present in marshes along the East Coast, and are known to be facilitators in those marshes, they do not serve the same function in these West Coast marshes. In fact, very few positive interactions between the existing communities and germinating seedlings were observed.

Although salt marshes throughout the world exist at similar latitudes and under similar tidal regimes, the results of this study indicate that it is inappropriate to assume that all salt marshes function in the same way. The marshes along the Pacific Coast are markedly different from other salt marshes and should be treated as unique communities.

APPENDIX A

STUDY MARSHES AND MAJOR SPECIES

This appendix contains aerial and ground level photographs of the six study marshes as well as images of the major species within the marshes from Cooke 1997.

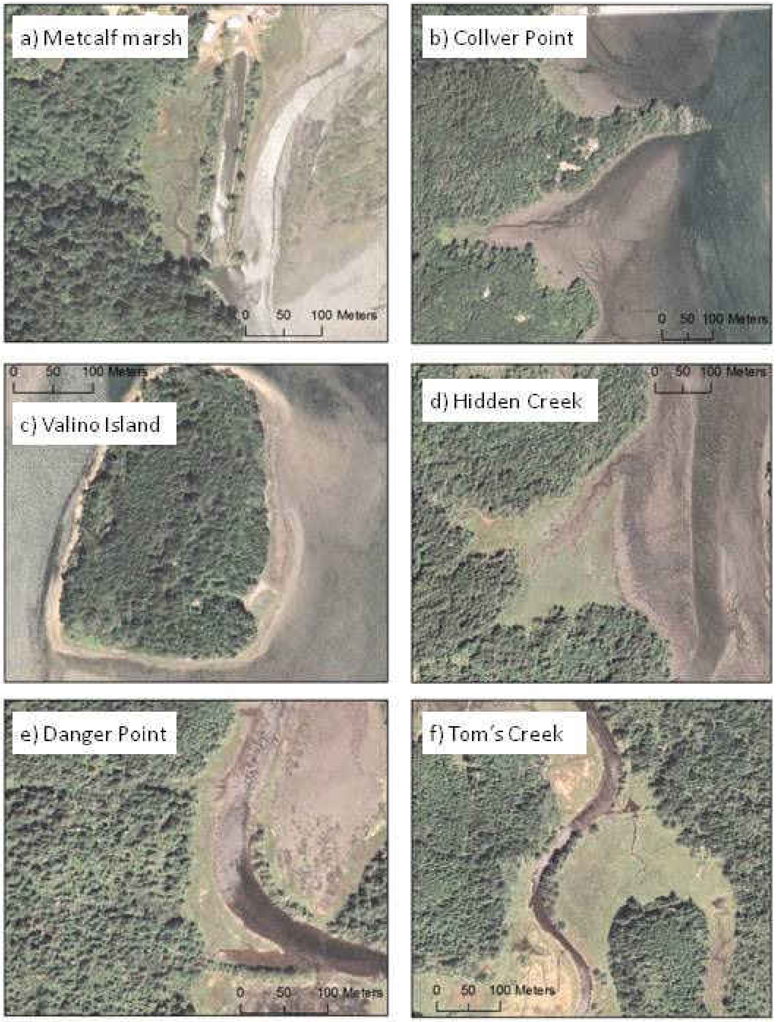

Figure A.1. Aerial photographs of the six study marshes along South Slough. Marshes area shown in order along the estuarine salinity gradient as a,b) marine dominated; c,d) mesohaline dominated; e,f) riverine dominated.

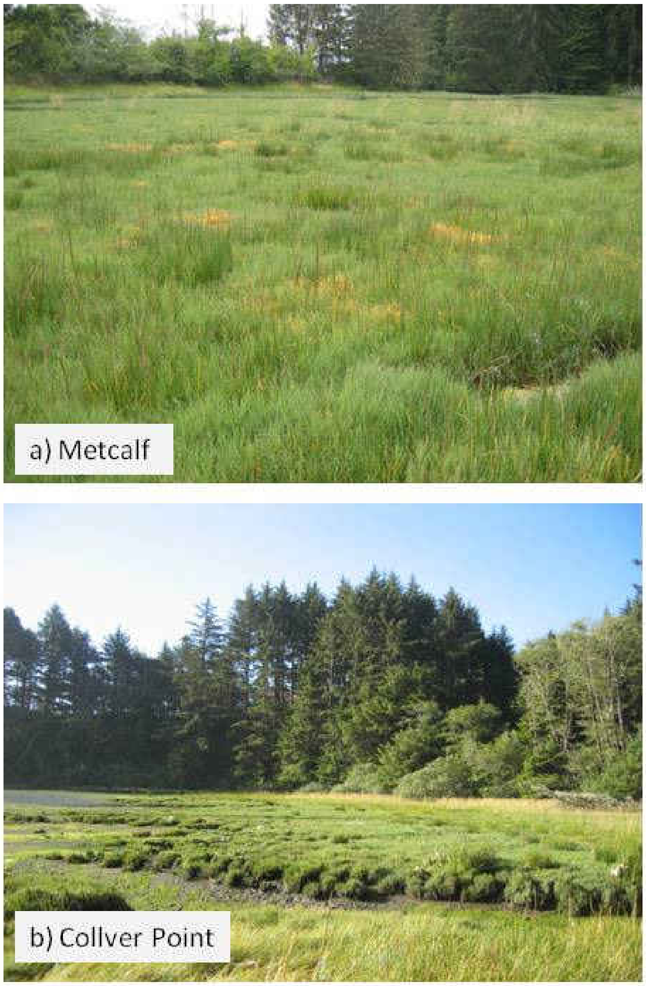

Figure A.2. Ground level photographs of the two marine dominated study marshes in South Slough.

Figure A.3. Ground level photographs of the two mesohaline dominated study marshes in South Slough.


a) Danger Point


b) Tom's Creek

Figure A.4. Ground level photographs of the two riverine dominated study marshes in South Slough.

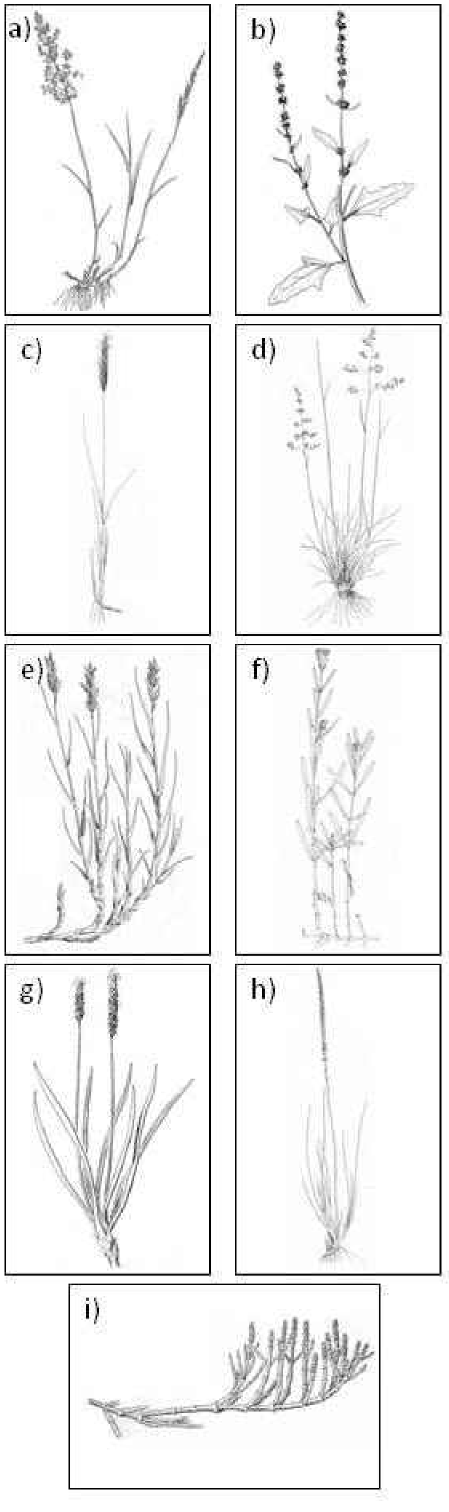

Figure A.5. Images of the major species in the South Slough marshes from Cooke 1997. Species: a) *Agrostis stolonifera*, b) *Atriplex patula*, c) *Carex lyngbyei*, d) *Deschampsia caespitosa*, e) *Distichlis spicata*, f) *Jaumea carnosa*, g) *Plantago maritima*, h) *Triglochin maritima*, i) *Salicornia virginica*.

APPENDIX B

COMMUNITY TYPE AND SUB-GROUP DESCRIPTIONS

This appendix describes in detail the composition of the subgroups within the four major community types (*Carex, Deschampsia, Distichlis/Salicornia* and *Salicornia*) found in the South Slough marshes (Chapter II). In particular refer to Chapter II for the relationship between the subgroups (Figure 2.2, cluster dendrogram) and species composition of each group (Table 2.1). Relative cover (RC) of each species was calculated for each plot as percent cover (of a given species) / total percent cover (of that plot). RC was used as a measure of species abundance within a community type for descriptive purposes (Table B.1). Relative biomass (RB) was calculated in the same way and used similarly (Table B.2).

Carex Community Type

The major community type dominated by *C. lyngbyei* is present in all six study marshes. The cluster analysis split this major community type into five subgroups (A, B, C, D and E) but every subgroup was not present in every marsh.

Subgroup A was found only in the three most riverine marshes, Hidden Creek, Danger Pt. and Tom's Creek. It was significantly defined by the introduced grass, *Agrostis stolonifera* (indicator species $p<0.05$, RC 33.6%, RB 47.8%). *C. lyngbyei* was the only other major species within the community (RC 62.5%, RB 42.4%) though seven other species were present.

Table B.1. Mean relative percent cover of emergent marsh plots within the 13 subgroups defined by the cluster analysis. Subgroups are separated by major marsh community type.

	Dominant Vegetation Type												
Relative Cover	*Carex*					*Deschampsia*			*Distichlis/ Salicornia*			*Salicornia*	
Group	A	B	C	D	E	F	G	H	I	J	K	L	M
Total	86.4	74.4	80.0	80.6	86.3	74.1	77.5	81.0	80.0	70.0	61.7	70.0	85.1
Agr sto	33.6	0.4	1.4	1.2	0.1	6.3	3.2	1.1	0	0	0	0	0
Arg ege	0	0	2.1	0	0	0	0.3	0	0	0	0	0	0
Atr pat	0	0.1	0	0.9	2.2	0.3	0	0.2	0.6	2.4	1.5	0	0.5
Car lyn	62.5	73.7	75.0	53.5	37.4	7.6	1.6	2.8	0	0	0	0	0
Cor mar	0	0	0	0	0	0	0	0	0.1	0.7	0	0	0
Cus sal	0	0	0	1.7	0.7	0.2	0.4	2.8	2.5	3.6	4.3	2.1	0
Des cae	0.4	0.8	8.4	8.4	0.6	50.1	50.8	46.2	0.1	0.7	0	0	1.1
Dis spi	0.4	16.9	0.1	15.7	18.1	19.6	5.2	16.7	65.5	57.2	20.6	2.5	10.0
Ele pal	0	0	0	0	0	0	0.3	0	0	0	0	0	0
Ele par	0	0.6	0.1	0	0	0	3.4	0.1	0	0	0	0	0
Gla mar	0.2	0	0	0.6	0.8	0	4.8	0.5	0	0.1	0	0	0
Gri int	0	0	1.1	0	0	0.1	10.7	0.1	0	0	0	0	0
Hor bra	0	0	0	0.4	0	0.4	0	0.3	0.3	0	0	0	0
Hor jub	0	0	0	0	0	0	0	0.2	0	0	0	0	0
Jau car	1.0	0.2	0.3	1.0	25.3	1.3	6.8	18.0	21.5	0.2	0	0	46.8
Jun bal	0.2	0	0	0	1.2	0	1.0	0.6	0	0	0	0	0
Jun ger	0	0	0	0	0	0	0	0.1	0	0	0	0	0
Lil occ	0	0	0.3	0	0	0.1	0	0	0	0	0	0	0
Lim cal	0	0	0	0	0	0	0.4	0.2	0	0.1	0	0	0
Pla mar	0	0	0	0	1.6	0	3.6	0.1	0	0	0	0	0
Sal vir	0	5.1	0	2.3	4.6	1.1	4.4	4.6	7.1	34.4	24.2	95.4	37.4
Sci ame	0	0	0	0	0	0	0	0	0	0	0	0	0
Spe mar	0	0	0	0	0.4	0	0.3	0	0.2	0.1	0	0	2.3
Tri con	0	0	0	0	0	0	0.7	0	0	0	0	0	0.1
Tri mar	1.6	2.2	10.4	14.2	7.0	12.9	1.9	5.3	2.0	0.4	45.5	0	1.8
Tri wor	0.2	0	0.7	0.2	0	0	0.3	0	0	0	3.8	0	0

Species: *Agrostis stolonifera* (Agr sto), *Argentina egedii* ssp. *egedii* (Arg ege), *Atriplex patula* (Atr pat), *Carex lyngbyei* (Car lyn), *Cordylanthus maritimus* (Cor mar), *Cuscuta salina* (Cus sal), *Deschampsia caespitosa* (Des cae), *Distichlis spicata* (Dis spi), *Eleocharis palustris* (Ele par), *Eleocharis parvula* (Ele par), *Glaux maritima* (Gla mar), *Grindelia integrifolia* (Gri int), *Hordeum brachyantherum* (Hor bra), *Hordeum jubatum* (Hor jub), *Jaumea carnosa* (Jau car), *Juncus arcticus* ssp. *balticus* (Jun bal), *Juncus gerardii* (Jun ger), *Lilaeopsis occidentalis* (Lil occ), *Limonium californicum* (Lim cal), *Plantago maritima* (Pla mar), *Salicornia virginica* (Sal vir), *Spergularia marina* (Spe mar), *Triglochin concinna* (Tri con), *Triglochin maritima* (Tri mar), *Trifolium wormskjoldii* (Tri wor).

Subgroup B was found in all marshes except Valino Island. Subgroup D was defined by *C. lyngbyei* (indicator species p<0.05, RC 75.0%, RB 71.0%) and *T. maritima* (RC 10.4%, RB 17.5%).

Subgroup C had no significant indicator species, but was characterized by high RC and RB of *C. lyngbyei* (RC 73.7%, RB 64.9%) and to a lesser extent, *D. spicata* (RC 16.9%, RB 16.8%). This group was not found at the most marine (Metcalf) or the most riverine (Tom's Creek) marshes.

Subgroup D was not defined by a significant indicator, but was characterized by high RC of *C. lyngbyei* (53.5%), *D. spicata* (15.7%) and *T. maritima* (14.2%). This group was found in four of the study marshes, Metcalf, Collver Pt, Hidden Creek and Danger Pt.

Subgroup E, defined primarily by the presence of *Atriplex patula* (significant indicator p<0.10; RC 2.2%; Table B.1), was a part of the greater *Carex* community type at Metcalf, Valino and Hidden Creek. This group had the lowest overall RC for *C. lyngbyei* (34.7%) and similarly low RB (26.5%; Table B.2). This group was also characterized by *D. spicata* (RC 18.1%, RB 23.9%) and *J. carnosa* (RC 25.3%, RB 21.4%).

Deschampsia Community Type

The *Deschampsia* community type was separated into three subgroups (F, G and H) by the cluster analysis. Subgroup F was present in all marshes except for Valino Island. This group had no significant indicator species, but was characterized by *D. caespitosa* (RC 50.1% RB 39.1%), *D. spicata* (RC 19.6% RB 12.1%) and *T. maritima*

(RC 12.9% RB 24.0%) in addition to *A. stolonifera* which accounted for a limited amount of the cover (RC 6.3%) but a higher percent of the biomass (RB 15.7%).

Table B.2. Mean relative biomass of emergent marsh plots within the 13 subgroups defined by the cluster analysis. Subgroups are separated by major marsh community type.

	Dominant Vegetation Type												
Relative Biomass	*Carex*					*Deschampsia*			*Distichlis/ Salicornia*			*Salicornia*	
Group	A	B	C	D	E	F	G	H	I	J	K	L	M
Total	753.6	557.6	697.2	658.4	620.2	691.3	486.4	714.5	660.6	495.8	521.2	679.0	641.3
Agr sto	47.8	0.1	1.2	1.4	1.2	15.7	2.4	1.3	0	0	0	0	0
Arg ege	0	0	0.6	0	0	0	0.2	0	0	0	0	0	0
Atr pat	0.0	0.0	0	0.3	1.1	0.0	0	0.1	0.3	0.9	0.7	0.0	0.2
Car lyn	42.4	64.9	71.0	38.5	26.5	5.9	8.6	2.4	0	0	0	0	0
Cor mar	0	0	0	0	0	0	0	0	0	0.3	0	0	0
Cus sal	0	0	0	0.0	0.1	0.0	0	0.4	0.6	0.4	0.2	0.2	0.0
Des cae	0.3	0	5.0	14.2	0.3	39.1	53.7	39.2	0.0	0.0	0	0.0	0.4
Dis spi	0.4	16.8	0.2	13.6	23.9	12.1	1.6	17.4	52.8	57.2	14.7	1.6	16.1
Ele pal	0	0	0	0	0	0	0	0	0	0	0	0	0
Ele par	0	1.4	0.1	0	0.3	0	3.2	0.0	0	0.0	0	0	0
Gla mar	0.0	0	0.5	0.4	0.7	0	3.9	0.2	0	0.1	0	0	0.0
Gri int	0	0	2.4	0	0	0	4.8	0.9	0	0	0	0	0
Hor bra	0	0	0	0.3	0	0.9	0	1.0	0.1	0	0	0	0
Hor jub	0	0	0	0	0	0	0	0.3	0.2	0	0	0	0
Jau car	1.4	0.7	0.7	3.9	21.4	0.9	7.1	18.8	28.3	0.3	0	0.1	61.3
Jun bal	1.8	0	0.5	0	1.0	0	0.8	1.0	0	0	0	0	0
Jun ger	0	0	0	0	0	0	0.0	0	0	0	0	0	0
Lil occ	0	0.0	0.0	0	0	0.0	0.0	0	0	0	0	0	0
Lim cal	0	0	0	0	0	0	0.7	0.3	0.3	0.0	0	0	0
Pla mar	0	0	0	0	0.3	0	4.8	0.1	0	0	0	0	0
Sal vir	0	11.4	0.1	3.0	6.2	1.3	5.2	6.6	14.8	39.9	28.1	98.0	20.4
Sci ame	0	3.0	0	0	0.6	0	1.0	0	0	0	0	0	0.0
Spe mar	0	0.5	0	0.0	0.1	0	0	0	0.0	0.2	0.4	0.1	0.1
Tri con	0	0	0	0	0.0	0	0.4	0	0	0	0	0	0
Tri mar	5.9	1.3	17.5	24.4	16.3	24.0	1.6	10.1	2.6	0.6	55.8	0	1.5
Tri wor	0.0	0	0.2	0	0	0	0.0	0	0	0	0	0	0

Species: Same as Table B.1.

Subgroup G was found only in the Valino Island marsh and in one sampled plot in Tom's Creek (Table 2.1). This group was defined by five significant indicator species ($p<0.05$): *D. caespitosa* (RC 50.82% RB 53.7%), *Glaux maritima* (RC 4.8% RB 3.9%), *Grindelia integrifolia* (RC 10.7% RB 4.8%), *Juncus arcticus* ssp. *balticus* (RC 1.0% RB 0.8%), and *Plantago maritima* (RC 3.6% RB 4.8%). This subtype had the highest species richness of all subtypes, with 14 species in addition to the five indicators present (Table 2.1).

Subgroup H was present in all marshes. This group was defined by the presence of the parasitic dodder (*Cuscuta salina*: indicator species $p<0.05$, RC 2.8%, RB 0.04%). *D. caespitosa* (RC 46.2% RB 39.2%), *D. spicata* (RC 16.7% RB 17.4%) and *J. carnosa* (RC 18.0% RB 18.8%) account for the majority of cover and yield within this group.

Distichlis/Salicornia Community Type

This community type was separated into three subgroups (I, J, and K) by the cluster analysis and occurred in the four marine and mesohaline marshes closest to the mouth of Coos Bay (Metcalf, Collver Pt., Valino Is., and Hidden Creek). Subgroup I was defined by the presence of *D. spicata* (indicator species $p<0.05$; RC 65.5%, RB 52.8%) as well as the relatively high proportion of *J. carnosa* (RC 21.5%, RB 28.3%). *S. virginica* accounted for little of the cover (RC 7.1%), but contributed a higher amount to the biomass (RB 14.8%).

Subgroup J was found only in the three most marine marshes (Metcalf, Collver Pt., and Valino Is., Table 2.1). This group had no significant indicator species, but was characterized by a co-occurrence of *D. spicata* RC 57.2%, RB 57.2%) and *S. virginica*

(RC 34.4%, RB 39.9%) with only 8.3% (RC) and 2.3% (RB) accounted for by the other nine species present.

Subgroup K was present only in Metcalf marsh and was characterized by *S. virginica* (RC 24.2%, RB 28.1%) and *D. spicata* (RC 20.6%, RB 14.7%). The group had two significant indicator species ($p<0.05$), *T. maritima* (RC 45.5, RB 55.8%) and *Trifolium wormskjoldii* (RC 3.8%, RB <0.1%).

Salicornia Community Type

The *Salicornia* community type was divided into only two subgroups (L and M). Subgroup L was described by the nearly monotypic stands of *S. virginica* (indicator species $p<0.05$, RC 95.4%, RB 98.0%) at Collver Pt. and Valino Is. Subgroup M, found at Metcalf, Valino Is. and Hidden Creek, was defined by *J. carnosa* (indicator species $p<0.05$, RC 46.8%, RB 61.3%) and *Spergularia marina* (indicator species $p<0.05$, RC 2.3%, RB 0.1%). *S. virginica* (RC 37.4% RB 20.4%) and *D. spicata* (RC 10.0%, RB 16.1%) were also present in addition to four other species.

APPENDIX C

RESULTS OF THE *DISTICHLIS* ‘SOD’ TRANSPLANTS

In the second year (2010) of the reciprocal transplant study across the high/low marsh boundary in Metcalf Marsh, larger plugs of *Distichlis* were also transplanted. The experimental design for this aspect of the study was the same as previously described (Chapter III, Figure 3.1). Plugs of *Distichlis* ‘sod’ containing 5-10 connected ramets were transplanted into vegetated (n=5) and cleared plots (n=5) in both the high and low intertidal marsh zones. Unmanipulated vegetated (n=5) and cleared (n=5) controls were also monitored within the low marsh. Transplants were established in April 2010 and monitored bi-weekly through the end of August 2010. At the conclusion of the study, the ‘sod’ was clipped at ground level, collected, dried to a constant mass at 80° C and weighed. Growth rate over the growing season was calculated as total mm growth divided by the total number of days after the transplant. Dry biomass and growth were compared using separate two-way ANOVAs with intertidal elevation (low, high or control) and vegetation (vegetated or cleared) as fixed factors. Data fit the assumptions of ANOVA and were therefore not transformed.

Biomass (dry grams) and growth (mm/day) differed significantly between intertidal elevations (Table C.1). In the high marsh, the cleared control treatment exhibited significantly higher biomass than the high-marsh transplanted individuals (Figure C.1a). Low marsh transplants had significantly more growth (mm/day) than high marsh transplants (Figure C.1b; significant elevation effect, Tukey post hoc $p<0.05$). These results follow the same pattern as was observed for the smaller *Distichlis* transplants (Chapter III, Figures 3.2, 3.3). Both biomass and growth rate were less in the high intertidal transplants, regardless of the presence of neighboring vegetation. This suggests that competition with *Carex* did not limit expansion of *Distichlis* into the high marsh at Metcalf.

Table C.1. ANOVA (F-ratio) results for full model (all treatments separately), intertidal elevation (low, high, control), vegetation (cleared, vegetated) and the interaction (E x V) for *Distichlis* 'sod' in 2010.

	df	*Distichlis* 'sod'	
Sources of Variation		Biomass	Growth
Model	5	6.406**	3.013*
Elevation	2	14.419**	7.341**
Vegetation	1	0.295	0.180
E x V	1	1.449	0.100
Error	24		

** $p<0.005$; * $p<0.05$

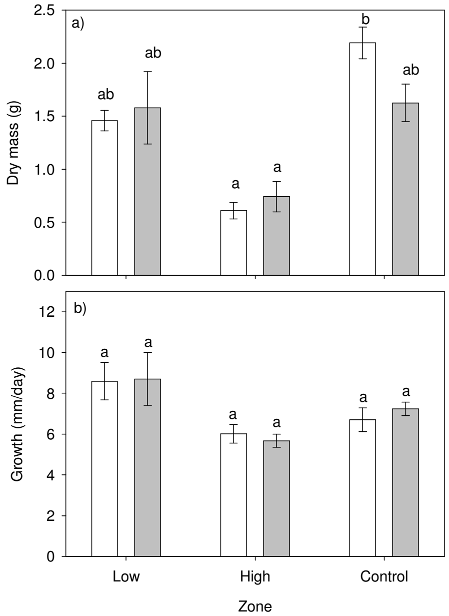

Figure C.1. a) Biomass (dry grams) and b) growth (mm/day) of the transplanted *Distichlis* 'sod' at the conclusion of the 2010 growing season in cleared (empty bars) and vegetated (filled bars) plots at two intertidal levels (low and high) and the control. Each bar represents mean (n=5) ± 1SE. Bars with the same letter above do not differ significantly (Tukey post hoc, $p<0.05$).

APPENDIX D

TABLES OF SEED DENSITY PER M^2

Table D.1. Mean number of seeds per m^2 based on sieved and counted samples for each of the three community types in two marine marshes. Counts presented as mean ± standard error of the mean

Marsh	Metcalf			Collver Point		
Community type	*Carex*	*Deschampsia*	*Distichlis/ Salicornia*	*Carex*	*Deschampsia*	*Distichlis/ Salicornia*
Species						
Agr sto	18 ± 18	30 ± 30	--	--	35 ± 35	--
Atr pat	666 ± 219	766 ± 133	704 ± 186	18 ± 13	200 ± 97	108 ± 79
Car lyn	6394 ± 1646	3356 ± 864	479 ± 168	10245 ± 1859	1235 ± 335	282 ± 71
Car obn	52 ± 52	6 ± 6	--	157 ± 157	--	--
Cus sal	150 ± 78	188 ± 83	435 ± 147	121 ± 90	--	185 ± 63
Des cae	435 ± 214	2775 ± 748	227 ± 113	795 ± 423	3068 ± 462	136 ± 56
Dis spi	602 ± 185	750 ± 219	3237 ± 629	553 ± 92	452 ± 133	279 ± 126
Gla mar	--	59 ± 28	18 ± 18	95 ± 45	90 ± 36	12 ± 12
Gri int	6 ± 6	614 ± 223	--	18 ± 18	215 ± 80	6 ± 6
Jau car	557 ± 172	482 ± 283	277 ± 118	70 ± 40	274 ± 194	321 ± 103
Jun bal	35 ± 35	24 ± 24	--	--	123 ± 92	12 ± 12
Jun ger	--	--	--	24 ± 24	6 ± 6	--
Pla mar	--	--	105 ± 61	226 ± 96	52 ± 52	157 ± 113
Rum mar	17±17	--	--	--	48 ± 48	--
Sal vir	2501 ± 483	3417 ± 721	10331 ± 127	2540 ± 674	1913 ± 405	7093 ± 1058
Spe mar	122 ± 91	139 ± 71	52±38	--	48 ± 48	--
Tri con	--	--	--	35 ± 24	--	--
Tri mar	3216 ± 653	9199 ± 3931	1864 ± 547	3306 ± 997	1324 ± 266	1947 ± 609
Tri wor	54 ± 29	17 ± 17	--	--	17 ± 17	--
Zos mar	--	--	--	--	--	76 ± 43

Species: *Agrostis stolonifera* (Agr sto), *Atriplex patula* (Atr pat), *Carex lyngbyei* (Car lyn), *Carex obnupta* (Car obn), *Cuscuta salina* (Cus sal), *Deschampsia caespitosa* (Des cae), *Distichlis spicata* (Dis spi), *Glaux maritima* (Gla mar), *Grindelia integrifolia* (Gri int), *Jaumea carnosa* (Jau car), *Juncus arcticus* ssp. *balticus* (Jun bal), *Juncus gerardii* (Jun ger), *Plantago maritima* (Pla mar), *Rumex maritimus* (Rum mar), *Salicornia virginica* (Sal vir), *Spergularia marina* (Spe mar), *Triglochin concinna* (Tri con), *Triglochin maritima* (Tri mar), *Trifolium wormskjoldii* (Tri wor), *Zostera marina* (Zos mar)

Table D.2. Mean number of seeds per m^2 based on sieved and counted samples for each of the three community types in two mesohaline marshes. Counts presented as mean ± standard error of the mean

Marsh	Valino Island			Hidden Creek		
Community type	*Carex*	*Deschampsia*	*Distichlis/ Salicornia*	*Carex*	*Deschampsia*	*Distichlis/ Salicornia*
Species						
Agr sto	--	--	24 ± 24	--	244 ± 244	--
Atr pat	--	218 ± 103	167 ± 69	121 ± 68	244 ± 80	131± 49
Car lyn	909 ± 188	1752 ± 323	1535 ± 243	1858 ± 784	779 ± 163	375 ± 111
Car obn	--	125 ± 63	70 ± 70	24 ± 24	--	--
Cus sal	85 ± 44	42 ± 25	12 ± 12	17 ± 17	18 ± 18	72 ± 33
Des cae	331 ± 155	495 ± 170	151 ± 126	1368 ± 237	1605 ± 316	672 ± 203
Dis spi	36 ± 25	182 ± 82	235 ± 80	382 ± 117	2634 ± 1285	779 ± 385
Gla mar	30 ± 21	575 ± 191	278 ± 107	17 ± 17	61 ± 61	30 ± 30
Gri int	--	88 ± 71	18 ± 18	18 ± 18	1003 ± 263	--
Jau car	12 ± 12	--	158 ± 98	748 ± 206	1429 ± 474	748 ± 310
Jun bal	1571 ± 606	13386 ± 3673	2339 ± 1780	--	17 ± 17	--
Jun ger	--	6 ± 6	36 ± 36	67 ± 67	254 ± 254	--
Pla mar	--	105 ± 71	18 ± 13	364 ± 154	300 ± 127	176 ± 81
Rum mar	18 ± 18	216 ± 109	--	17 ± 17	234 ± 96	--
Sal vir	350 ± 242	1262 ± 754	4152 ± 1017	615 ± 164	653 ± 283	1236 ± 244
Spe mar	--	--	30 ± 21	--	--	--
Tri con	--	780 ± 397	30 ± 21	--	--	--
Tri mar	76 ± 40	132 ± 63	607 ± 198	9493 ± 2256	5628 ± 1034	4569 ± 1257
Tri wor	--	--	--	17 ± 17	506 ± 351	--
Zos mar	141 ± 92	18 ± 18	--	--	--	54 ± 25

Species: *Agrostis stolonifera* (Agr sto), *Atriplex patula* (Atr pat), *Carex lyngbyei* (Car lyn), *Carex obnupta* (Car obn), *Cuscuta salina* (Cus sal), *Deschampsia caespitosa* (Des cae), *Distichlis spicata* (Dis spi), *Glaux maritima* (Gla mar), *Grindelia integrifolia* (Gri int), *Jaumea carnosa* (Jau car), *Juncus arcticus* ssp. *balticus* (Jun bal), *Juncus gerardii* (Jun ger), *Plantago maritima* (Pla mar), *Rumex maritimus* (Rum mar), *Salicornia virginica* (Sal vir), *Spergularia marina* (Spe mar), *Triglochin concinna* (Tri con), *Triglochin maritima* (Tri mar), *Trifolium wormskjoldii* (Tri wor), *Zostera marina* (Zos mar)

Table D.3. Mean number of seeds per m^2 based on sieved and counted samples for each of the three community types in two riverine marshes. Counts presented as mean ± standard error of the mean

Marsh	Danger Point		Tom's Creek	
Community type	*Carex*	*Deschampsia*	*Carex*	*Deschampsia*
Species				
Agr sto	52 ± 28	645 ± 256	7543 ± 1772	5095 ± 1690
Atr pat	36 ± 24	172 ± 65	230 ± 217	77 ± 41
Car lyn	7601 ± 1450	3593 ±576	6994 ± 1326	12237 ± 3818
Car obn	--	17 ± 17	17 ± 17	436 ± 198
Cus sal	--	--	--	--
Des cae	3974 ± 859	3234 ± 1407	822 ± 311	4033 ± 809
Dis spi	218 ± 113	682 ± 247	222 ± 79	432 ± 100
Gla mar	36 ± 24	73 ± 42	260 ± 200	82 ± 40
Gri int	18 ± 18	343 ± 167	36 ± 21	185 ± 57
Jau car	52 ± 38	12 ± 12	--	12 ± 12
Jun bal	87 ± 61	17 ± 17	84 ± 56	441 ± 163
Jun ger	--	--	--	--
Pla mar	--	--	--	61 ± 61
Rum mar	18 ± 18	17 ± 17	--	--
Sal vir	213±77	520 ± 148	47 ± 25	494 ± 266
Spe mar	--	--	--	--
Tri con	17 ± 17	30 ± 20	--	1760 ± 974
Tri mar	3029 ± 562	1688 ± 339	1141 ± 323	4273 ± 1138
Tri wor	--	17±17	--	173 ± 61
Zos mar	88 ± 71	--	60 ± 32	35 ± 35

Species: *Agrostis stolonifera* (Agr sto), *Atriplex patula* (Atr pat), *Carex lyngbyei* (Car lyn), *Carex obnupta* (Car obn), *Cuscuta salina* (Cus sal), *Deschampsia caespitosa* (Des cae), *Distichlis spicata* (Dis spi), *Glaux maritima* (Gla mar), *Grindelia integrifolia* (Gri int), *Jaumea carnosa* (Jau car), *Juncus arcticus* ssp. *balticus* (Jun bal), *Juncus gerardii* (Jun ger), *Plantago maritima* (Pla mar), *Rumex maritimus* (Rum mar), *Salicornia virginica* (Sal vir), *Spergularia marina* (Spe mar), *Triglochin concinna* (Tri con), *Triglochin maritima* (Tri mar), *Trifolium wormskjoldii* (Tri wor), *Zostera marina* (Zos mar)

APPENDIX E

TABLE OF IDENTIFIED EMERGED SEEDLINGS PER M^2

Table E.1. Total number of identified seedlings emerged per m^2 of each species from both collected samples (lab emergence) and field observations. Counts are presented as lab (field). Samples collected from *Carex lyngbyei* (Cl), *Deschampsia caespitosa* (Dc) or *Distichlis spicata/Salicornia virginica* dominated communities (Ds/Sv)

Marsh	Metcalf			Collver Pt			Valino Is		
Community type	Cl	Dc	Ds/Sv	Cl	Dc	Ds/Sv	Cl	Dc	Ds/Sv
Agrostis stolonifera	1161 (0)	996 (0)	1328 (0)	498 (‡)	747 (‡)	415 (‡)	0 (‡)	166 (‡)	249 (‡)
Argentina egedii ssp. *egedii*	166 (0)	0 (128)	0 (0)	0	0	0	83	0	0
Atriplex patula	0 (96)	83 (992)	0 (272)	83	0	0	0	0	0
Carex lyngbyei	83 (0)	0 (0)	0 (0)	83	0	0	0	0	0
Cuscuta salina	0 (32)	0 (224)	0 (560)	0	0	83	0	0	0
Eleocharis parvula	0 (0)	0 (0)	0 (0)	0	0	0	1328	996	0
Hordeum sp†	0 (0)	0 (0)	0 (0)	0	0	0	0	0	0
Jaumea carnosa	747 (80)	664 (464)	581 (96)	581	249	0	0	249	249
Juncus arcticus ssp. *balticus*	0 (64)	0 (0)	0 (0)	83	83	249	0	83	83
Deschampsia caespitosa	664 (0)	2988 (944)	0 (64)	747	3983	166	0	5145	0
Distichlis spicata	83 (0)	83 (16)	249 (16)	249	166	0	0	249	83
Grindelia integrifolia	0 (32)	166 (160)	0 (0)	0	0	0	0	166	0
Glaux maritima	0 (0)	0 (80)	0 (0)	0	415	0	0	2656	83
Limonium californicum	0 (0)	0 (0)	0 (0)	0	0	0	0	0	83
Plantago maritima	2158 (0)	1909 (80)	5643 (80)	5892	249	7967	83	249	4315
Salicornia virginica	1909 (0)	1826 (0)	498 (208)	1079	913	996	249	2988	1328
Spergularia marina	83 (0)	0 (0)	0 (0)	83	249	0	0	83	0
Triglochin maritima	0 (80)	0 (352)	0 (80)	249	0	0	0	0	1577
Trifolium wormskjoldii	0 (0)	83 (0)	83 (0)	83	0	0	0	249	83

† either *H. brachyantherum* or *H. jubatum* ‡ only lab emergence tested

Table E.1 Continued

Marsh	Hidden Crk			Danger Pt		Tom’s Crk	
Community type	Cl	Dc	Ds/Sv	Cl	Dc	Cl	Dc
Agrostis stolonifera	249 (0)	332 (0)	83 (0)	0 (‡)	0 (‡)	0 (1024)	0 (160)
Argentina egedii ssp. *egedii*	166 (0)	0 (160)	1162 (0)	0	0	0 (0)	0 (288)
Atriplex patula	249 (0)	83 (160)	0 (0)	2158	1411	6058 (32)	3900 (72)
Carex lyngbyei	664 (0)	0 (0)	0 (0)	0	0	0 (0)	0 (0)
Cuscuta salina	83 (80)	83 (416)	0 (96)	0	0	0 (0)	0 (0)
Eleocharis parvula	0 (0)	0 (0)	0 (0)	0	0	0 (0)	0 (0)
Hordeum sp†	249 (0)	0 (0)	0 (0)	0	83	0 (0)	0 (0)
Jaumea carnosa	1494 (224)	747 (80)	83 (176)	332	249	83 (0)	1079 (96)
Juncus arcticus ssp. *balticus*	0 (0)	0 (0)	0 (0)	0	0	83 (0)	83 (0)
Deschampsia caespitosa	1328 (0)	2822 (544)	415 (32)	415	2407	5228 (0)	8299 (448)
Distichlis spicata	1245 (0)	415 (0)	332 (0)	0	0	0 (0)	0 (0)
Grindelia integrifolia	0 (0)	498 (144)	0 (0)	0	0	2241 (80)	1328 (64)
Glaux maritima	332 (144)	830 (224)	0 (0)	0	415	0 (0)	0 (0)
Limonium californicum	0 (0)	0 (0)	0 (0)	83	83	83 (0)	0 (0)
Plantago maritima	581 (352)	249 (32)	1162 (112)	0	83	0 (0)	0 (64)
Salicornia virginica	5892 (256)	1411 (0)	3402 (160)	664	1162	1743 (0)	1660 (0)
Spergularia marina	0 (0)	0 (0)	0 (0)	0	0	83 (0)	0 (0)
Triglochin maritima	415 (304)	0 (128)	830 (128)	83	0	415 (272)	0 (176)
Trifolium wormskjoldii	0 (0)	0 (0)	0 (0)	0	0	0 (16)	0 (0)

† either *H. brachyantherum* or *H. jubatum* ‡ only lab emergence tested

APPENDIX F

TABLE OF SEED VIABILITY

Table F.1. Percent viability of species present based on emergence from collected seed bank samples. Percent shown ± standard error of the mean. nd: no seeds present in sieved sample

Marsh	Metcalf			Collver Pt			Valino Is		
Community type	Cl	Dc	Ds/Sv	Cl	Dc	Ds/Sv	Cl	Dc	Ds/Sv
Agr sto	0	0	nd	nd	0	nd	nd	nd	0
Atr pat	34 ± 20	13 ± 7	22 ± 9	0	4 ± 2	22 ± 10	nd	0	0
Car lyn	0	0	0	<1 ± <1	0	0	0	0	0
Cus sal	0	0	0	0	nd	7 ± 5	0	0	0
Des cae	19 ±5	14 ± 4	0	6 ± 4	8 ± 4	13 ± 6	0	59 ± 22	0
Dis spi	1 ± 1	<1 ± <1	1 ± 1	4 ± 3	0	0	0	2 ± 1	0
Gla mar	nd	0	0	0	10 ± 6	0	0	28 ± 11	6 ± 4
Gri int	0	1 ± 1	nd	0	0	0	nd	4 ± 2	0
Jau car	8 ± 3	13 ± 7	2 ± 1	28 ± 7	4 ± 2	0	0	nd	11 ± 5
Pla mar	nd	nd	0	5 ± 3	0	0	nd	0	0
Sal vir	4 ± 2	6 ± 2	6 ± 2	22 ± 8	2 ± 1	10 ± 3	0	3 ± 2	12 ± 4
Tri mar	9 ± 6	3 ± 1	2 ± 1	5 ± 2	5 ± 3	3 ± 2	17 ± 9	84 ± 31	7 ± 4
Tri wor	0	0	nd	nd	0	nd	nd	nd	nd

Species: *Agrostis stolonifera* (Agr sto), *Atriplex patula* (Atr pat), *Carex lyngbyei* (Car lyn), *Cuscuta salina* (Cus sal), *Deschampsia caespitosa* (Des cae), *Distichlis spicata* (Dis spi), *Glaux maritima* (Gla mar), *Grindelia integrifolia* (Gri int), *Jaumea carnosa* (Jau car), *Plantago maritima* (Pla mar), *Salicornia virginica* (Sal vir), *Triglochin maritima* (Tri mar), *Trifolium wormskjoldii* (Tri wor)

Table F.1 Continued

Marsh	Hidden Crk			Danger Pt		Tom's Crk	
Community type	Cl	Dc	Ds/Sv	Cl	Dc	Cl	Dc
Agr sto	nd	0	nd	63 ± 9	23 ± 10	17 ± 8	0
Atr pat	3 ± 1	2 ± 1	3 ± 2	0	0	0	0
Car lyn	1 ± 1	0	0	0	0	0	0
Cus sal	0	0	0	nd	nd	nd	nd
Des cae	10 ± 5	18 ± 5	12 ± 8	2 ± 2	9 ± 4	56 ± 31	28 ± 9
Dis spi	22 ± 7	2 ± 1	11 ± 6	0	0	0	0
Gla mar	0	0	0	0	56 ±26	0	0
Gri int	0	1 ± 1	nd	0	0	0	38 ± 22
Jau car	10 ± 4	3 ± 1	0	0	0	nd	50 ±13
Pla mar	0	0	0	nd	nd	nd	0
Sal vir	11 ± 5	19 ± 10	6 ± 2	0	1 ± 1	0	0
Tri mar	4 ± 1	3 ± 2	4 ± 1	3 ± 2	10 ± 7	7 ± 4	11 ± 7
Tri wor	0	0	nd	nd	0	nd	0

Species: *Agrostis stolonifera* (Agr sto), *Atriplex patula* (Atr pat), *Carex lyngbyei* (Car lyn), *Cuscuta salina* (Cus sal), *Deschampsia caespitosa* (Des cae), *Distichlis spicata* (Dis spi), *Glaux maritima* (Gla mar), *Grindelia integrifolia* (Gri int), *Jaumea carnosa* (Jau car), *Plantago maritima* (Pla mar), *Salicornia virginica* (Sal vir), *Triglochin maritima* (Tri mar), *Trifolium wormskjoldii* (Tri wor)

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Appendix A

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