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THE ECOLOGY OF A PARASITIC PLANT AND ITS HOST PLANT IN A CENTRAL CALIFORNIA SALT MARSH

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THE ECOLOGY OF A PARASITIC PLANT AND ITS HOST PLANT IN A CENTRAL CALIFORNIA SALT MARSH

Katie Alt Griffith

ABSTRACT

Parasitic plants are understudied despite their prevalence in natural communities. *Cuscuta salina*, salt marsh dodder, grows in association with its preferred host, *Sarcocornia pacifica*, in salt marshes along the western coast of the United States. This dissertation is an experimental investigation of (1) the distribution and abundance of *C. salina*, (2) the interaction between *C. salina* and *S. pacifica* across multiple levels of nitrogen and salinity, and (3) the effect of artificial tidal restrictions on marsh sediment and *S. pacifica*.

The distribution and abundance of *C. salina* in the Elkhorn Slough watershed is constrained by abiotic conditions (mainly the intertidal and estuarine gradient), *S. pacifica* quality (tissue salinity levels), and recruitment (in wrack deposits). Seed germination is greatest in freshwater and declines with increasing salinity. Germination also trends toward being lower at lower tidal heights. There is a greater probability of a *C. salina* seedling establishing successfully on *S. pacifica* with increasing tidal heights. This chapter demonstrates the importance of multiple factors in determining pattern and process in *C. salina* distribution and abundance at Elkhorn Slough.

The interaction between *C. salina* and *S. pacifica* was examined in the greenhouse under 3 levels of nitrogen additions and 4 levels of salt additions. Although *C. salina* did not affect *S. pacifica* biomass, it did significantly affect *S. pacifica* tissue salinity and tissue nitrogen. However, these effects interacted with salinity and nitrogen treatments. *S. pacifica* was also affected by a strong interaction between nitrogen and salinity treatments. *C. salina* coiled more *S. pacifica* stems under the two lower nitrogen treatment levels compared to the highest treatment level. This chapter demonstrates the importance of the abiotic environment in structuring this parasitic plant – host plant interaction.

The final chapter of this dissertation examines the effects of artificial tidal restrictions on sediment and *S. pacifica* tissue. Tidal restriction affected sediment quality, but not *S. pacifica* tissue quality. However, the large effects of spatial and temporal variation associated with site, season and tidal height may exert an even greater control over marsh dynamics than the effects of tidal restriction alone.

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INTRODUCTION

"We therefore have no choice but to cast them together, as oddities, into their own category, much as in an asylum we bring together the mentally ill, whose mania are extremely varied, but of whom no one is really what he pretends or imagines to be. Our Sarcophytae also imitate, in a baroque fashion, something which they are not...."

- Rationale for giving parasitic plants their own systematic grouping, offered by botanists in 1828 (Kuijt 1969).

Parasites have long inspired fascination in naturalists. However, for nearly a century since parasitic plants were officially recognized in 1828, very few studies examined parasitism in higher plants (Kuijt 1969). The first big strides in the field of parasitic angiosperm biology coincided with the discovery of witchweed (*Striga asiatica*), a parasitic plant that threatened US maize cultivation in the 1950s. National funding was made available to initiate a large research program devoted to this crop pest (Sand and Westbrooks 1991). Then, in 1969, Job Kuijt published a book detailing the biology and ecology of parasitic plants (Kuijt 1969). This was the only published reference on parasitic plants for nearly 25 years. Finally, in the 1970s and 1980s, famines in Africa drew international attention to the parasitic plants that were ravaging crops, and a new collaborative research effort began across multiple countries. The study of parasitic plant ecology, separate from its applied foci, has begun to grow over the last couple of decades (Kelly 1990, Gomez 1994, Callaway

and Pennings 1998, Marvier 1998, Koskela et al. 2000, Adler 2003, Press and Phoenix 2005, Meulebrouck et al. 2007).

Over 3,000 species of parasitic plants are known to exist in seven orders: Laurales, Santalales, Rafflesiales, Polygales, Solanales, Lamilales, and Scrophulariales (Press and Graves 1995). These species, which may take the form of trees, shrubs, vines, or herbs, make their living by tapping into the host plant's vascular system with root-like plugs of tissue called haustorium and extracting water, nutrients, and organic solutes (Musselman and Press 1995). The point of attachment and level of dependency differ greatly among species. Roughly 60% of species live above ground and attach to the host via the shoot, whereas 40% of species live partially or completely below ground and attach to the host's root system (Musselman and Press 1995). The presence of chlorophyll in the parasite determines whether the parasite is a holoparasite (no chlorophyll, depends completely on the host, approximately 20% of species) or a hemiparasite (some chlorophyll, uses the host as a supplement, approximately 80% of species). However, some species are not easily categorized. For example, the *Cuscuta* genus includes species that lack chlorophyll along with species that contain small amounts. Other genera may only have chlorophyll during certain stages of their life cycles. For example, Striga species contain no chlorophyll while they live underground, parasitizing host roots. But once they emerge from the ground, photosynthesizing shoots develop. The effect of parasites on their hosts is usually controlled by a variety of factors including the size

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of the parasite, the rate of growth and metabolic activity of the parasite, the parasite's level of dependency on the host, and the developmental stage of the host (Graves 1995).

One of the most intriguing genera of parasitic plants is *Cuscuta*. As early as 1825, this parasitic genus was compared to mythical monsters:

Round sire and sons with scaly monsters roll'd, Ring above ring, in many a tangled fold, Close and more close their writhing limbs surround, And fix with foamy teeth the envenom'd wound.

-Erasmus Darwin,1825

Cuscuta is broadly distributed world-wide, with 158 species named (Yuncker 1920). This orange, stoloniferous plant has no visible leaves (they occur as orange scales along the stolons), no roots beyond its initial germination, and is minimally photosynthetic. As a shoot holoparasite, *Cuscuta* relies on its host for water, nutrients, and sugars which are obtained by inserting haustoria into the host's vascular system. This interaction can suppress and often kill the host plant. Although *Cuscuta* species are annuals, there is evidence that many can survive throughout the year as thick stolons or haustoria plugs (Dean 1954).

Cuscuta flowers have four ovules, although not all ovules will produce seeds. The size and shape of the seeds depend on how many ovules produce seeds. Seeds may germinate directly in the capsule (Molau 1995), an adaptation to the parasitic lifestyle which often requires epiphytic growth. There has been very little research conducted on the dispersal of this genus (Gomez 1994, Meulebrouck et al. 2007), which is assumed to be haphazard and unspecialized (Kuijt 1969). Once germinated, a *Cuscuta* seedling is attracted to moisture and certain chemicals found in leaf extracts (Kuijt 1969). Without a host, a seedling can grow up to 35 cm long over the course of several weeks before dying. If it does find a host, and haustoria are formed, *Cuscuta* will then "cut its umbilical cord" to the soil or germinating media and become wholly dependent on its host (Kuijt 1969).

The effect of *Cuscuta* on the host plant is an intriguing area of research because of the feedbacks that occur between the parasite and host. For example, *Cuscuta* can cause sink-stimulated photosynthesis and nitrate uptake in its host which explains why more nitrogen is often found in a parasitized host compared to an unparasitized host (Jeschke and Hilpert 1997). Similarly, the carbon sink caused by *Cuscuta* is responsible for stimulating an increase in photosynthesis of the host (Jeschke et al. 1994). Although the mechanisms governing the attraction of solutes to the parasite are not well understood (Hibberd and Jeschke 2001), *Cuscuta* gains access to host materials (water, nutrients, and sugars) through the phloem, even though there are higher levels of these nutrients in the xylem (Jeschke et al. 1994). *Cuscuta* cells in the haustoria are connected to the host phloem cells by plasmodesmata (Birschwilks et al. 2006).

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At least twenty species of *Cuscuta* (including *C. capestris*, *C. australis*, *C. reflexa*, *C. pedicellata*, *C. gronovii*, and *C. epilinum*) are considered weeds or agricultural pests (Riches and Parker 1995). Although there is a range of host specificity, annual crops and ornamental flowers are the most favored hosts for *Cuscuta* (Marambe et al. 2002). Controlling *Cuscuta* has been the focus of much research. Measures taken include flaming and harrowing, applying herbicide, and rotating crops (Dawson et al. 1994, Hunsberger et al. 2006). Many species of *Cuscuta* are remarkably resistant to insect damage, although galls formed by weevils have been reported (Dawson et al. 1994). Post-attachment control procedures are the most successful with *Cuscuta* because it is difficult to clear seeds from the seedbank (Eplee and Norris 1995).

Despite this large body of research on the agricultural impacts and control of *Cuscuta*, there is comparatively little research on *Cuscuta* in natural communities (but see Gomez 1994, Kelly and Horning 1999, Meulebrouck et al. 2007). In California salt marshes, the native *Cuscuta salina* is commonly seen in the mid to upper intertidal zones parasitizing *Sarcocornia pacifica* (Pennings and Callaway 1996). *S. pacifica* is not only the preferred host of *C. salina* (Pennings and Callaway 1996), but also forms virtual monocultures as the competitive dominant in many Pacific salt marshes. By killing or suppressing areas of *S. pacifica*, *C. salina* creates gaps in the monoculture which facilitate colonization by lesser competitors (Pennings and Callaway 1996, Callaway and Pennings 1998). In this dissertation, I examine the

distribution and abundance of *C. salina* in the field, the interaction between *C. salina* and *S. pacifica* across multiple levels of salinity and nitrogen, and the effect of artificially restricted tidal exchange on sediment and *S. pacifica* tissue quality.

The first chapter is an experimental investigation of the distribution and abundance of *C. salina* across the entire Elkhorn Slough watershed in central California. Through surveys at multiple spatial scales, I show that patterns emerge across the estuarine and intertidal gradients, that *C. salina* recruits to new sites with wrack deposits, and that the tissue salinity of *S. virginica* can predict *C. salina* presence. This chapter also examines *C. salina* germination and seedling establishment on *S. virginica* across the tidal gradient as the experimental component of the study.

The second chapter examines how multiple levels and combinations of salinity and nitrogen affect physiological response variables in *S. pacifica* and *C. salina*, as well as their interaction. The results of this greenhouse experiment demonstrate strong interactions between salinity and nitrogen on *S. virginica*, as well as an effect of *C. salina* on *S. pacifica* physiology that varied according to nitrogen and salinity levels. *C. salina* was affected by nitrogen additions to *S. pacifica* but not salinity. Understanding the interactive effects of salinity and nutrients on marsh plants is critical not only for understanding shifting marsh function and species distributions, but for informing restoration efforts either in salt marshes often

challenged by sediment hypersalinity (Zedler et al. 2003) or in estuaries where nutrient-enriched effluent from wastewater treatment plants has been applied to offset freshwater diversions (Alexander and Dunton 2006).

The third chapter teases apart the effects of artificial tidal restriction on sediment and *S. virginica* tissue quality. Artificial tidal restriction at Elkhorn Slough mainly affects the salt marsh by altering sediment quality, but not tissue quality, of *S. virginica*. Moreover, the large effects of spatial and temporal variation associated with site, season and elevation may exert an even greater control over marsh dynamics than the effects of tidal restriction alone.

Future Work

The findings from Chapter 1 provide baseline data on the distribution and abundance of *C. salina*. In this study, I measured host quality in May when *C. salina* was established and growing vegetatively. It is possible that *C. salina* is more sensitive or selective of particular hosts during its seedling phase compared to the adult phase. Thus, a potential next step may include pinpointing germination time in order to examine host quality at that time to confirm that host quality (nitrogen content and salinity) does not play a larger role in *C. salina* distribution and abundance. Additionally, further work on dispersal from the parent plant and across

the estuary would be useful for understanding the relative contributions of recruitment to the distributional patterns. Finally, reciprocal transplants of *S. pacifica* from low to high tidal heights and vice versa may be necessary to tease apart roles of tidal inundation and host quality in *C. salina* seedling establishment.

The work in chapter 2 could be continued by conducting an identical study in the field. An experiment with salinity and nitrogen additions in the field would take into account precipitation, tidal inundation and land runoff, thereby making the conclusions much more robust and applicable to other marsh sites. Understanding the long term effects of shifts in salinity and nitrogen levels would also be informative to land managers. In this regard, a researcher might locate sites with existing differences in salinity and nitrogen to assess long term effects on *S. pacifica* and *C. salina* variables.

Continuing my work on artificial tidal restrictions, researchers may further divide study sites into more than two categories. In chapter 3, 11 study sites had full tidal exchange and 11 had restricted exchange. The restricted exchange category was defined by sites that had 50% or less of the tidal amplitude of flushed sites. Splitting this category into two groups: minimal exchange and muted exchange (Ritter et al. In press) may elucidate the more subtle effects of tidal exchange on sediment and plant characteristics. Additionally, taking measurements of *S. pacifica* biomass at each site

is an important next step in understanding the effects of tidal restrictions on the salt marsh ecosystem.

Significance

Parasitic plant ecology has been largely dominated by laboratory research and studies of crop pests rather than research conducted in natural communities (Pennings and Callaway 2002). This dissertation contributes to the growing number of studies dedicated to understanding parasitic plants in the field and how their distribution, abundance, and interactions with host plants vary with the abiotic environment. In addition to expanding our knowledge of parasitic plants in natural communities, this body of work also provides baseline data on *C. salina* in the salt marshes of Elkhorn Slough.

The Elkhorn Slough watershed in Moss Landing, California is an estuary with tremendous diversity and species richness (Caffrey et al. 2002). It lends beauty and biological function to a coastline that has already lost more than 90% of its coastal marshes (Scharffenberger 1999). Not surprisingly, Elkhorn Slough lists the coastal marsh habitat as one of five resources that are of highest priority for protection against significant threats. These threats include eutrophication from agricultural runoff (Caffrey et al. 2003) and tidal erosion or restriction resulting from hydrological

manipulations (Scharffenberger 1999). The ultimate goal of natural habitat restoration requires a fundamental understanding of the underlying biological and physical processes of healthy wetlands. Accordingly, many estuarine reserves, including Elkhorn Slough National Estuarine Research Reserve, have set a high priority on the accumulation of baseline data through native species monitoring. By investigating the patterns of C. salina distribution and abundance, as well as its interaction with S. virginica, my work has contributed to this reserve-wide goal. It is astonishing that C. salina has been a member of Elkhorn Slough's salt marsh community for over 6,000 years (Caffrey et al. 2002), and yet so little is known about its basic biology (Kuijt 1969). With such a dearth of knowledge, it is difficult to predict how inevitable changes to our wetlands might affect the distribution and abundance of C. salina and, in turn, how this will affect the salt marsh community. This dissertation demonstrates the roles of multiple factors in determining the distribution and abundance of C. salina, the interaction between C. salina and S. pacifica, and the effects of artificial tidal restrictions on the S. pacifica marsh. By surveying the existing trends in the abiotic and biotic salt marsh, this work also provides a baseline for the marsh as a whole ecosystem within the Elkhorn Slough watershed.

CHAPTER 1

DISTRIBUTION OF A PARASITIC PLANT IN A CALIFORNIA SALT MARSH

Introduction

Understanding what limits the distribution of organisms is a major goal in ecology. One of the most tractable systems for studying species distributions is the intertidal habitat, because small changes in elevation are usually associated with large changes in environmental variables (Pennings and Bertness 2001). Thus, species are often distributed in horizontally narrow, discrete zones. In the rocky intertidal, where most organisms are marine in origin, the lower limits of these zones are usually set by biotic forces like predation (Paine 1974) or competition (Connell 1961), while the upper limits reflect abiotic forces such as desiccation (Connell 1972). The zonation of plant species across the intertidal gradient of salt marshes has also been well studied, although here the pattern is often reversed. The lower limit for marsh plants is attributed to the physical stress of flooding and high salinities that can diminish growth (Bertness et al. 1992), thicken leaves (Longstreth and Nobel 1979), hinder germination (Shumway and Bertness 1992), and uproot seedlings (Ellison 1987). The upper limit is often set by interactions between species. For example, a superior competitor may dominate physically benign zones and displace other plants to more stressful areas (Bertness and Ellison 1987, Bertness 1991b, a, Pennings and Callaway 1992). Facilitation between species may play a role in salt marsh zonation either

directly by buffering harsh abiotic conditions (Hacker and Bertness 1995, 1999) or indirectly by alleviating competition (Bertness 1991a, Pennings and Callaway 1996, Callaway and Pennings 1998, 2000).

Salt marsh species that form virtual monocultures at a particular tidal elevation, such as cordgrass, Spartina spp., and pickleweed, Sarcocornia pacifica (Sarcocornia hereafter), have received the most attention (Josselyn 1983, Bertness 1991b, a), with fewer studies examining plants with patchy distributions (Bertness and Ellison 1987). Patchy distributions are of interest to ecologists because the factors governing them are often more complex than those involved in the broader distributions of dominant plants. For example, some species may rely on disturbances for generating gaps in areas dominated by other plants (Bertness and Ellison 1987). The parasitic salt marsh dodder, Cuscuta salina (Cuscuta hereafter), has a patchy distribution in salt marshes along the Pacific coast of the US. In the Elkhorn Slough watershed in Central California, Cuscuta is absent at some sites, forms small, isolated patches at other sites, and nearly blankets the entire intertidal zone at others. The mechanisms behind this pattern are unknown. However, it is found in close association with its preferred host plant, Sarcocornia (Callaway and Pennings 1998), which is broadly distributed across the entire estuary, suggesting that the distribution of *Cuscuta* is governed by factors more complex than the presence of the host.

The goal of this study was to examine the distribution and abundance of *Cuscuta*, focusing on the roles of environmental factors, host quality, and recruitment. In an examination of environmental factors, I quantified *Cuscuta* distribution, abundance, establishment, and germination along the intertidal gradient (from low to high tidal heights) and distribution and abundance along the estuarine gradient (from the mouth to the head of the estuary). Both of these environmental gradients commonly affect the distribution of many salt marsh plants (Bertness and Ellison 1987, Crain et al. 2004). I also tested for associations between *Cuscuta* and sediment salinity, moisture, nitrate and ammonium, and water salinity, and examined the effect of water salinity on seed germination in the laboratory. The roles of Sarcocornia tissue salinity and total nitrogen content on Cuscuta distribution and abundance were examined as measures of host quality. Finally, I tested the hypothesis that wrack is a dispersal agent for Cuscuta seeds. Wrack consists of dead plant litter that is often stranded by tidal action in the upper marsh (Bertness and Ellison 1987). There is evidence that wetland plant seeds are dispersed by clinging to the litter and germinating once it is deposited (Ellison 1987, Xiong and Nilsson 1999). Cuscuta infections are commonly seen superimposed on old wrack lines the following summer (K. Griffith, Per. Obs.), suggesting that wrack may transport *Cuscuta* seeds.

Methods and Results

Study Species

The native, parasitic plant *Cuscuta salina* Engelm. var. *major* Yunck. is distributed from British Columbia to Mexico (Zedler 1982, Ferren 1985). *Cuscuta* is an obligate shoot parasite and reproduces by seed and clonal growth. Seeds are passively released and may sometimes germinate within the fruit (Molau 1995). A summer annual, *Cuscuta* forms conspicuous orange patches by entangling the habitat's competitive dominant, *Sarcocornia*, with long tendrils. Lacking roots and functional leaves, *Cuscuta* accumulates carbon, water, and nutrients by inserting plugs of tissue (haustoria) into the host's vascular system (MacLeod 1961).

Sarcocornia pacifica (Standley) A.J. Scott, the preferred host of *Cuscuta* (Callaway and Pennings 1998), is a perennial, C₃ plant distributed along the US west coast from California to Baja Mexico (MacDonald and Barbour 1974) and on the US east coast from New England to Florida (Peinado et al. 1994). It grows mainly in coastal salt marshes, occupying a zone from mean high water to the highest high tides (Mahall and Park 1976b, Josselyn 1983). *Sarcocornia* is most productive (with green succulent tissue) in the summer months and dormant (with woody stems) in the winter (Boyer et al. 2001). It maintains low water potentials in its tissues by accumulating solutes from the sediment environment (Davy et al. 2001).

Study Site

This study was conducted in the estuarine habitats of the Elkhorn Slough watershed. This estuary, located near Moss Landing, California, on the Monterey Bay (Fig. 1.1), is comprised of multiple channels, the largest of which is Elkhorn Slough. Smaller channels include Moro Cojo Slough, the Old Salinas River channel, and Bennett Slough. This region experiences a Mediterranean climate (11° to 15.4° C annually) with a distinct rainy season, from October through May, when rainfall averages 55.2 cm (Caffrey et al. 2002). Marshes dominated by *Sarcocornia* border the main channel and tidal creeks. Other species of the salt marsh plant community include *Disticilis spicata*, *Atriplex* spp., *Jaumea carnosa*, *Frankenia salina*, *Spergularia* spp., and *Cuscuta salina*. *Cuscuta* has been present at Elkhorn Slough for over 6,000 years (Caffrey et al. 2002). As the competitive dominant of salt marshes at Elkhorn Slough, *Sarcocornia* is responsible for the second largest primary production in the Elkhorn Slough watershed (149 gC/m² per year) (Reilly 1979).

Fully tidal portions of the estuary have mixed semi-diurnal tides with a range of 2.5 m (Caffrey et al. 2002). About 900 ha of estuarine habitat in the Elkhorn Slough watershed receives unrestricted tidal exchange, with the same tide range as the adjacent open coast; the remaining 500 ha have artificially restricted tidal exchange due to water control structures (dikes, culverts, and tide and flap gates). In early 2005, 22 study sites were established: 11 received full tidal exchange and 11 received restricted tidal exchange (Figure 1.1). The tidal amplitude was measured with graduated tide staffs at restricted sites on December 12, 2005. All restricted sites experienced less than 50% of the full tidal range.

These 22 sites were chosen to include the wide range of environmental variability in the Elkhorn Slough watershed and to examine edaphic variation that is likely to influence marsh plant distributions. The distance of each site from the mouth of the estuary along the closest main channel was measured using ArcView software.

Abiotic Factors and Host Quality

To examine the distribution and abundance of *Cuscuta* across the intertidal and estuarine gradient, I conducted a field survey in May 2005. At each of the 22 sites described above, I established 9 sampling stations at 3 different tidal heights: 3 at the lower border of the site, 3 in the middle of the site, and 3 at the upland border of the site (Fig. 1.2). Sampling stations located at the same tidal heights were 15m apart. I quantified *Cuscuta* distribution as presence/absence at each site, and at each tidal height within sites. I quantified *Cuscuta* abundance as proportion cover using a $0.25 \times 0.25 \text{ m}^2$ quadrat and counting all 5 cm² squares that contained *Cuscuta* stems. The area of *Cuscuta* cover was divided by the total rectangular area of the site (designated by the dashed line in Fig. 1.2) to obtain *Cuscuta* proportion cover per site. Proportion cover at each tidal height within sites was obtained by scoring each *Cuscuta* patch as low, middle, or high according to which tidal height it was located nearest. To examine the effect of tidal height on *Cuscuta* abundance, I used a randomized block ANOVA (with site as a random variable and location as a fixed variable) with the *Cuscuta* proportion cover data at each tidal height. The effect of tidal height on *Cuscuta* presence was analyzed using a chi-square test (2 x 3 table). A t-test was used to examine the effect of tidal exchange (full vs. restricted) on *Cuscuta* proportion cover. A chi-square test (2 x 2 table using a Fisher's exact test) was used to examine the effect of tidal exchange on *Cuscuta* presence. The relationship between the distance from the estuarine mouth and the presence of *Cuscuta* at each site was examined using a logistic regression. This analysis excluded sites with restricted tidal exchange since their distance from the mouth of the estuary is not likely to be related to water quality or residence time. The relationship between distance from the estuarine mouth and *Cuscuta* proportion cover was examined with a linear regression. To meet assumptions of normality, *Cuscuta* proportion cover data was fourth-root transformed prior to analysis.

To examine associations between *Cuscuta* and sediment variables, I collected sediment cores (2 cm diameter, 25 cm deep) at each sampling station during low tide. The salinity of water at each site was measured with a refractometer (Vee Gee STX-3, Kirkland, Washington). All sediment samples were sealed in bags immediately in the field and returned to the lab in a cooler to maintain the temperature at which they were collected. In the laboratory, sediment samples were homogenized and KCl extracts were performed. Extracts were analyzed using a flow injection analyzer (Lachat Instruments, Loveland, Colorado) for NO₃-N and NO₂-N (hereafter referred to as NO₃-N) and NH₄-N (Hofer 2003, Knepel 2003). Sediment moisture was

measured gravimetrically. Since sediments can be very dry in these marshes, I created a solution of sediment and water to measure sediment salinity (Rhodes 1982). Salinity of the supernatant was measured with a refractometer.

To examine associations between *Cuscuta* and host quality variables, I collected *Sarcocornia* tissue at each sampling station during low tide. *Sarcocornia* tissue was analyzed for salinity by expressing liquid from the succulent stems using a garlic press and measuring its salinity with a refractometer. *Sarcocornia* samples were dried in an oven at 60°C for 96 hours (or until all moisture was lost), ground in a Wiley Mill, and analyzed for total %N using the combustion method (vario MAX CN, Elementar, Hanau, Germany). All laboratory analyses were performed at the University of California, Santa Cruz.

Sediment and *Sarcocornia* subsamples (n=3) were averaged to obtain a single value per tidal height (low, middle, high) per site. Because the measured variables were expected to covary, I used principal components analysis (PCA) with varimax rotation to derive composite factors, which by definition are independent of each other (Quinn and Keough 2002). The PCA yielded 2 composite factors (PC1 and PC2) with eigenvalues greater than 1.0. Relationships between PC scores and *Cuscuta* presence/absence (at each tidal height) were examined with a logistic regression. Relationships between PC scores and *Cuscuta* proportion cover were examined with a linear regression. Where PC scores trended toward significantly predicting *Cuscuta* presence or proportion cover, I examined the highly loaded

variables in that composite variable individually. The effects of tidal height and distance from the mouth of the estuary on *Sarcocornia* tissue salinity were examined with an ANOVA, and linear regression, respectively. To meet assumptions of normality, sediment NO₃-N and sediment NH₄-N were fourth-root transformed prior to analysis.

To test the hypothesis that germination success is constrained by tidal height, I deployed seed bags to 10 uniformly-spaced locations along a transect perpendicular to the shoreline at 4 sites. Seed bags were made out of tulle material; each bag contained 10 *Cuscuta* seeds. I used pin flags to anchor the bags to the surface of the sediment in November 2007 and collected them in March 2008. I used an ANOVA to test for the effect of site on the percentage of seeds that germinated, and a logistic regression to test for a relationship between distance from the shoreline and the probability of at least one seed germinating.

To test the hypothesis that increasing salinity constrains *Cuscuta* germination, I conducted a germination trial in the greenhouse in January, 2007. *Cuscuta* seeds were placed in Petri dishes containing filter paper soaked with water of varying salinity. Each salinity treatment (0‰, 10‰, 20‰, 30‰, 40‰, 50‰) was replicated 10 times; each dish contained ten seeds. Dishes were sealed with parafilm and left in the incubator to germinate (10°C at night and 13°C during the day, with a 14 hour day-length). Germinations were scored every 4 days for 2 months. I used an ANOVA to test for the effect of salinity on *Cuscuta* germination, and pairwise comparisons were made with a Tukey Test. Treatment levels that resulted in zero germination were omitted from the analysis due to lack of variance.

To test the hypothesis that seedling establishment (coiling onto the host's stem) on *Sarcocornia* hosts is constrained by tidal height, I transplanted *Cuscuta* tissue onto *Sarcocornia* plants along transects perpendicular to the shoreline at 5 field sites (site numbers 2, 11, 14, 16, 20). Tissue to be transplanted was collected by cutting infected *Sarcocornia* stems from naturally occurring infections. I placed each of these pieces in individual water-filled vials that were tied to new *Sarcocornia* plants at equidistant (every meter) locations at that the same site. *Cuscuta* was transplanted in July, 2006 and scored (yes or no) for attachment to the new *Sarcocornia* in August, 2006. I used an ANOVA to test for the effect of site on stem coiling by the transplants. I used a logistic regression to test for a relationship between distance from the shoreline and the probability of *Cuscuta* attaching to *Sarcocornia*. Because the elevational gradient differed among the five study sites, the distance from the shoreline was adjusted to scale from 0 (shoreline and lower border of *Sarcocornia* band) to 100 (upland border of *Sarcocornia* band).

Recruitment

To test the hypothesis that wrack (dead plant litter that is often stranded by tidal action at high tidal heights) transports *Cuscuta* seeds, I collected and examined wrack samples for *Cuscuta* seeds and seedlings. In January 2006, after a large storm,

I collected three wrack samples (12 oz. each) per site at 10 sites (site numbers 2, 3, 4, 5, 7, 8, 9, 10, 11, 12). I used a dissecting microscope to count the number of seeds and seedlings in each sample. Sites with restricted tidal flow and one tidally flushed site (site number 13) did not have any wrack and were thus eliminated from this survey.

If *Cuscuta* is recruiting to sites with wrack, then there should be no relationship between *Cuscuta* in wrack and *Cuscuta* adults in the marsh on which the wrack was deposited (the presence of a relationship suggests the possibility of seeds dispersing from adults to wrack deposits at the same site). I used a chi-square test (2 x 2 table using a Fisher's exact test for sparse cells) to compare the presence of *Cuscuta* in wrack with the presence of adult *Cuscuta* growing at each site.

All statistical analyses were performed with SYSTAT 12.0.

Results

Abiotic factors and host quality

Patterns of *Cuscuta* distribution and abundance emerged at different spatial scales. Within sites, *Cuscuta* proportion cover was the highest at high tidal heights compared to low tidal heights (Table 1.1, Fig. 1.3). However, there was only a trend towards this pattern with *Cuscuta* presence data (chi-square test, p = 0.066). At the scale of the whole estuary, there was a higher probability of *Cuscuta* presence with increasing distance from the estuarine mouth (logistic regression, Z = 1.556, df = 1, p

= 0.055, Fig. 1.4). There was no relationship between distance from the estuarine mouth and *Cuscuta* proportion cover (linear regression, $r^2 = 0.083$, df = 1, 20, p = 0.194). Tidal exchange regime had no effect on either *Cuscuta* proportion cover (t-test, t = -1.120, df = 20, p = 0.276), or *Cuscuta* presence (chi-square test, p = 1).

There was a significant effect of both host quality and abiotic factors on *Cuscuta*. The sediment, water, and *Sarcocornia* data were reduced by principal components analysis to two composite variables (Table 1.2). Sediment salinity, NO₃-N, NH₄-N and moisture loaded heavily on the PC 1 axis. Water salinity, *Sarcocornia* salinity, and Sarcocornia %N loaded heavily on the PC 2 axis. There was a higher probability of *Cuscuta* presence at higher values of PC 2 (logistic regression, Z = -2.068, df = 1, p = 0.039). This relationship was driven by *Sarcocornia* tissue salinity: as Sarcocornia salinity rose, the probability of a Cuscuta infection fell (logistic regression, Z = -2.220, df = 1, p = 0.026, Fig. 1.5). There was no effect of either PC1 or PC2 on *Cuscuta* proportion cover (linear regressions, $r^2 = 0.039$, df = 1, 64, p = 0.110: $r^2 = 0.022$, df = 1, 64, p = 0.238, respectively), nor was there a relationship between the presence of *Cuscuta* and PC1 (logistic regression, Z = 0.768, df = 1, p = 0.442). Sarcocornia salinity was not affected by distance from the mouth of the estuary (linear regression, $r^2 = 0.005$, df = 1, 20, p = 0.753), or tidal height (ANOVA, df = 2, 63, F = 2.392, p = 0.100).

Germination was not significantly affected by tidal height but local site conditions had a large effect on the number of seeds that germinated. There was a significant effect of site on the percentage of seeds that germinated (ANOVA, df = 3, 36; F = 75.82, p = 0.000), and a non-significant trend towards a higher probability of germination with increasing tidal height (logistic regression, Z = 1.716, df = 1, p = 0.074). The germination trial in the laboratory showed a significant effect of salinity on *Cuscuta* germination (ANOVA, F = 9.979, df = 3, 36; p = 0.000, Fig. 1.6). The greatest percentage of seeds germinated in freshwater, with fewer seeds germinating in 10‰, 20‰ and 30‰, and no seeds germinating in 40‰ or 50‰.

There was a significant effect of tidal height on the probability of *Cuscuta* attaching to *Sarcocornia* (logistic regression, Z = 1.865, df = 1, p = 0.048, Fig. 1.7). *Cuscuta* transplants were more likely to attach to *Sarcocornia* with increasing distance from the shoreline. There was no effect of site on *Sarcocornia* stem coiling by the *Cuscuta* transplants (ANOVA, df = 4, 33; F = 18.62; p = 0.137).

Recruitment

Cuscuta seeds and seedlings were found in the wrack samples (Fig. 1.8). There was no relationship between the presence of *Cuscuta* arriving in wrack and the presence of *Cuscuta* adults at a particular site, suggesting that seeds recruit to new sites with wrack (chi² test: p = 1).

Discussion

For plants living in the intertidal zone of salt marshes, many factors affect distribution and abundance including tidal inundation, disturbance, and species interactions. Those species with zonal distributions are usually limited from lower tidal heights by the stress of tidal inundation whereas interactions with other species limit growth toward higher tidal heights. Patchily distributed species may rely on wrack for suppressing competitive dominants, dispersing seeds, and providing a suitable germination environment (Bertness and Ellison 1987). The results of this study suggest that *Cuscuta* is most abundant in a distinct zone at high tidal heights. Some of the factors that limit the distribution of *Cuscuta* to this zone are similar to those of other zonally distributed, non-parasitic species. For example, the lower limit of the Cuscuta distribution is likely to be set by salinity and other correlates of tidal height that affect seed germination. Other factors affecting the distribution of Cuscuta, however, are unique its parasitic habit. For example, the quality of the host may affect distribution and abundance since Cuscuta was more likely to occur on hosts with lower tissue salinity, and seedling establishment on host plants was a function of tidal height. This study has shown that, in the case of a parasitic marsh plant, multiple factors influence the parasite at different stages of its life cycle (Fig. 1.9).

Abiotic Factors

The distribution and abundance of *Cuscuta* in the Elkhorn Slough watershed is affected by salinity, tidal height, and the estuarine gradient. High tidal heights are associated with the greatest *Cuscuta* abundance compared to low tidal heights. In their study of *Cuscuta* in a southern California salt marsh, Pennings and Callaway (1996) reported that *Cuscuta* was most abundant in the high *Sarcocornia* zone, and declined with decreasing elevation. They did not find *Cuscuta* at the highest zones of the marsh (dominated by plants other than *Sarcocornia*). In the Elkhorn Slough watershed *Sarcocornia* is distributed across all tidal heights of the marsh. Thus, our results suggest that the presence of the *Sarcocornia* host may be more important than tidal elevation for *Cuscuta*.

This pattern along the tidal gradient suggests a negative effect of salinity on *Cuscuta*. Indeed, the germination trial supported this common phenomenon among many halophytes, where declining salinities are associated with increasing germination (Shumway and Bertness 1992, Noe and Zedler 2000, Alexander and Dunton 2002). Although seed germination in the field was significantly affected by site variation, there was still a trend towards a higher probability of germination at higher tidal heights, again suggesting the role of salinity. Many marshes exhibit a predictable salinity gradient from low to high tidal heights, although this feature is highly variable due to frequent tidal flushing, topography, evaporation, and precipitation (Callaway and Sabraw 1994).

The presence of *Cuscuta* is also associated with the estuarine gradient across the whole estuary. An increasing presence with increasing distance from the mouth of an estuary is a common pattern of distribution for many fresh and brackish marsh plant species that are less tolerant of salinity than salt marsh plants (Crain et al. 2004). However, at Elkhorn Slough, the combination of strong tidal flushing and water control structures that limit freshwater input prevent a salinity gradient occurring from the mouth to the head (Caffrey et al. 2002). There may be some other correlate of distance from the mouth that is driving this pattern (eg. water residence time). My results suggest that regardless of its parasitic habit, *Cuscuta* distribution and abundance may be partially driven by similar environmental factors as other zonallydistributed, non-parasitic plants.

Host Quality

The effect of biotic factors on *Cuscuta* sets it apart from other non-parasitic marsh plants due to the parasite-host relationship. For example, *Cuscuta* is more likely to attach to *Sarcocornia* stems with increasing tidal height. Although I found an association between *Cuscuta* presence and host tissue salinity, suggesting that host quality may be a factor in the likelihood of *Cuscuta* attachment across the intertidal gradient, there was no effect of tidal height on *Sarcocornia* salinity. Thus, the low probability of attachment at low tidal heights may be a result of mechanical disturbance by tidal inundation or some other correlate of tidal height. These results
are in agreement with work by Pennings and Callaway (1996) who found *Cuscuta* virulence (the percent reduction in *Sarcocornia* cover) to increase with tidal height in the *Sarcocornia* zone. Similarly, herbivorous insects tend to prefer plants growing in less saline conditions (Hemminga and Van Soelen 1988), although herbivore preference is highly dependent on the plant and herbivore studied (Goranson et al. 2004). There may be other measures of plant quality that affect *Cuscuta* since tidal inundation is known to reduce *Sarcocornia* tissue quality (Seliskar 1985) and stunt growth (Mahall and Park 1976a). It is unclear whether the interaction with the host or simply mechanical disturbance by tidal inundation sets the lower limits of *Cuscuta* distribution.

Recruitment

Wrack is a major form of natural disturbance in salt marsh communities (Bertness and Ellison 1987, Valiela and Rietsma 1995, Minchinton 2002). Primarily composed of plant litter, wrack deposits are often stranded by tidal action along high tidal heights (Bertness and Ellison 1987). This study suggests that *Cuscuta* is dispersed by wrack, although the method by which seeds are retained in wrack is unclear. While *Sarcocornia* seeds, also dispersed by wrack, are covered with little hooks that attach to floating debris (Ellison 1987), *Cuscuta* may be equipped to disperse with wrack by other means. At Elkhorn Slough, wrack is primarily composed of dead *Sarcocornia* litter. Because *Cuscuta* parasitizes *Sarcocornia* by

forming dense mats of tendrils that often persist beyond the life span of the parasite (K. Griffith, Pers. Obs.), it is possible that portions of this mat (with seeds still attached) break off with *Sarcocornia* stems and recruit to new sites with the floating host stems. *Cuscuta* species are known to germinate while still in fruit, without being dehisced (Kuijt 1969). Aside from wrack and hydrochory, there are probably other modes of dispersal because *Cuscuta* infections occur at sites with very limited tidal exchange. Little is known about *Cuscuta* spp. dispersal other than it is non-specialized and often referred to as "haphazard" (Kuijt 1969).

The benefit of wrack for many patchy, non-parasitic marsh species lies primarily in its suppression of the competitive dominant, thus allowing these rafting seeds a suitable place to germinate and grow before the slower dominant species recolonize the area (Bertness and Ellison 1987). For *Cuscuta*, the presence of other plants is crucial to its survival and thus the benefit of wrack may lie both in its dispersal capabilities and its placement on the *Sarcocornia* canopy. Seeds that germinate here may not need to grow far in order to find a host compared to a seed germinating on the soil surface. For both *Cuscuta* and other, non-parasitic marsh plants, wrack may promote high germination rates due to lower salinities and/or higher temperatures than the nearby soil (Parker and Richies 1993, Noe and Zedler 2001b, a).

Conclusions

Because the growth and performance of parasitic plants are often a function of the host species on which they depend (Kuijt 1969), the mechanisms involved in their distribution are likely to be more complex than those of non-parasitic species. For example, the effect of tidal inundation on *Cuscuta* may have pre-settlement effects similar to those on other non-parasitic marsh plants (i.e. hindered germination at lower elevations), but post-settlement effects may be entirely different since the parasite may experience the abiotic or biotic stress indirectly, mediated by the host plant. As one of the few studies to examine the distribution of a parasitic plant across the intertidal gradient, this study highlights not only the importance of spatial scale, but also the roles of both the environment and the host in driving patterns of distribution. **Table 1.1**. Results of ANOVA examining the effect of tidal height on *Cuscuta*proportion cover. Site was included in the model to partition out spatial variance.

Source	df	MS	F-ratio	Р
Tidal Height	2	0.085	3.695	0.033
Site	21	0.063	2.720	0.003
Error	42	0.023		

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Variable	PC 1	PC 2
Sarcocornia Salinity	-0.066	0.870
Sarcocornia %N	-0.301	-0.696
Sediment Moisture	0.864	0.274
Sediment Salinity	0.801	0.501
Sediment NO ₃ -N	0.722	-0.213
Sediment NH ₄ -N	0.738	-0.114
Water Salinity	-0.120	0.794
% of Total Variance Explained	36.6%	32.2%



Figure 1.1. Map of study sites in the Elkhorn Slough watershed. Bold numbers indicate tidally restricted study sites (sites 1, 6, 15, 16, 21 and 22 contain culverts; sites 14, 19, and 20 contain flap gates; sites 17 and 18 contain tide gates).



Figure 1.2. A diagram of the sampling stations at a single study site. At each "x" I collected a soil core and *Sarcocornia* tissue for analysis. I quantified proportion cover of *Cuscuta* within the area surrounded by the dashed-line. The presence or absence of *Cuscuta* was recorded in the high, middle and low marsh, as well as at the site as a whole.



Figure 1.3. Effect of tidal height on *Cuscuta* proportion cover. Error bars represent \pm 1 s.e. Tukey pairwise comparisons test: bottom-middle, p = 0.355; bottom-top, p = 0.025; middle-top, p = 0.388.



Figure 1.4. Relationship between the distance from the mouth of Elkhorn Slough and the probability of *Cuscuta* infection. Boxes are bounded by the 25th and 75th percentiles with the median displayed. Outer fences represent the 5th and 95th percentiles. Circles represent outliers. Probability curve was generated by a logistic regression.



Figure 1.5. The relationship between *Sarcocornia* tissue salinity and the probability of *Cuscuta* infection. Boxes are bounded by the 25th and 75th percentiles with the median displayed. Outer fences represent the 5th and 95th percentiles. Circles represent outliers. Probability curve was generated by a logistic regression.



Figure 1.6. The effect of salinity on germination of *Cuscuta*. Values represent means ± 1 s.e. Letters represent results of a tukey test (p < 0.05).



Figure 1.7. The relationship between distance from the shoreline and the probability of *Cuscuta* attaching to *Sarcocornia*. Boxes are bounded by the 25th and 75th percentiles with the median displayed. Outer fences represent the 5th and 95th percentiles. Circles represent outliers. Probability curve was generated by a logistic regression.



Figure 1.8. Counts of seeds/seedlings in wrack samples (black bars) and proportion cover of *Cuscuta* (gray bars). Seed/seedling counts in wrack are averaged across three samples collected at each site. Proportion cover data is averaged over low, mid, and high sampling locations at each site. Error bars represent ± 1 SD. Only the sites where wrack was collected are shown here. Site numbers are the same as those in Fig. 1.



Figure 1.9. A conceptual diagram of factors that affect *Cuscuta* germination, establishment, adult distribution, and dispersal. Solid lines represent a significant effect or relationship, the dashed line represents a non-significant trend, and dotted lines represent hypotheses generated by this work.

CHAPTER 2

NITROGEN AND SALINITY MEDIATE AN INTERACTION BEWTEEN A PARASITIC PLANT AND ITS HOST PLANT

Introduction

A central goal in ecology is to understand the dynamics of species interactions. Although negative species interactions have received a great deal of attention in this regard, parasitism between plants is comparatively understudied, despite the prevalence of parasitic plants in natural communities (Press and Phoenix 2005). Researchers have focused largely on their role as crop pests (Parker and Riches 1993, Eplee and Norris 1995, Marambe et al. 2002, Hunsberger et al. 2006) with fewer studies examining their ecology in natural systems (Gomez 1994, Pennings and Callaway 1996, Meulebrouck et al. 2007). One of the most intriguing aspects of this interaction is the potential for parallels between parasitic plants and herbivores in their effects on prey species (Atsatt 1977, Pennings and Callaway 2002).

Plant-herbivore relationships have been studied extensively in direct tests of the plant vigor hypothesis (vigorous plants are more palatable for herbivores, Price 1991) and the plant stress hypothesis (stressed plants are more palatable for herbivores, White 1974, White 1984). In support of the plant vigor hypothesis, increased soil nitrogen content often leads to an increase in plant tissue content (i.e. a

more vigorous plant), and this results in higher densities of herbivorous insects (Bowdish and Stiling 1998, Levine et al. 1998). Similarly, parasitic plants often choose host plants with higher nitrogen contents (Kelly 1992), and accumulate more biomass on these hosts (Parker and Riches 1993). In addition to nutrients, which often enhances the vigor of plants, factors associated with plant stress can also significantly affect both plant-parasite and plant-herbivore interactions. Soil salinity is a major source of stress for terrestrial plants living in the intertidal zone of salt marshes. It has led to a variety of adaptations, including succulence, salt exclusion, salt secretion, and shedding (Cronk and Fennessy 2001). Herbivorous insects tend to prefer plants growing in less saline conditions (Hemminga and Van Soelen 1988), although herbivore preference is highly dependent on the plant and herbivore studied (Goranson et al. 2004). Parasitic plants from salt marshes prefer hosts from both ends of the salinity spectrum, compared with hosts of intermediate salinity (Frost et al. 2003), and their virulence there may differ as a function of tidal elevation (Pennings and Callaway 1996).

Investigating how multiple environmental factors affect the strength of species interactions is central to understanding the structure and dynamics of a community (Agrawal et al. 2007). Although studies have examined the separate roles of salinity and nitrogen on herbivores and, to a lesser extent, on parasitic plants, the complex interaction between these two abiotic factors has received far less attention. Salt marshes are very tractable systems for examining multiple environmental factors because small changes in elevation are associated with large changes in edaphic variables such as salinity, flooding, and nutrients (Pennings and Bertness 2001). Previous studies have found significant interactions between salinity and nitrogen on plants and their herbivores. For example, Moon and Stiling (2000) report that herbivores were more abundant on salted plots when no nitrogen was added, and that nitrogen additions masked the effect of salt additions on herbivores. Salinity can also reduce tissue nitrogen of marsh plants (Moon and Stiling 2002), and have large impacts on herbivores (Hemminga and Van Soelen 1988, Moon and Stiling 2000). The effects of these factors on parasitic plants and how they compare and contrast with herbivores in the same system remains unexplored.

The goal of this study was to investigate the effect of multiple abiotic factors on a parasitic plant-host plant interaction in order to examine how multiple levels and combinations of salinity and nitrogen affects physiological response variables in the host plant and coiling of the parasite, as well as their interaction. I used the parasitic plant, *Cuscuta salina* and its host, *Sarcocornia pacifica*, as a model system.

Methods

Study Species

Sarcocornia pacifica (Standley) A.J. Scott (*Sarcocornia* hereafter) is a perennial, C₃ plant distributed along the US west coast from California to Baja Mexico and on the US east coast from New England to Florida (Peinado et al. 1994).

It grows mainly in coastal salt marshes, occupying a zone from mean high water to the highest high tides (Mahall and Park 1976b, Josselyn 1983). *Sarcocornia* is most productive (with green succulent tissue) in the summer months and dormant (with woody stems) in the winter (Boyer et al. 2001). It maintains low water potentials in its tissues by accumulating solutes from the sediment environment (Davy et al. 2001).

Cuscuta salina Engelm. var. *major* Yunck. (*Cuscuta* hereafter) is an annual, parasitic plant found in salt marshes along the western US coast (Zedler 1982). *Cuscuta* forms conspicuous orange patches by entangling *Sarcocornia* with long tendrils. Lacking roots and functional leaves, *Cuscuta* accumulates carbon, water, and nutrients by inserting plugs of tissue (haustoria) into the host's phloem (MacLeod 1961).

Plant Collection and Propagation

All plant tissue and seeds used in this study were collected from Elkhorn Slough, near Moss Landing, California. Elkhorn Slough is an estuary located on the Monterey Bay. This region experiences a Mediterranean climate (11° to 15.4° C annually) with a distinct rainy season (October through May), when rainfall averages 55.2 cm (Caffrey et al. 2002). Elkhorn Slough has mixed semi-diurnal tides with a range of 2.5 m (Caffrey et al. 2002).

I collected succulent *Sarcocornia* stems randomly from multiple sites at Elkhorn Slough in March, 2006. At the greenhouses at the University of California, Santa Cruz, I propagated 240 plants by making cuttings and rooting them in a misting table (with 10‰ salt additions). In April, plants were potted in plastic pots (8.25 cm^2 pots, 7 cm deep) and fertilized with Dyna-Gro 7-9-5 at a rate of 1/4 tsp/gal every 2 weeks. No additional salt was added. By late June, when plants had grown 10 cm tall on average, they were repotted into larger pots (8.9 cm^2 pots, 9.2 cm deep) to begin receiving experimental treatments. Dyna-Gro applications ceased at this time.

Experimental Design

To test for the effects of salinity, nitrogen, and *Cuscuta* on *Sarcocornia*, I conducted a greenhouse experiment in a 3-way factorial ANOVA design. Within this experiment I also tested for the effects of salinity and nitrogen treatments on *Cuscuta* (via *Sarcocornia*) in a 2-way factorial ANOVA design. *Sarcocornia* plants received one of four levels of salinity (Instant Ocean salt mix: 0‰, 10‰, 20‰, and 34‰), one of three nitrogen treatments (applied as dissolved urea granules: 0 g/l, 3.33 g/l, and 6.66 g/l), and one of two levels of *Cuscuta* (present or absent). There were originally four nitrogen treatments; but the highest level killed plants prematurely, and so it was removed from the analysis. All salinity and nitrogen treatments were delivered to plants dissolved in 40 ml of DI water. Salinity and nitrogen treatments were administered every two days, alternating between salt and nitrogen treatments.

After one month of treatments, I assessed nitrogen treatment effects by analyzing tissue from a subsample of 6 plants from each treatment level for total Kjeldahl nitrogen using the block digester method (Diamond 2001) and a flow injection analyzer (Lachat Instruments, Loveland, Colorado) at the University of California, Santa Cruz. There was a significant effect of nitrogen additions on tissue TKN (no added N: 136.6 \pm 3.759 mg N/l, mid-N: 199.6 \pm 8.334 mg N/l, high-N: 245.0 \pm 6.639 mg N/l, Table 2.1). All levels were significantly different from one another (Tukey test, p < 0.00).

Cuscuta was then introduced to *Sarcocornia* plants. I collected *Cuscuta*infected *Sarcocornia* stems from three sites at Elkhorn Slough and randomly selected half of all the greenhouse *Sarcocornia* plants to inoculate by placing an open eppendorf tube filled with water and an infected *Sarcocornia* stem near the plant. Once *Cuscuta* grew from the field host to the greenhouse host I cut the connection to the field host and removed the tube.

Data Collection and Analysis

The experiment concluded two months after *Cuscuta* was introduced. I quantified *Cuscuta* growth by counting the number of host stems coiled per host plant as well as the number of coils per host plant. *Sarcocornia* (with *Cuscuta* removed) was analyzed for tissue salinity by expressing solution from the succulent stems onto a refractometer (Vee Gee STX-3, Kirkland, Washington). Some plants were not succulent enough to analyze for tissue salinity and thus were omitted from that analysis. These missing replicates were equally spread across treatments. Plants were then dried in an oven at 60°C for 96 hours (or until all moisture was lost) and weighed. Finally, a random subset of 5 plants was analyzed for Total Kjeldahl Nitrogen (TKN) using the block digester method (Diamond 2001) and a flow injection analyzer (Lachat Instruments, Loveland, Colorado) at the University of California, Santa Cruz.

Sarcocornia TKN was log-transformed, and Cuscuta coils were fourth root transformed to meet assumptions of normality. Because Sarcocornia tissue salinity data were highly skewed (2/3 of the data were 100‰ which was the highest reading on the refractometer) and impossible to transform, I analyzed them without a transformation. All other variables were normally distributed and thus did not require additional transformations. I tested the effects of salinity treatments, nitrogen treatments, and Cuscuta on Sarcocornia dry weight, tissue TKN, and tissue salinity with a 3-way ANOVA. I tested the effects of salinity and nitrogen treatments on the number of Cuscuta coils and the number of host stems coiled with a 2-way ANOVA. Post hoc Tukey Tests were performed where appropriate. I tested for a relationship between Cuscuta (coils and number of host stems coiled) and Sarcocornia tissue salinity and TKN with linear regressions. All statistical analyses were conducted with SYSTAT 10.2.

Results

Effects of salinity, nitrogen, and Cuscuta on Sarcocornia

Sarcocornia biomass was affected by an interaction between salinity and nitrogen (Table 2.2, Fig. 2.1A). Without salt, biomass stayed low regardless of N additions. At intermediate salinities (10‰ and 20‰), *Sarcocornia* biomass showed the greatest interaction with N additions. Plants nearly doubled in size with mid-N additions, and were smaller without N and with high-N additions. There was no effect of *Cuscuta* on *Sarcocornia* biomass (Table 2.2).

Sarcocornia tissue salinity was also affected by an interaction between salinity and nitrogen additions (Table 2.3, Fig. 2.1B). Without added N, tissue salinity increased with increasing salt concentrations. With mid-N additions, tissue salinity was near 100‰ for all plants given salt (10‰, 20‰, 34‰), but much lower for plants grown without salt. With high-N additions, plants grown in 34‰ and 20‰ had tissue salinities near 100‰, while plants grown at 10‰ showed declining tissue salinities and plants grown at 0‰ had the lowest tissue salinities. In addition to nitrogen and salinity treatments, there was also an interacting effect of nitrogen and *Cuscuta* on *Sarcocornia* tissue salinity (Table 2.3, Fig. 2.2). Without added nitrogen, and with high-N addition, the presence of *Cuscuta* increased the tissue salinity. However, the greatest effect was at mid-N additions, where *Cuscuta* parasitism greatly decreased the tissue salinity of *Sarcocornia*. These values fall within the normal range found at Elkhorn Slough (Griffith, Chapter 3, Griffith and Crain, unpublished data).

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Sarcocornia tissue nitrogen (TKN) was affected by a three-way interaction between *Cuscuta*, salinity, and nitrogen treatments (Table 2.4, Fig. 2.3). Nitrogen additions increased *Sarcocornia* TKN (none < mid < high) except in the freshwater treatment. For all other plants, the increase was not additive. In other words, although plants grown with high-N additions were given twice the amount of N as plants grown with mid-N additions, tissue TKN was not twice as high. *Cuscuta* drew down *Sarcocornia* TKN, and this effect was most pronounced in plants grown in fullstrength seawater. With the exception of plants grown in freshwater, salt additions generally decreased TKN in no-N and with mid-N treatments.

Effects of salinity, nitrogen, and Sarcocornia on Cuscuta

Cuscuta was affected by nitrogen treatments and *Sarcocornia* tissue TKN. Nitrogen additions significantly affected the number of host stems coiled by *Cuscuta* (Table 2.5, Fig. 2.4). Specifically, *Cuscuta* coiled around more *Sarcocornia* stems with mid-N additions than with high-N additions. There was a negative relationship between *Sarcocornia* tissue TKN and the number of *Cuscuta* coils (F = 6.225, df = 1, p = 0.016, y = -0.216 x + 1.494), and also a negative relationship between *Sarcocornia* tissue TKN and the number of *Sarcocornia* stems coiled by *Cuscuta* (F = 5.737, df = 1, p = 0.020, y = -0.567 x + 2.849). Neither salinity treatments nor *Sarcocornia* tissue salinity had an effect on *Cuscuta*.

Discussion

There is a large body of research examining the effects of various Cuscuta spp. on host plant variables including biomass (Koskela et al. 2001, Marambe et al. 2002, Shen et al. 2005), nitrogen uptake (Jeschke and Hilpert 1997), and carbon fixation (Jeschke et al. 1994, Watling and Press 2001). *Cuscuta* spp. are frequently documented as having a negative effect on host biomass (Koskela et al. 2001, Marambe et al. 2002, Shen et al. 2005). It is likely that the small size of *Cuscuta* infections in my study may explain why they did not affect Sarcocornia biomass. However, the fact that the parasite still had a significant effect on host physiology suggests that *Cuscuta* can affect host plants, regardless of parasite size or biomass effects. Cuscuta's negative effect on Sarcocornia tissue nitrogen content was dependent on nitrogen and salinity treatments, but was largely driven by hosts grown in full strength seawater. While many studies have reported the role of Cuscuta in drawing down host nitrogen levels (Marambe et al. 2002), others have shown just the opposite: that Cuscuta is associated with increased nitrogen content in the host, due to sink-stimulated uptake (Jeschke and Hilpert 1997). Whether Cuscuta is capable of inducing sink-stimulated uptake effect on Sarcocornia is unclear, since infections in this study were so small.

In addition to host nitrogen levels, there was a large effect of *Cuscuta* on *Sarcocornia* tissue salinity. *Cuscuta* either increased or decreased host tissue salinity depending on nitrogen additions. A higher tissue salinity in response to *Cuscuta* may

be due to increased transpiration since parasites often maintain a higher transpiration rate than their hosts (Stewart and Press 1990, Graves 1995). A lower tissue salinity may be due to *Cuscuta* sequestering sodium ions to create an osmotic gradient greater than *Sarcocornia* to facilitate water flux from the host to the parasite (Kelly and Horning 1999). Host tissue salinity as a response variable has received little attention from studies of host-parasite interactions (Frost et al. 2003), and this study has shown that host salinity can be affected by parasitic plants, even in succulent, saltconcentrating halophytes with small parasitic infections.

The effects of the host on the parasite also varied according to the abiotic environment. However, only nitrogen additions were important. *Cuscuta* infected significantly fewer *Sarcocornia* stems when the host was given the high nitrogen treatment. There was no effect of nitrogen treatment on the number of coils per host, which suggests that *Cuscuta* may be foraging less on these hosts than on hosts with lower levels of nitrogen. Possibly, by coiling on fewer stems of high nitrogen hosts, *Cuscuta* acquires as much nitrogen as it would if coiling on more stems of lower nitrogen hosts. Supporting this idea is the weak negative relationship between *Sarcocornia* TKN and *Cuscuta* coiling. Alternatively, *Cuscuta* may have coiled around fewer stems in the high nitrogen treatment because it found these hosts unfavorable (by discriminating against them before any resource uptake). Kelly (1990) found that chemicals present on the outside of stems are altered by the nitrogen additions and can activate *Cuscuta* coiling. Regardless of the mechanism, the effect of nitrogen on this parasitic plant differs from the effect on herbivores. Most herbivores are attracted to plants with higher nitrogen levels, and small differences in plant tissue nitrogen can yield large effects on herbivore density (Mattson 1980, Moon and Stiling 2000, 2002).

The effects of salinity on herbivore-plant relationships are much more nuanced than those of nitrogen. Some salt marsh herbivores may respond positively to salt-stressed plants (Brodbeck and Strong 1987), whereas others prefer low-salinity plants (Hemminga and Van Soelen 1988, Bowdish and Stiling 1998). Sarcocornia, a salt accumulating plant, is known to produce varied effects on herbivores. Goranson et al. (2004) found contrasting herbivore preferences for Sarococrnia: crabs preferred high-salinity plants, but insects preferred low-salinity plants. This kind of result is not unusual: a plant that one insect herbivore deems favorable may be completely unsuitable for another insect herbivore (Stiling 1994). Even though Cuscuta and Sarcocornia grow in salt marshes, where environmental stress to terrestrial plants is largely a function of salinity levels, I found no effect in the greenhouse of salinity treatment or host tissue salinity on Cuscuta coiling. This finding contrasts with field observations, in which Sarcocornia with low tissue salinity had a higher probability of Cuscuta infection (Chapter #). My results suggest that processes occurring during other stages of the life cycle (recruitment, germination, seedling establishment) may be generating this pattern in the field.

Coastal ecosystems are increasingly altered by multiple anthropogenic stressors. Two major problems tidal wetlands are facing are eutrophication and hydrological manipulations. Altered hydrology (by means of water control structures like tide gates, berms, and culverts) can shift salinity regimes and make wetlands either more or less saline than normal. When tidal flow is restricted from a salt marsh, the marsh usually becomes hypersaline (if there is no freshwater input) or hyposaline (if a freshwater input exists). Increasing salinity in coastal marshes is also predicted due to sea-level rise and the increasing frequency of drought due to climate change. Because Sarcocornia is so widely distributed in California salt marshes, strong responses in biomass and physiology to various combinations of salinity and nitrogen may not only affect those organisms that rely on Sarcocornia as a food source, but also the ability of the Sarcocornia marsh as an ecosystem to filter high nutrient runoff by sequestering nitrogen in its tissues. The interaction between salinity and nitrogen on Sarcocornia biomass suggests that high nitrogen levels alone may not be as important in fresh or brackish marshes as they are in more saline marshes. Thus, at Elkhorn Slough and other marshes dominated by Sarcocornia, maintaining tidal influence to marshes heavily impacted by agricultural runoff may increase the retention of excess nutrients by Sarcocornia. In marshes that are impounded and contain mostly freshwater, eutrophication may pose a greater threat to the estuary overall.

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Conclusions

Within the *Cuscuta-Sarcocornia* system, this study has demonstrated that a parasitic plant can affect host physiology in the absence of any effects on host biomass, and that these physiological effects of the parasite on the host are mediated by the abiotic environment. This work also suggests that *Cuscuta* may forage less on high nitrogen *Sarcocornia* plants, a finding that implies substantial differences between *Cuscuta* and herbivores in their response to host plants. Overall, this study demonstrates the importance of the abiotic environment in structuring this parasitic plant – host plant interaction. The results of this study also yield important insight to the effects of eutrophication in estuaries where salinity regimes are highly variable.

Table 2.1. ANOVA output showing the effect of nitrogen additions on SarcocorniaTKN before the start of the experiment.

Source	df	MS	F	Р
Nitrogen	2	17,802.99	418.33	0.000
Error	15	42.557		

Source	df	MS	F	Р
Salinity	3	25.382	76.834	0.000
Nitrogen	2	26.482	80.165	0.000
Cuscuta	1	0.032	0.097	0.756
Salinity*Nitrogen	6	3.221	9.750	0.000
Salinity*Cuscuta	3	0.475	1.438	0.233
Nitrogen*Cuscuta	2	0.053	0.159	0.853
Salinity*Nitrogen*Cuscuta	26	0.376	1.137	0.342
Error	208	0.330		

Table 2.2. ANOVA output showing the effect of nitrogen, salinity, and *Cuscuta* on *Sarcocornia* biomass.

Source	df	MS	F	Р
Salinity	3	11,845.421	87.447	0.000
Nitrogen	2	2,383.016	17.592	0.000
Cuscuta	1	195.215	1.441	0.232
Salinity*Nitrogen	6	731.327	5.399	0.000
Salinity*Cuscuta	3	273.621	2.020	0.113
Nitrogen*Cuscuta	2	493.232	3.641	0.028
Salinity*Nitrogen*Cuscuta	6	217.119	1.603	0.149
Error	178	135.458		

Table 2.3. ANOVA output showing the effect of salinity, nitrogen, and *Cuscuta* onSarcocornia tissue salinity.

Source	df	MS	F	Р
Salinity	3	0.896	12.476	0.000
Nitrogen	2	36.006	501.179	0.000
Cuscuta	1	0.142	1.983	0.163
Salinity*Nitrogen	6	1.144	15.921	0.000
Salinity*Cuscuta	3	0.055	0.772	0.513
Nitrogen*Cuscuta	2	0.001	0.011	0.989
Salinity*Nitrogen*Cuscuta	6	0.202	2.811	0.015
Error	85	0.072		

Table 2.4. ANOVA output showing the effect of salinity, nitrogen, and *Cuscuta* onSarcocornia tissue TKN.

df	MS	F	Р
3	0.480	0.158	0.924
2	12.990	4.279	0.016
6	0.533	0.176	0.983
108	3.036		
	df 3 2 6 108	df MS 3 0.480 2 12.990 6 0.533 108 3.036	df MS F 3 0.480 0.158 2 12.990 4.279 6 0.533 0.176 108 3.036

Table 2.5. ANOVA output showing the effect of nitrogen and salinity treatments on*Cuscuta* coiling.



Figure 2.1. The interaction between salinity and nitrogen treatments on (A) *Sarcocornia* dry weight and (B) *Sarcocornia* tissue salinity. Values are means ± 1 s.e.



Figure 2.2. The interaction between *Cuscuta* and nitrogen additions on *Sarcocornia* tissue salinity. Solid line represents *Cuscuta* absent, dotted line is *Cuscuta* present. Values represent means ± 1 s.e.



Figure 2.3. The interaction between salinity, nitrogen, and *Cuscuta* on *Sarcocornia* tissue TKN. Value represent means ± 1 s.e.


Figure 2.4. The effect of nitrogen additions on the number of *Sarcocornia* stems coiled by *Cuscuta*. Values represent means ± 1 s.e. Letters represent results of a tukey test (p < 0.05).

CHAPTER 3

THE EFFECT OF ARTIFICIAL TIDAL RESTRICTION IN A CALIFORNIA SALT MARSH

Introduction

The extent and health of salt marshes world-wide are in decline (Adam 2002, Zedler and Kercher 2005). While many factors contribute to this degradation, the alteration of natural hydrology regimes may be the most widespread threat (Kennish 2002). Restricting tidal action in a salt marsh poses a significant problem to marsh structure and function because hydrology drives geomorphology (Friedrichs and Perry 2001), sediment deposition (Anisfeld et al. 1999), sediment chemistry (Portnoy and Giblin 1997), marsh elevation, and, in turn, plant community composition (Roman et al. 1984). Historically, alterations to tidal hydrology have been extensive throughout the United States; estimates of salt marsh loss range from 50-80% in New England (Bromberg and Bertness 2005) to over 90% in California (Larson 2001). Marshes worldwide continue to be extensively manipulated by water control structures that permit various human activities, such as agriculture and urban development. Some structures (tide gates and culverts) may provide limited tidal exchange to landward marshes, while others (dikes and berms) can completely restrict the flow. Despite the extent of altered marsh hydrology, there are still sizable gaps in our understanding of the effects of tidal restriction. For example, while several studies have investigated the impacts of tidal restriction in East Coast estuaries

(Roman et al. 1984, Sinicrope et al. 1990, Portnoy and Giblin 1997, Buchsbaum et al. 2006), few have examined similar impacts on West Coast estuaries. Moreover, few studies anywhere have thoroughly investigated how tidal restriction interacts with natural spatial and temporal variability in marshes. These areas of study are crucial for directing management efforts and augmenting our understanding of this ecosystem.

The consequences of restricting tidal exchange in salt marshes along the US Atlantic coast are well known. In this region, tidal restriction often leads to a reduction in sediment salinity (Roman et al. 1984, Buchsbaum et al. 2006), higher sediment nutrients (Portnoy and Giblin 1997), and a shift in the plant community from more salt-tolerant species to less salt-tolerant ones (Roman et al. 1984, Sinicrope et al. 1990). The few studies that have investigated these responses in estuaries on the US Pacific coast suggest more complicated patterns. In San Francisco Bay, St. Omer (1994) found that reduced tidal exchange can increase sediment salinity, which supports a community dominated by more salt-tolerant plants. The resultant community was less diverse, lacked typical zonation, and exhibited bare sediment patches (St. Omer 1994). However, a southern California marsh with impounded freshwater exhibited reduced sediment salinities and increased nutrients, and it was associated with higher net primary productivity of the dominant vegetation (Zedler et al. 1980). A key driver of such variability in these results is the Mediterranean climate, which can profoundly affect the influence of tidal restrictions on both plant and sediment dynamics (Zedler 1982, Josselyn 1983).

While basic shifts in sediment and vegetation dynamics between restricted and flushed marshes have been documented on both the east and west coasts of the US, we scarcely understand the natural spatial and temporal variability in these mechanistic factors that lead to long term patterns. Sediment salinity, moisture, and nutrients are highly variable both temporally (Jefferies 1977, Allison 1992, Ralph and Manley 2006) and spatially (Zedler et al. 1980, Seliskar 1985a). Spatial variability often reflects sediment type, freshwater inputs, or topography. Elevation gradients, too, cause spatial variability in salt marshes and have significant effects on sediment salinity (Nestler 1977, Zedler 1982) and vegetation morphology (Seliskar 1985b). Seasonal patterns also generate temporal variability in salt marshes. For example, in West Coast salt marshes most of the precipitation is limited to the winter months. Thus, marsh sediments are often saltier during the dry summer months when evaporation is high and river inputs diminish (Callaway and Sabraw 1994). Such variability in sediment salinity can greatly affect plant community composition (Allison 1992, Callaway and Sabraw 1994), biomass and nutrient content of marsh vegetation (Boyer et al. 2001), and tissue salinity (Ralph and Manley 2006).

The interaction between natural spatio-temporal variability and artificial tidal restriction is likely to elicit complex responses by marsh sediments and vegetation. Without accounting for these other sources of variation, it becomes difficult to

identify the sole effects of tidal restriction. The goal of this study was to examine the effects of tidal restriction on marsh sediments and on the dominant vegetation, *Sarcocornia pacifica*, of a central California salt marsh, while explicitly incorporating the spatial and temporal variation associated with multiple sites, seasons, and tidal heights.

Methods

Study Site

This study was conducted in the estuarine habitats of the Elkhorn Slough watershed. This estuary, located near Moss Landing, California, on the Monterey Bay (Fig. 3.1), is comprised of multiple channels, the largest of which is Elkhorn Slough. Smaller channels include Moro Cojo Slough, the Old Salinas River channel, and Bennett Slough. This region experiences a Mediterranean climate (11° to 15.4° C annually) with a distinct rainy season (October through May) when rainfall averages 55.2 cm (Caffrey et al. 2002). Figure 3.2 shows the precipitation data during the sampling period. The mixed semi-diurnal tides reach a maximum range of 1.2 m (Caffrey et al. 2002).

About 900 ha of estuarine habitat in the Elkhorn Slough watershed receive unrestricted tidal exchange; the remaining 500 ha have artificially restricted tidal exchange due to water control structures (dikes, culverts, and tide and flap gates). In early 2005, 22 study sites were established: 11 received full tidal exchange and 11 received restricted tidal exchange (Figure 3.1). The tidal amplitude was measured with graduated tide staffs at restricted sites on December 12, 2005. All restricted sites experienced less than 50% of the full tidal range.

Sarcocornia pacifica (Sarcocornia hereafter) is the competitive dominant plant in the watershed's salt marshes and covers most of the vegetated marsh from the lower (shoreline) limit to the upland border. *Sarcocornia* is broadly distributed at all 22 sites in this study. As a perennial, C₃ plant, *Sarcocornia* is most productive (with green succulent tissue) in the summer months and dormant (with woody stems) in the winter (Boyer et al. 2001). The shallow roots penetrate 10-20 cm into the marsh sediment and it maintains low water potentials in its tissues by accumulating solutes from the sediment environment (Davy et al. 2001). Other species, including *Distichlis spicata, Atriplex* spp., *Jaumea carnosa, Frankenia salina*, and *Cuscuta salina*, are distributed in patches along the upland ecotone.

Field Survey

In order to examine the effects of tidal restriction, season, and tidal height on marsh sediments and *Sarcocornia* tissue, I conducted field surveys in May 2005, September 2005, and January 2006 during low tide. At each site, I established 3 permanent transects running from the shoreline border to the upland border of the marsh (this distance varied across sites). Transects were located 15m apart, with sampling positions along the located at 3 different tidal heights: the shoreline (low), middle, and upland border (high) of the salt marsh (methods detailed in Griffith, Chapter 1). At each sampling location, I collected a sediment core (2 cm diameter, 25 cm deep) and a succulent *Sarcocornia* tissue sample. All samples were sealed in bags immediately in the field and returned to the lab in a cooler to maintain the temperature at which they had been collected.

Laboratory Work

Upon return from the field, sediment samples were homogenized and KCl extracts were performed. Extracts were analyzed using a flow injection analyzer (Lachat Instruments, Loveland, Colorado) for NO₃-N and NO₂-N (hereafter referred to as NO₃-N) and NH₄-N (Hofer 2003, Knepel 2003). Sediment moisture was measured gravimetrically. Since sediments can be very dry in these marshes, I created a solution of sediment and water to measure sediment salinity (Rhodes 1982). Salinity of the supernatant was measured with a refractometer (Vee Gee STX-3, Kirkland, Washington).

Sarcocornia tissue was analyzed for salinity by expressing solution from the succulent stems and measuring the salinity with a refractometer. Sarcocornia samples were dried in an oven at 60°C for 96 hours (or until all moisture was lost), ground in a Wiley Mill, and analyzed for total %N and %C using the combustion method (vario MAX CN, Elementar, Hanau, Germany). Tissue samples collected during January were also analyzed for δ^{15} N and δ^{13} C using a Carlo Erba model

CE1108 elemental analyzer coupled to a ThermoFinnigan Delta Plus XP isotope ratio mass spectrometer with a Conflo III interface. I did not analyze tissue samples from the other sampling times due to logistical issues. All analyses were performed at the University of California, Santa Cruz.

Data Analysis

Subsamples (n=3) were averaged to obtain a single value per tidal height (low, middle, high) per site. Data were square-root or fourth root transformed when necessary to achieve normal distributions. Because the measured variables were expected to covary, I used principal components analysis (PCA) with varimax rotation to derive composite factors, which by definition are independent of each other (Quinn and Keough 2002). The PCA yielded 2 composite factors (PC1 and PC2) with eigenvalues greater than 1.0. A repeated measures ANOVA tested for the effect of sampling time (May, September, January), tidal height (high, middle, low), tidal exchange (restricted, flushed), and site (nested within tidal exchange) on each composite variable univariately. A 2-way ANOVA tested for the effect of tidal height and tidal exchange on stable isotope values from the *Sarcocornia* samples collected in January. All statistical analyses were conducted with SYSTAT 10.2.

Results

The multiple dependent variables were reduced to two composite variables by principal components analysis that, together, explained over 67% of the variance in the data (Table 3.1). PC1 represents sediment moisture, sediment salinity and sediment NH₄-N. All these variables loaded heavily on the positive end of the PC1 axis. PC2 represents sediment NO₃-N, *Sarcocornia* salinity, and *Sarcocornia* C:N. *Sarcocornia* salinity and C:N loaded heavily on the positive end of the PC2 axis, whereas sediment NO₃-N loaded heavily on the negative end of the PC2 axis.

There was a significant interaction between sampling time and site on both PC1 (p = 0.000, Table 3.2) and PC2 (p = 0.000, Table 3.3). The effect of site on PC1 and PC2 is shown in Figure 3.3. Despite this interaction, the main effect of sampling time on PC1 and PC2 was interpretable (Fig. 3.4). Described by PC1, sediment salinity, moisture, and NH₄-N values were the highest in May, intermediate in September, and lowest in January. Decomposing PC2 shows that September coincided with the highest *Sarcocornia* salinity, and *Sarcocornia* C:N, and lowest sediment NO₃-N; May had the lowest *Sarcocornia* salinity, *Sarcocornia* C:N, and highest sediment NO₃-N; and January had intermediate levels of all three variables.

There was a significant 3-way interaction between sampling time, tidal exchange, and tidal height on PC1 (p = 0.002, Table 3.2, Fig. 3.5). Despite this interaction, all the main effects are interpretable. Tidally restricted sites were associated with lower sediment salinity, moisture, and NH₄-N values than flushed sites. Low and middle tidal heights had higher levels of sediment salinity, moisture,

and NH_4 -N than did high tidal heights. The main effect of sampling time was stated in the previous paragraph (Fig. 3.4). The interaction between tidal height and sampling time was the strongest. In May the three tidal heights (low, middle, high) separated along the PC1 axis the most. In September and January all tidal heights showed much more overlap. The most overlap between tidal heights occurred in restricted sites in January; the least overlap between tidal heights occurred in restricted sites in May. Middle tidal heights appeared to be most affected by tidal restriction. In flushed sites, middle tidal height means had slightly higher PC1 values than did low or high tidal heights (especially in May, although there was a high degree of overlap then) while in restricted sites, means fell between low and high tidal heights. High tidal heights were the most different from middle and low tidal heights in flushed sites, and there was a high degree of overlap between middle and low tidal heights. The largest difference between flushed and restricted sites occurred in May. During this sampling period, flushed sites had higher values of sediment salinity, moisture, and NH₄-N than did restricted sites.

PC2 was significantly affected by tidal height (p = 0.000, Table 3.3, Fig. 3.6). Low and middle tidal heights were associated with high levels values of *Sarcocornia* salinity and *Sarcocornia* C:N, and low levels of sediment NO₃-N. In contrast, high tidal heights were associated with low *Sarcocornia* salinity, low *Sarcocornia* C:N, and high sediment NO₃-N values. The backtransformed data for all combinations of the independent factors are shown in Table 3.4. There was a highly significant effect of site on *Sarcocornia* $\delta^{15}N$ (p = 0.000) and $\delta^{13}C$ (p = 0.000) from the January sampling period (Table 3.5, Fig. 3.7), suggesting spatial variation in both parameters. Tidal height also had a significant effect on $\delta^{13}C$ (p = 0.025, Table 3.5b, Fig. 3.8A). Higher tidal heights were more depleted than low or middle tidal heights. There was a marginally significant effect of tidal exchange on $\delta^{15}N$ (p = 0.060, Table 3.5a, Fig. 3.8B). Restricted sites trended towards being more depleted than flushed sites.

Discussion

Effects of Tidal Restriction

In general, tidal restriction was associated with drier, less saline sediments with less NH₄-N. This finding agrees with studies conducted on the east coast of the United States, where sediments respond to tidal restriction by becoming less saline (Roman et al. 1984, Buchsbaum et al. 2006) and retaining more NH₄-N (Portnoy and Giblin 1997). In San Francisco Bay, tidally restricted sediments were drier and saltier, but no different than flushed sediments in terms of the total available nitrogen (St. Omer 1994). In a southern California estuary, tidal restriction was associated with lower sediment salinities that varied according to the existence of a freshwater input source (Zedler et al. 1980). California's Mediterranean climate, with separate dry and rainy seasons, is often a strong driver of salinity in marshes (Zedler 1982, Josselyn 1983). The combination of tidal restriction and climate results in

hypersaline sediments in the summer, when evaporation is high, and hyposaline sediments in the winter due to rainfall (Josselyn 1983). In my study, however, restricted sites were usually drier and less saline than flushed sites in May and September and showed no difference from each other in January (although there was a great deal of variance among sites). It is likely that precipitation in January blurred differences in sediment salinity between sites. More restricted tidal inundation at the Elkhorn Slough watershed compared to restricted sites in other studies may partially explain drier and less saline sediments during May and September. Such interactions between tidal restriction and sampling time are important for identifying the sometimes subtle effects of tidal restriction on marsh sediments.

Understanding the interaction between tidal exchange and tidal height is equally important when investigating tidal restriction. A study sampling sediments only from the low or high marsh tidal heights might not find differences resulting from tidal exchange. In the Elkhorn Slough watershed, middle tidal heights revealed the largest effects of tidal restriction. This may be due to the fact that, regardless of the tidal exchange regime, low marsh tidal heights were often flooded and high tidal heights were often dry. Tidal inundation at flushed sites resulted in middle tidal heights that were regularly flooded (K. Griffith, pers. obs.). Perhaps due to the same mechanism, middle tidal heights were nearly identical to low tidal heights in flushed sites but were drier and less saline with less NH₄-N than low tidal heights in restricted sites. Furthermore, high tidal heights pulled away from low and middle tidal heights

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more in flushed sites compared to restricted sites where there was a near linear progression from low to middle to high tidal heights in sediment quality. Overall, low and middle tidal heights were more similar across tidal exchange regimes than they were to high tidal heights within the same regime. This finding is likely due to the more intimate association of low and middle tidal heights with tidal exchange than high tidal heights.

Despite the effects of tidal restriction on marsh sediments, there was no apparent effect on *Sarcocornia* except in its stable isotope signature: δ^{15} N values trended towards being enriched in flushed marshes (10.51‰) compared to restricted marshes (8.76‰). Others have found δ^{15} N of *Sarcocornia* in the range of 11‰ (Kwak and Zedler 1997) and 12.8‰ (Cloern et al. 2002). There are several possible mechanisms of variation in stable isotope fractionation. First, nitrogen transformations can often result in changes in the stable isotope ratios of nitrogen pools (Handley and Raven 1992). Denitrification (the conversion of NO₃ to NO₂) discriminates against ¹⁵N, thereby leaving residual NO₃-N enriched in ¹⁵N (Heaton 1986). Another possibility is that restricted marshes may be receiving more landbased than marine-based inputs. Terriginous material tends to have an isotopically lighter δ^{15} N signature than marine material (Peterson and Fry 1987). Tidally restricted sites may not be receiving more runoff from surrounding uplands than are flushed sites, but they are likely to be receiving less marine influence and the resulting ratio between land and marine inputs may generate this pattern. Other work in a California salt marsh has shown that *Sarcocornia* becomes enriched with increasing proximity to the lower limit of the salt marsh (Page 1995). Finally, this trend could reflect the proximity to agricultural fields. Synthetic fertilizers have a lighter signal than natural nitrogen (Heaton 1986) which may be accumulating in restricted marshes (Page 1995, Caffrey et al. 2002).

There was a large amount of variation among sites in this study. In the Elkhorn Slough watershed, a simple dichotomy between restricted and flushed sites may not take into account the variability associated with tidal exchange (Ritter et al. In press). Whether a site receives 5% or 50% of the tidal amplitude can have large effects on plants and animals living in the system. For example, while communities at sites with extremely restricted tidal exchange (~5% of tidal amplitude) are significantly different from those with unrestricted tidal exchange, communities at restricted sites with moderate tidal exchange (~50% of tidal amplitude) were only slightly different from those with full tidal exchange (Ritter et al. In press).

Whether tidal restriction affects other parameters of *Sarcocornia* such as biomass, fecundity, or growth rate remains an intriguing possibility. A range of responses by *Sarcocornia* to tidal restriction has been documented in California salt marshes. In the Elkhorn Slough watershed, *Sarcocornia* has a higher percent cover in flushed marshes, yet greater biomass in restricted marshes (Parravano 2004). Other studies show that flushed marshes host more vigorous *Sarcocornia* plants than do restricted sites (Seliskar 1985b, St. Omer 1994), and Zedler et al. (1980) found higher primary productivity of *Sarcocornia* in restricted marshes in Southern California. Sediments low in salinity and high in nutrients may partially explain reports of higher biomass and productivity in such sites, since *Sarcocornia* responds well to such sediment types (Zedler et al. 1980). Directly linking these patterns to their mechanistic counterparts and understanding how different measures of plant growth (biomass, productivity, percent cover) differ remain important avenues for research.

Effect of Sampling Time and Tidal Height

Temporal and spatial variation may exert even greater control over sediment and vegetation dynamics than does tidal restriction alone. The patterns I have found have often differed from those reported in other California estuaries. For example, during my study, the Elkhorn Slough watershed had its highest sediment salinities in September similar to what St. Omer (1994) found in San Francisco Bay. But it also had its highest sediment NO₃-N and NH₄-N in May, whereas Boyer et al. (2001) found sediment TKN highest in January, and St. Omer (1994) found the most total available nitrogen in sediments in fall. In this study, I found that high marsh tidal heights had drier and less saline sediments than middle or lower tidal heights. While some studies conducted in West Coast estuaries agree with this finding (Seliskar 1985b, Ralph and Manley 2006), other studies have found that upper marshes can become hypersaline during the summer (Jefferies 1977), and may even be classified as euryhaline (Mahall and Park 1976a, Zedler 1977, Callaway et al. 1990). Still others have found no relationship between tidal height and sediment salinity (Silvestri et al. 2005). Sediment salinity and sediment moisture values vary greatly according to fluctuations in seasonal rainfall, tidal patterns and height, and even the slope of the marsh (Callaway et al. 1990).

This variability of California salt marshes often makes it difficult to draw hard, causal conclusions regarding vegetation and sediment trends (Zedler 1982, Josselyn 1983, Allison 1992). However, taking into account the interaction between sampling time and tidal height may help improve our understanding of marsh dynamics. In the Elkhorn Slough watershed, sediments showed the least overlap between low, middle and high tidal heights in May, whereas in January tidal heights exhibited the most overlap in sediment variables. Thus, sampling sediment salinity across tidal heights in the winter may well show no effect of tidal height, but the same effort during the spring months may reveal a clear salinity gradient. Similarly, sediment traits at low and middle tidal heights are more similar in flushed sites than they are in restricted sites, and the differences between sediments at high tidal heights and sediment at low or middle tidal heights are more pronounced in flushed sites than in restricted ones. These results may help explain the large range of sediment salinities found in salt marshes, and some of the differences among multiple studies.

The effect of tidal height on stable isotope values of *Sarcocornia* was significant. I found more negative δ^{13} C values of *Sarcocornia* at high tidal heights, where sediment salinity and moisture are lowest. These results agree with those of

Chmura and Aharon (1995); they found marsh sediments and their associated flora to have the most negative δ^{13} C values (~29‰) in freshwater marshes, with increasingly less negative (~ -14‰) values as marshes become saltier. Guy et al. (1980) found that, in *Salicornia europaea*, δ^{13} C values reflect the water potential of the sediment in which it grows. It is likely that *Sarcocornia* becomes increasingly water stressed at lower tidal tidal heights, and that its δ^{13} C values reflect this stress.

The relationship between sediment salinity and vegetation salinities was complex. For example, although sediment salinity was generally highest in September, tissue salinity remained between 55‰ and 65‰ throughout the year. *Sarcocornia* has often been described as flexibly tolerant of wide ranging of sediment salinities (Mahall and Park 1976a, Zedler et al. 1980), and Ralph and Manely (2006) report no relationship between *Sarcocornia* tissue salinity and sediment salinity in a southern California salt marsh. Freshwater input during the rainy season may be leveling differences in sediment quality between flushed and restricted sites such that later in the year, when differences become stark, *Sarcocornia* is already established and therefore not significantly affected (Beare and Zedler 1987, Allison 1992, Onuf 2006). In contrast to sampling time, plant and sediment salinities were more closely linked across spatial gradients. *Sarcocornia* had the saltiest tissues at lower and middle tidal heights, mirroring the pattern of sediment salinity. *Sarcocornia* can tolerate hypersaline sediments by accumulating solutes in cell vacuoles which allow the plant to maintain plant water potentials lower than soil water potentials (Davy et al. 2001).

Conclusions

Artificial tidal restriction at Elkhorn Slough affects the salt marsh by altering sediment quality. This effect differs according to sampling time and the tidal height of the marsh. It is therefore crucial to develop a robust sampling design when investigating the effects of water control structures because the salt marsh system is extremely variable both spatially and temporally. This point is especially true of salt marshes on the US west coast where the Mediterranean climate results in separate dry and wet seasons. Here, the large effects of spatial and temporal variation associated with site, season and tidal height may exert an even greater control over marsh dynamics than the effects of tidal restriction alone. Investigating the responses of multiple salt marsh indicators, including both sediment and vegetation parameters, is equally important because, under some circumstances, links between the two that may seem obvious (e.g. sediment salinity and tissue salinity) do not exist. Thus, using one variable as a proxy for another may mislead interpretations of the dynamics of marsh ecology.

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Table 3.1 F	actor	loadings	trom the	principal	i comp	onents :	anaivs	1S -
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Variable	PC 1	PC 2
Salicornia Salinity	0.253	0.778
Salicornia C:N	-0.169	0.656
Sediment Moisture	0.912	-0.161
Sediment Salinity	0.902	0.188
Sediment NO ₃ -N	0.195	-0.75
Sediment NH ₄ -N	0.761	-0.209
% of Total Variance Explained	39.3%	28.4%

A. Between Subjects						
Source	SS	df	MS	Error df	F	Р
Tidal Exchange	4.153	1	4.153	20	2.226	0.151
Tidal Height	24.688	2	12.344	40	32.491	0.000
Tidal Exchange*Tidal Height	1.566	2	0.783	40	2.062	0.141
Site(Tidal Exchange)	37.298	20	1.865	40	4.909	0.000
Error	15.197	40	0.380			
D. Within California						
B. within Subjects				-		
Source	SS	df	MS	Error df	F	Р
Time	103.15	2	51.575	80	497.072	0.000
Time*Tidal Exchange	0.436	2	0.218	40	0.724	0.491
Time*Tidal Height	6.210	4	1.553	80	14.963	0.000
Time*Tidal Exchange*Tidal Height	2.007	4	0.502	80	4.837	0.002
Time*Site(Tidal Exchange)	12.040	40	0.301	80	2.901	0.000
Error	8.301	80	0.104			

Table 3.2. Repeated measures ANOVA results showing the effects of tidal exchange, tidal height, site and sampling time on PC1.

A. Between Subjects						
Source	SS	df	MS	Error df	F	Р
Tidal Exchange	1.337	1	1.337	20	0.718	0.406
Tidal Height	8.569	2	4.285	40	12.801	0.000
Tidal Exchange*Tidal Height	1.262	2	0.631	40	1.885	0.165
Site(Tidal Exchange)	37.198	20	1.860	40	5.557	0.000
Error	13.389	40	0.335			

Table 3.3. Repeated measures ANOVA results showing the effects of tidal exchange, tidal height, site and sampling time on PC2.

B. Within Subjects

5						
Source	SS	df	MS	Error df	F	Р
Time	85.860	2	42.93	80	210.87	0.000
Time*Tidal Exchange	0.585	2	0.293	40	1.437	0.690
Time*Tidal Height	0.349	4	0.087	80	0.429	0.788
Time*Tidal Exchange*Tidal Height	0.835	4	0.209	80	1.026	0.399
Time*Site (Tidal Exchange)	31.329	40	0.783	80	3.847	0.000
Error	16.286	80	0.204			

FactorTissueTissueMoistureSediment NO_3-N NH_4-N CombinationSalinityC:N(%)Salinity(mg/L)(mg/L)May, Restr.,57.311.948.637.42.3853.75Low(44.6, 70.1)(10.5, 13.3)(40.2, 57.7)(20.6, 62.7)(1.20, 4.27)(11.5, 162)May, Restr.,58.612.242.733.22.5815.13Mid(48.2, 69.1)(10.9, 13.5)(30.9, 56.4)(17.9, 56.6)(1.71, 3.77)(4.88, 36.5)May, Restr.,55.111.227.413.42.198.29High(49.2, 60.7)(9.08, 13.4)(17.9, 38.7)(6.3, 25.2)(1.62, 2.89)(3.91, 15.6)May, Flush.,60.113.354.355.12.5621.1Low(55.7, 64.5)(11.3, 15.2)(36.9, 75.1)(27.1, 100)(1.17, 4.91)(8.65, 43.7)May, Flush.,60.313.960.372.23.3824.5Mid(56.8, 63.8)(11.9, 15.9)(41.4, 82.6)(35.8, 131)(1.88, 5.61)(8.86, 55.2)May, Flush.,53.711.831.621.32.527.01High(49.2, 58.2)(10.1, 13.5)(17.3, 50.1)(11.6, 36.2)(1.32, 4.38)(3.26, 13.3)Sept., Restr.,66.316.423.129.50.00813.7Low(55.7, 76.9)(13.7, 19.2)(12.1, 37.6)(18.0, 46.0)(0.0219)(4.17, 34.2)Sept.,
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Table 3.4. Back-transformed data (means shown with lower and upper bounds in parentheses) for all combinations of independent factors (sampling time, tidal exchange, and tidal height).

Table 3.5. ANOVA results showing the effects of site, tidal height and tidal exchange on (a) δ^{15} N and (b) δ^{13} C stable isotope values of *Sarcocornia*.

А.						
Source	SS	df	MS	Error df	F-ratio	Р
Tidal Exchange	50.270	1	50.270	20	3.95	0.06
Tidal Height	4.240	2	2.120	40	1.338	0.274
Tidal Exchange *Tidal Height	0.087	2	0.043	40	0.027	0.973
Site(Tidal Exchange)	254.496	20	12.725	40	8.031	0.000
Error	63.377	40	1.584			

B.						
Source	SS	df	MS	Error df	F-ratio	Р
Tidal Exchange	0.066	1	0.066	20	0.0344	0.854
Tidal Height	3.508	2	1.754	40	4.036	0.025
Tidal Exchange * Tidal Height	0.332	2	0.166	40	0.381	0.685
Site(Tidal Exchange)	38.359	20	1.918	40	4.413	0.000
Error	17.386	40	0.435			



Figure 3.1. Map of study sites in the Elkhorn Slough watershed. Bold numbers indicate tidally restricted sites (sites 1, 6, 15, 16, 21 and 22 contain culverts; sites 14, 19, and 20 contain flap gates; sites 17 and 18 contain tide gates).



Figure 3.2. Daily and cumulative precipitation at Elkhorn Slough from January 1, 2004 through January 1, 2007. Three lines (asterisks) across top of figure represent sampling times. Data from National Oceanic and Atmospheric Administration, Office of Ocean and Coastal Resource Management, National Estuarine Research Reserve System-wide Monitoring Program. 2004. Centralized Data Management Office, Baruch Marine Field Lab, University of South Carolina http://cdmo.baruch.sc.edu.



Figure 3.3. The effect of site on PC1 and PC2. Numbers represent sites, as shown in figure 3.1. Error bars represent ± 1 s.e.



Figure 3.4. The effect of sampling time on sediment and *Sarcocornia* properties. Solid lines represent PC 1 values, dotted lines represent PC 2 values. Error bars represent ± 1 s.e.



Figure 3.5. The effect of sampling time, tidal height and tidal exchange on PC1. Error bars represent \pm 1s.e.



Figure 3.6. The effect of tidal height on PC2. Error bars represent ± 1 se.



Figure 3.7. The effect of site on (a) δ^{13} C and (b) δ^{15} N stable isotopes of *Sarcocornia*. Error bars represent ± 1 s.e.



Figure 3.8. The effects of (a) tidal height on δ^{13} C and (b) tidal exchange on δ^{15} N stable isotopes of *Sarcocornia*. Boxes are bounded by the 25th and 75th percentiles with the median displayed. Outer fences represent the 5th and 95th percentiles. Circles represent outliers.

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