Title

Species Diversity in Northern California Salt Marshes: Functional Significance of Parasitic Plant Interactions

Author

Grewell, Brenda J.

Publication Date

2004

Species Diversity in Northern California Salt Marshes: Functional Significance of Parasitic Plant Interactions

By

BRENDA JOY GREWELL

B.S. (University of California, Davis) 1982

DISSERTATION

Submitted in partial satisfaction of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

Ecology

in the

OFFICE OF GRADUATE STUDIES

of the

UNIVERSITY OF CALIFORNIA

DAVIS

Approved:

Eliska Rejm

Edwin D. Grosholz

Committee in Charge

2004

ProQuest Information and Learning Company
300 North Zeeb Road
P.O. Box 1346
Ann Arbor, MI 48106-1346

TABLE OF CONTENTS

Species Diversity in Northern California Salt Marshes:

Functional Significance of Parasitic Plant Interactions

by Brenda Joy Grewell

University of California, Davis

Thesis Committee Chair: Professor Eliška Rejmánková,
Department of Environmental Science and Policy

ABSTRACT

I studied how parasitic plant interactions contribute to species coexistence in tidal wetlands of northern California. First, I address the effects of the native parasite *Cuscuta salina* on species interactions and plant community structure. I showed that *Cuscuta* is restricted to nutrient poor areas with significant canopy gaps and high species diversity. I examined timing, level, and frequency of host infectivity and identified *Plantago maritima* as the primary host. I experimentally removed *Cuscuta* from the community and measured host fitness, rare plant fitness, and plant community response. *Cuscuta* reduction of host biomass and reproductive effort resulted in indirect positive effects on a rare hemiparasite, and enhanced community diversity.

Then I present results demonstrating how parasitic plant – host interactions ameliorate physical stress conditions and generate environmental heterogeneity. Experimental bare plots, artificially shaded bare plots, and parasite removal plots across intertidal elevations were compared to controls with hemiparasites at two sites representing a steep stress gradient. Over three years, plant species richness was enhanced with parasites at both locations. Parasitic plants improve sediment salinity and redox potential, and parasite-generated habitat heterogeneity contributes to species coexistence.

Lastly, I present results of an experimental reintroduction of an endangered hemiparasite to a restoration site. I tested disturbance management methods for enhancement of plant establishment and fitness. I identified critical life stages and used failure time survival analysis models for a demographic comparison of restoration and reference populations. I demonstrate that successful restoration requires a unique, productive host community to support the introduced parasite load. Disturbance-gap creation is a successful restoration technique that will enhance rare plant establishment and fitness, but benefits can be offset by exotic plant invasions. Applied conservation significance of the study points to a critical need for regional invasive plant control as the first step in restoration efforts.

Overall, my dissertation clarifies the functional role of parasitic plants within mid-Pacific Coast salt marshes of North America. Results demonstrate that preferential parasitism, spatial contingency of species interactions, and creation of habitat heterogeneity through parasitic amelioration of physiological stress conditions all play a role in supporting coexistence within the salt marsh community.

ACKNOWLEDGEMENTS

The contributions of many people made completion of this dissertation research possible. First, I thank my major professor Eliška Rejmánková for her scientific rigor, guidance, friendship, and countless cups of Peet's coffee. Her in-depth knowledge of aquatic botany, global view, and enthusiasm for wetlands has forever altered my perspective. Professor Rejmánková generously provided support towards my participation in the INTECOL wetland conference in Quebec City, and wetland biogeochemistry symposia at Duke and Ghent Universities.

I thank Kevin Rice and Ted Grosholz for serving on my committee, for eternal optimism, and for suggestions that greatly improved this research. I also thank Kevin Rice for countless equipment loans, and for levity and laughs when they were the best medicine. I am indebted to Debbie Elliott-Fisk and Michael Barbour for encouraging me to pursue this goal, and for leading me to the trailhead. Peggy Lee Fiedler offered helpful suggestions, and has taught me a great deal about conservation biology. Gary Polis was a mentor and role model, and I will never forget his sincerity, cheerful outlook and enthusiasm for ecology. I am grateful to Silvia Hillyer for her help, chocolate, and service to the Graduate Group in Ecology.

I thank Rick Karban for encouragement and suggestions that helped me start my first manipulative field experiment at Bodega Marine Reserve. Mark Bertness made great suggestions that inspired Chapter 2, and research contributions from his lab have improved my understanding of salt marsh ecology.

Graduate student colleagues enhanced my academic experience at UC Davis. I especially thank Megan Donahue, Ada Fowler, and Wendy Trowbridge for stimulating discussions (over delicious food and wine!) and friendship. I would like to recognize the contributions of members of Kevin Rice's "Big Science Lab," with particular thanks to Cini Brown, John Gerlach, Michael Goedde, Eric Knapp, Elizabeth Leger, Jaymee Marty, and Kimberly Reever Morghan for constructive critiques of my experimental plans in the early stages of this work when an intellectual yet supportive environment was invaluable. I could always count on Miles DaPrato for help with the restoration project, and I thank him for being such a pleasure to work with in even the most demanding field conditions.

I thank my colleagues Jan Květ, Hana Šantrůčková, Jiří Šantrůček, and Jarka Komárková at the University of South Bohemia for helping with my research, generously sharing both their scientific knowledge and culture, for inviting me into their homes, and for botanical excursions in the Šumava Mountains and Třeboň Basin Biosphere Reserve wetlands. I thank each of them for thinking out loud and candidly sharing the way they see the world, and for helping me see it in a new way. I thank them for making my Fulbright experience in the Czech Republic a time I will always cherish. Děkujeme!

I appreciate the financial support provided by a William and Patricia Switzer Foundation fellowship, the CALFED Ecosystem Restoration Program, and a J. William Fulbright Foreign Scholarship Board fellowship. Additional funding provided by UC Davis Jastro-Shields research awards, Bodega Marine

Laboratory grants, and a Society of Wetland Scientists research award made all the difference. I thank Peter Connors and Kitty Brown (Bodega Marine Laboratory), John Kelly (Audubon Canyon Ranch), Diana Hickson (Dept. of Fish and Game), Marla Hastings (Dept. of Parks and Recreation), and Ken Poerner and Julian Meisler (Solano Land Trust) for enthusiastic facilitation of my research in some very special California wetlands

Lastly, I thank Steve Kidner. His love, patience, encouragement and assistance throughout this experience were a true gift.

I dedicate this thesis to the memory of Michelina (Marie) A. Sica and Paolo (Paul) Sica who moved half way around the world for a better life with educational opportunities for their children. I am greatly in their debt.

INTRODUCTION

California estuarine salt marshes have been drastically altered since pre-settlement times by changes in land use and hydrology. These changes pose monumental conservation challenges. Relict tidal wetlands have been reduced to fragmented habitat patches that support both endangered and invasive species. Success in conservation management of tidal wetlands and restoration of biological diversity has been limited by gaps in knowledge of California salt marsh community ecology.

In the quest to protect biological diversity, ecologists have argued that species are not interchangeable although ecosystem response to extinction is poorly understood (Loreau et al. 2001). An “idiosyncratic response hypothesis” suggests that the number of species per se may not be important to ecosystem functioning, but individual species and their characteristics can be crucial (Lawton 1994, Vitousek and Hooper 1994). Experimental evidence supports this idea (Naeem et al. 1995). Plants can be key regulators of ecosystem function as they respond to and change their environments altering factors such as nutrient and water availability. It is not fully known which species are important, why they are important, and how their importance changes with variable environmental conditions. An understanding of the multiple roles influential plants can play is essential if we are to predict the consequences of species losses and gains in human-impacted natural systems and achieve restoration success.

Parasites are ubiquitous in wetland ecosystems, and understanding how they affect biodiversity and ecosystem dynamics is also a central question in conservation biology (Thomas et al. 1997). Parasitic lifestyles by definition invoke some level of harm to hosts, but in reality a continuum of negative to positive interactions exists coupled with variation in degree of symbiosis that may alter population dynamics and shape community structure (Toft 1991). Parasitic plants are locally abundant in coastal salt marshes and may play a key role in maintaining species diversity.

In this thesis, I present results of experiments testing the functional role of parasitic plants within tidal wetlands and methods for restoration of endangered parasitic plant populations. In chapter one, I assess the direct and indirect effects of the native obligate parasite *Cuscuta salina* on species interactions and salt marsh community structure. In chapter two, I investigate the effects of root hemiparasite – host interactions on amelioration of physical stress conditions in the rhizosphere. In addition, I investigate how salt marsh plant community diversity responds to parasite-generated habitat heterogeneity across climate and estuarine stress gradients. In the final chapter, I present results of an experimental reintroduction of an endangered hemiparasite to a restoration site in the San Francisco Estuary. In three years of field experiments, I test disturbance management methods for enhancement of rare plant establishment and fitness. I identify critical life stages and use failure time survival analysis models for a demographic comparison of restored and reference populations. Overall, these results serve to clarify the functional role of parasitic plant interactions within mid-Pacific Coast salt marshes of North America and advance our practical and scientific knowledge of rare plant restoration.

LITERATURE CITED

Lawton, J.H. 1994. What do species do in ecosystems? Oikos 71:1-8.

Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J.P. Grime, A. Hector, D.U. Hooper, M.A. Huston, D. Raffaelli, B. Schmid, D. Tilman, and D.A. Wardle. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294:804-808.

Naeem, S., L.J. Thompson, S.P. Lawler, et al. 1995. Empirical evidence that declining species diversity may alter the performance of terrestrial ecosystems. Phil. Trans. Roy. Soc. London 347:249-262.

Thomas, F., F. Cezilly, T. de Meeus, A. Crivelli, and F. Renaud. 1997. Parasitism and Ecology of Wetlands: A Review. Estuaries 20:646-654.

Toft, C.A. 1991. An ecological perspective: the population and community consequences of parasitism. Chapter 16 in: C.A. Toft, Andre Aeschlimann, and L. Bolis (eds.) Parasite-Host Associations: Coexistence or Conflict? Oxford Science Publications, Oxford U. Press, Oxford.

Vitousek, P.M. and D.U.Hooper 1994. Biological diversity and terrestrial ecosystem biogeochemistry. p. 255-270 in: E.D. Schulze and H.A. Mooney (eds.) Biodiversity and Ecosystem Function. Springer-Verlag, Berlin, Germany.

CHAPTER 1

CRITICAL INTERACTIONS OF THE PARASITIC PLANT *CUSCUTA SALINA* ENHANCE RARE PLANT FITNESS AND DIVERSITY IN A CALIFORNIA SALT MARSH

ABSTRACT

Recent advances in estuarine ecology suggest that processes influencing salt marsh community structure are a balance between competitive and facilitative biological interactions ranging from direct commensalisms to mutualisms. Parasitic angiosperms are prevalent in mid-Pacific Coast salt marshes of North America, and complex interactions involving these plants also may play a role in community organization. I investigated the effects of a holoparasitic vine (*Cuscuta salina* ssp. *major*) on its primary host plant (*Plantago maritima* L.), a rare hemiparasitic angiosperm (*Cordylanthus maritimus* ssp. *palustris*), and the salt marsh plant community. *Cuscuta* simultaneously parasitizes several halophytes, but *Plantago* was the most frequent and highly infected host in this wetland. In two years of field experiments, I removed *Cuscuta* from experimental treatments and measured host plant performance and community response. In this system, *Cuscuta* clearly suppressed its preferred host and rare plant fitness and community plant species richness were enhanced through indirect effects. Competitive release may not fully explain the indirect effects of *Cuscuta* in this open wetland community. Priority effects play a role in the strength of the effect due to the timing of host life history characteristics. The differential influence of interplant parasitism on host plant fecundity may change population dynamics, benefit rare species, and alter salt marsh community structure. The continuum of negative to positive consequences of parasitic interactions deserves more attention if we are to understand tidal wetland community structure, successfully conserve community diversity, and restore functional salt marsh communities.

INTRODUCTION

A fundamental concern in ecology is to understand the processes that shape community structure and promote species coexistence. Knowledge of the mechanisms underlying changes in species diversity within communities is of paramount importance to applied conservation and restoration science. Experimental evidence suggests changes in species richness within communities potentially will feedback through ecosystem functions and influence future community structure (Naeem et al. 1994, Tilman and Downing 1994, Lawler et al. 2002). Rapid human population growth along the Pacific coast of California has resulted in the loss of nearly 90% of coastal wetland ecosystems, and relict fragments of these tidal wetlands support numerous endangered species. Substantial evidence that some plant species are a powerful community organizing force makes the potential loss of species a serious concern (Grime 1997; Hooper and Vitousek 1997). Because one universal conservation goal is to restore fragmented or otherwise degraded communities, it is crucial to understand the consequences of species loss, the identity of particular species that perform critical functions, and how the role of influential species changes with variable environmental conditions (see Kareiva and Levin 2003).

Coastal salt marshes experience daily tidal immersion that results in elevational gradients of soil salinity and hypoxia stress. These gradients correspond to variation in plant species composition, a wetland community dynamic of interest to early 20th century ecologists (Johnson and York 1915, Cooper 1926). Such initial observations led to an early view of edaphic control of plant zonation and community diversity (Adams 1963). But while physico-chemical factors change gradually over the intertidal gradient, sharp boundaries often are found between halophyte assemblages, a feature suggesting the importance of biological interactions in determining community structure (Bertness and Ellison 1987, Bertness1991a,b, and see Ungar 1998). While many early studies focused on a single interaction, it is recognized now that competition, herbivory, facilitation and parasitism are interactive processes whose outcome may depend on environmental conditions (Clay 1990, Bronstein 1994). Recent advances in salt marsh ecology suggest that processes influencing community structure are a balance between competitive and facilitative species interactions ranging from direct commensalisms to mutualisms These interactions occur across steep environmental gradients, but positive interactions often are masked and under-appreciated (Bertness and Callaway 1994, Bertness and Leonard 1997, Hacker and Gaines 1997). The conceptual model of plant community structure that has evolved suggests that competition and consumer pressure should prevail in benign environmental conditions, while the frequency of facilitative interactions should increase with physical stress (Bertness and Callaway 1994). An alternative view is that environmental stress favors coexistence only when it creates spatial or temporal niche opportunities (Chesson and Huntly 1997).

Parasite – host interactions are thought to be a major force in generating biological diversity (Thompson 1999). Parasites are ubiquitous in wetland systems, and understanding how they affect biodiversity and ecosystem dynamics is also a central question in conservation biology (Thomas et al. 1997, McCallum and Dobson 1995). Parasitic lifestyles by definition invoke some level of harm to their hosts, but in reality a continuum of negative to positive interactions exists coupled with variation in the degree of symbiosis (Toft 1991). A similar continuum of plant responses to herbivory exists (Maschinski and Whitham 1989), ranging from negative to neutral to positive effects, and parallels have been drawn between the effects of parasitic plants and herbivores (Pennings and Callaway 2002). Interplant parasitism is a consumer-resource interaction involving direct removal of host-synthesized carbon and nitrogen compounds (Press et al. 1988, Seel et al. 1992). Parasites may show strong host preferences, directly influencing host fitness, and therefore indirectly altering the result of interspecific interactions and community structure (Atsatt and Strong 1970, Gibson and Watkinson 1991, Marvier 1998). Pennings and Callaway (1996) identified *Salicornia virginica* L. as the preferred host of *Cuscuta salina* Engelm. var. *major* Yunck. in a southern California coastal marsh. Through correlative patterns they revealed convincing evidence of holoparasite influence on community structure. Other field observations on a related holoparasite suggest the neutral effect of *Cuscuta epithymum* on its host shrub due to an array of balancing positive and negative indirect effects (Gomez 1994). Rigorous field experiments to test hypotheses regarding the effects of parasite – host interactions and community response, such as removal of parasitic plants from natural communities, are few and have been limited to studies of root hemiparasites with photosynthetic capability in grasslands (ter Borg and

Bastiaans 1973, Gibson and Watkinson 1992, Marvier 1996). Experimental tests of effects of *Cuscuta* on tidal wetland diversity are lacking and leave us uncertain about its role in the community.

Building on the studies of Pennings and Callaway (1996), I report the results of two years of field research in which I investigated the role of *Cuscuta salina* in a northern California salt marsh community. My objectives were threefold. First, I determined how parasitism by *Cuscuta* relates to plant species composition and to environmental variables across the intertidal gradient to refine hypotheses regarding its community role, and provide local context. Second, I recorded field observations of host preference and infectivity of *Cuscuta* to determine if (a) potential hosts are equally infected, (b) *Cuscuta* infection pattern changes over time, and (c) there are differences in infectivity among hosts. Previous observational work suggested *Cuscuta* to be a keystone species relative to the maintenance of plant species diversity within California salt marshes (Pennings and Callaway 1996). My final objective was to manipulate the abundance of *Cuscuta* in a fully randomized removal experiment, to simultaneously examine infection by *Cuscuta* on multiple hosts in a natural setting.

METHODS

Study site, natural history

My study was conducted in the University of California Bodega Marine Reserve (BMR) salt marsh at Bodega Head, Sonoma County (38° 19’N 123° 04’W) approximately 100 km north of San Francisco, California (Fig. 1.1). The study site is 0.5 km from the Pacific ocean within the Bodega Harbor marine embayment. It experiences mixed semi-diurnal tidal cycles throughout the year, and is typical of high tidal elevation back-barrier salt marshes of the northern California and Oregon coasts. This region of California experiences a Mediterranean-type climate with most precipitation falling from November through April; cool foggy summers follow. Distinct salt marsh vegetation assemblages are evident along a subtle intertidal gradient. *Cuscuta* is restricted to the high elevational zone of the BMR salt marsh that is regularly, but infrequently inundated by high tides (Barbour et al. 1973). Sand accretion from adjacent dunes and extreme tidal events contribute to the development of a diverse, open plant community in this highest salt marsh zone where bare successional patches continually are being created. Vegetation within this open community is diminutive in stature (generally < 15 cm tall) and includes salt-tolerant species such as *Salicornia virginica*, *Distichlis spicata* (L.) E. Greene, *Limonium californicum* (Boiss.) A.A. Heller and *Plantago maritima* L. Within this community, *Cuscuta salina* interacts with a variety of hosts with contrasting life history characteristics and seasonal phenological patterns. Further description of the site and its dominant species is provided in Barbour et al. (1973).

Focal species

Cuscuta salina var. *major* (Salt marsh dodder; Cuscutaceae) is an annual holoparasitic plant native to Pacific Coast salt marshes from British Columbia to Baja California, Mexico. This obligate heterotroph requires scarification for seed germination, and relies on endosperm resources to reach a host quickly.

Cuscuta reproduces sexually, and is rootless and effectively leafless (Kuijt 1969). The vine coils around above-ground parts of its host and extracts water, nutrients, and carbon via haustorial connections to host conductive tissues (Kelly 1990). Holoparasites of the Cuscutaceae are powerful sinks of host photosynthate, and can also effectively deprive hosts of nitrogen (Jeschke, et al. 1994, 1997). While initial parasitism of a single individual is limited to a single host, the vine may eventually form multiple connections with several hosts. At high levels of infection, *Cuscuta* can form dense mats over hosts by the end of the growing season that are conspicuous because of its bright orange color. As such, *Cuscuta* presents a unique opportunity to study parasite-host interactions.

Plantago maritima L. (sea plantain; Plantaginaceae) is a rosette- and taproot-forming perennial herb widespread through the coastal northern hemisphere. It is wind-pollinated, self-incompatible, and exhibits limited vegetative reproduction (Jerling 1983). The seed bank is not persistant (van Damme 1992). *Plantago* adjusts to salinity fluctuations through stomatal closures, and regulates intracellular levels of carbon for synthesis of sorbitol for osmotic adjustment to counteract salinity stress (Jefferies et al. 1979, Flanagan and Jefferies 1989). This early successional species typically is confined to open sites where much of the incident solar radiation reaches ground level (Dormann et al. 2000). *Plantago* is one of the earliest species to break winter dormancy at Bodega Head. Linear, succulent leaves emerge from basal rosettes in December and January. *Plantago* begins transition to reproductive stage as *Cuscuta* first emerges in March, some six weeks prior to significant above-ground growth of other potential hosts such as *Salicornia* and *Distichlis.*

Cordylanthus maritimus Benth. ssp. *palustris* (Behr) Chuang and Heckard (Point Reyes bird's-beak; Scrophulariaceae) is an annual, root hemiparasite that typically emerges in April. It often is associated with, and directly hyper-parasitized by *Cuscuta*. This rare plant is endemic to salt marshes from San Francisco Bay (37° 23'N 122° 11'W) to Tillamook County, Oregon (45° 25'N 123° 56'W). Where extant, it may be locally abundant. *Cordylanthus maritimus* ssp. *palustris* is a conservation species of concern in California, and is listed as an endangered plant in Oregon as a result of habitat loss and fragmentation (CNPS 2001).

***Distribution of* Cuscuta salina**

I conducted an observational study to document spatial associations among *Cuscuta*, potential host species, and environmental variables. Six randomly dispersed 12-m^2 plots were established in each of four distinct vegetation zones to describe vegetation pattern, vegetation structure, and soil conditions within the salt marsh at peak *Cuscuta* abundance. Within each plot, percent cover of plant species, gaps, and maximum canopy height were recorded. Photosynthetically-active radiation (PAR) and sunfleck fraction were measured 5 cm above the soil surface within 90 min of solar noon on clear days with a Decagon SF-80 sunfleck ceptometer. Biomass (dry weight) was determined by removing all above-ground vegetation from four 0.0625-m^2 samples randomly located within each plot. Undisturbed 5 cm diameter X 10 cm deep soil core samples were collected and evaluated for bulk density, water content, organic matter, and total nitrogen, carbon and phosphorus. Soil samples were weighed before and after oven drying at 105°C for 48 hours. Bulk density was determined as grams of oven-dry soil per volume of soil, and gravimetric soil water content was calculated as the ratio of water mass to dry soil mass. Organic matter content was analyzed by the loss-on-ignition method. Total nitrogen and carbon concentrations were assessed with a Carlo-Erba Series 5000 CHN-S analyzer. Total phosphorus was determined by sample digestion followed by a colorimetric method for orthophosphate analysis. Soil nutrients were standardized by bulk density for comparisons among zones. Soils in some plots were too dry to extract interstitial water in the field. Therefore, core samples were collected from all plots and standard soil saturation pastes were prepared for salinity analysis (Rhoades 1982). Soil extract solutions were expressed from a 10 ml syringe loaded with filter paper for salinity determination with a Leica Model 10419 temperature-compensating refractometer (PERL 1990).

Because distinct intertidal vegetation zones were identified *a priori,* observed vegetation and sampling plot relationships were confirmed by subjecting species abundance data to hierarchical cluster analysis using Euclidean distance as a measure of plot dissimilarity and an average group linkage algorithm. Because *Cuscuta* abundance and plant species diversity at BMR are a unimodal function of position along the intertidal gradient, I used canonical correspondence analysis (CCA) in CANOCO 4.5 (ter Braak and Šmilauer 2002) to investigate correlations between plant species and environmental variables by the forward selection procedure ($p \leq 0.05$). The statistical significance of these relationships was evaluated with Monte Carlo permutation tests

Host preferences and infectivity of **Cuscuta salina**

To determine if preferential parasitism could influence salt marsh community structure, I conducted an observational study to quantify the identity and temporal variation of *Cuscuta* host infectivity at BMR. I located 80 stratified random 0.01-m^2 plots in areas where *Cuscuta* was present. Within this wetland, *Cuscuta* does not occur in monospecific host stands and individual host plants are quite small. All plots were positioned on a mixture of species, and all plants within each plot were examined for presence of *Cuscuta* infection.

In this study, I distinguish between parasite infectivity and virulence. It is important to define these terms, as there often is overlap in their use (Dybdahl and Storfer 2003). Infectivity (infection success) is an important measure of parasite fitness. I assessed infectivity of *Cuscuta* through direct observation as the ability of the parasite to infect hosts. Following Pennings and Callaway (1996) plants were scored as uninfected (0), lightly infected with 1 – 10 haustoria attached (1), moderately infected with 10-30 haustoria attached (2), or heavily infected with > 30 haustoria attached. To determine if there is a difference in infection level among initial potential hosts, the first observations were recorded in mid-April two weeks following the emergence of *Cuscuta*. To determine if infection level varies among potential host at peak infection, observations were repeated in July when *Cuscuta* is most abundant. Data were analyzed with a Kruskal-Wallis nonparametric ANOVA to test the hypothesis that all species were equally infected. Rank-sum post hoc tests were used to determine differences in infectivity among species.

Cuscuta salina *manipulation experiment*

To investigate the impact of *Cuscuta* on the plant community, and also on its primary host and a rare hemiparasite, I conducted a two-year *Cuscuta* removal experiment. The primary host, *Plantago maritima,* was well established at BMR salt marsh at the initial onset of *Cuscuta* parasitism in late March. *Plantago* was the only parasitized host encountered at experiment establishment, as most perennials in the community such as *Salicornia* had not broken winter dormancy. Thirty 0.25 m^2 control plots and thirty 0.25 m^2 removal plots were identified, marked, and randomly interspersed throughout the high marsh zone. All identified experimental plots included at least one initial coil of *Cuscuta* attached to *Plantago* host. All *Cuscuta* present in the 30 removal plots was carefully removed from the intact *Plantago* leaves. *Cuscuta* coils were easy to detect and remove at this early stage of parasitism. I initially inspected all experimental units daily, and gradually reduced the frequency of hand removal of *Cuscuta* to at least once a week. The procedure was repeated in the permanently-marked plots a second year.

To assess parasite – host interactions, I evaluated the impact of *Cuscuta* on its primary host through the first season. I used an ecological definition of parasite virulence (i.e. the degree of host damage resulting from infection). I assessed the virulence by measuring the degree of host damage indicated by host fitness response to infection compared to fitness of uninfected hosts.

Infected *Plantago* plants in experimental plots were individually marked prior to initiation of *Cuscuta* removal, and measurements were made of rosette diameter, number of inflorescence spikes, and aggregated length of inflorescences to assess growth and reproductive fitness. If more than one parasitized host was present in the plot, I haphazardly selected one individual to mark and monitor. At the start of the experiment, marked *Plantago* individuals in control and removal plots did not differ in size or fecundity (MANOVA: Wilks' $\lambda = 0.957$; $F_{3,56} = 0.843$; $p = 0.476$). Final measurements of host fitness were made following 16 weeks of parasitism before *Plantago* senescence, and marked plants were harvested for final biomass and reproductive fitness determination. It was not possible to determine accurately seed production of this species under field conditions. The difference between initial and final data were natural log transformed prior to analysis. As the response variables (change in rosette diameter, inflorescence number, and aggregated inflorescence length; and final biomass) potentially were correlated, I used MANOVA followed by "protected" univariate F tests with control and removal treatments as the main effects to evaluate host fitness response using the General Linear Modeling procedure (GLM). Post hoc treatment comparisons were made with sequential Bonferroni-adjusted probabilities. Statistical analyses were performed in SYSTAT 9.0 (SPSS 1999).

To assess the impact of *Cuscuta* on a rare hemiparasite associate of conservation concern, five subsamples of *Cordylanthus maritimus* ssp. *palustris* were selected haphazardly from experimental plots and harvested. Presence or absence of *Cuscuta* hyperparasitism was recorded prior to *Cuscuta* removal from samples. Hemiparasite height and branch, flower, and seed capsule counts were recorded prior to oven drying for biomass determination. I used MANOVA to examine rare plant fitness (GLM, SYSTAT v. 9.0, SPSS, Inc.). When MANOVA sufficiently detected the strength of the effect, univariate tests were evaluated for treatment significance. Post hoc treatment comparisons were made with Bonferroni adjusted probabilities.

Initially when treatments were established, I evaluated plant community composition of 0.25-m^2 plots. Grids with 100 subdivisions were placed over plots for evaluation of initial community composition. The number and identity of species present were recorded. Percent cover by plant species and community gaps were determined by the point intercept method. Initially, when plots were established, species composition and abundance did not differ between treatments. I reassessed community composition after one and two years of removals to follow changes in community composition over time. I used repeated measures ANOVA with treatment (control or removal) as the main effect to examine the effect of parasite removal on species richness and canopy gap dynamics. To examine the effect of parasite removal on the host community, I simultaneously examined the relative abundance of species in a multivariate analysis of variance (MANOVA). Paired t-tests were used to compare species abundance between controls and parasite removal plots. Species that were extremely rare in the random experimental plots (present in < 2% of plots; e.g., *Frankenia salina* (Molina), *Polygonum marinese* T.Mert. & Raven) were excluded from these analyses.

RESULTS

Community pattern and distribution of Cuscuta

Cluster analysis confirms four unique vegetation groups across intertidal elevations at BMR (Fig. 1.2). *Cuscuta* infection is limited to the highest intertidal zone. The multivariate ordination diagram from CCA further reveals the distribution of species relative to environmental gradients, and suggests which environmental factors best explain the occurrence of *Cuscuta* (Fig. 1.3). The relationship between plant community and environmental data was highly significant (F = 8.134, p=0.002, Monte Carlo test), and the first three canonical axes explained 38.6%, 29.5%, and 15.2% response of the variance in plant species abundance distribution. CCA ordination results suggest that variation in canopy height and above ground biomass are most distinctive between the zone that supports *Cuscuta*, and areas of the marsh where this parasite is absent. *Scirpus maritimus* L.- *Salicornia* stands were distinguished by greatest canopy heights and above ground biomass, while *Cuscuta* is associated with diminutive vegetation in areas with highest environmental stress. Soil water content and above ground plant biomass were lowest, while soil salinity and bulk density, sunfleck fractions, and below canopy photosynthetically active radiation were highest in the infrequently flooded *Cuscuta* host community. *Cuscuta* is restricted to an open area of the marsh with the lowest levels of soil nutrients. In contrast, *Scirpus pungens* Vahl, *Triglochin maritima* L., *Scirpus cernuus* Vahl, and *Jaumea carnosa* (Less.) A. Gray are associated with increasing soil nitrogen, carbon, organic matter, and water content. It is important to note that *Distichlis* *spicata* and *Salicornia virginica* are generalist species that occur across the entire intertidal gradient, and are not distinguished by association with any measured environmental variable.

The mere presence of potential hosts is not a reliable indicator of a suitable host community for *Cuscuta*. *Salicornia* and *Distichlis* are found with *Cuscuta*, but the correlation is weak and they are not parasitized in all intertidal zones of the marsh where they occur. Potential hosts most strongly associated with *Cuscuta* include *Plantago maritima*, *Cordylanthus maritimus* ssp. *palustris*, *Spergularia macrotheca* (Hornem.) Heynh., and *Atriplex triangularis* Willd. Other closely linked community species include *Triglochin concinna* Burtt Davy, *Frankenia salina*, *Limonium californicum*, *Atriplex californica* Moq., *Puccinellia nutkaensis* (J.S. Presl) Fern. & Weath., *Polygonum marinense*, and the exotic *Parapholis incurva* (L.) C.E. Hubb.

Host infectivity of **Cuscuta**

The level and frequency of infection by *Cuscuta* varies among potential hosts, and over the course of the season. *Plantago maritima* was the most frequent initial host for *Cuscuta*, and *Plantago* supported the highest level of *Cuscuta* infection (Fig. 1.4a). Spring infection of *Jaumea carnosa*, *Salicornia virginica*, *Spergularia macrotheca, and Atriplex triangularis* was observed at very low levels. Only a small number of *Salicornia*, *Distichlis*, and other potential hosts plants have transitioned from winter dormancy at the time *Cuscuta* germinates and forms initial host attachments in northern California tidal wetlands, and most lagged behind this initiation of parasitism by nearly 6 weeks.

Atriplex californica, Triglochin concinna, and *Limonium californicum* were present when *Cuscuta* shoots appeared, but were not selected as early hosts.

A different pattern of host infection was observed in summer at the time of peak summer growth of *Cuscuta* (Fig. 1.4b). *Plantago* continued as the most frequently selected host, and supported the highest level of *Cuscuta* infection. *Jaumea*, *Salicornia*, *Spergularia*, *Atriplex californica*, and *Cordylanthus* were secondary summer hosts that were infected equally at low levels. *Cuscuta* formed host connections with relatively tall tillers of *Distichlis* and *Puccinellia* grasses, but frequency and level of infection of the grasses were very low. *Cuscuta* twines around the reproductive culms, attaches with a few haustoria, but appears to use these erect grasses as structural supports to bridge to other more preferred hosts.

***Cuscuta* Removal Experiment**

Direct effect of* Cuscuta *on primary host fitness. - *Cuscuta* exerted a powerful, virulent effect on its primary host after 16 weeks of parasitism. *Cuscuta* parasitism impaired growth, transition to reproductive life stage, and reproductive fitness of *Plantago maritima.* All marked *Plantago* in parasite removal plots achieved reproductive maturity, while 17% of parasitized marked plants did not produce inflorescence spikes. *Cuscuta* directly suppressed growth and reproduction of *Plantago* as indicated by rosette diameter, host biomass, and production and cumulative length of inflorescence spikes (Table 1.1, Fig. 1.5).

Indirect effects of* Cuscuta *on rare hemiparasite fitness – Experimental manipulations reveal an indirect positive effect of *Cuscuta* on the rare

Cordylanthus hemiparasite. *Cordylanthus* was frequently hyper-parasitized by *Cuscuta* as a secondary host at low infection levels (Fig. 1.4b). A preliminary analysis of *Cordylanthus* in control plots did not provide statistical evidence for a difference in fitness between hyperparasitized individuals and those that were not directly infected by *Cuscuta* (MANOVA, Wilk's $\lambda = 0.92$, $F = 1.86$, $df = 5$, $p = 0.107$). However, there is a highly significant indirect positive effect of *Cuscuta* on this rare hemiparasite associate (Table 1.2, Fig. 1.6). *Cordylanthus* grew taller, exhibited more branching, and produced more flowers, biomass, and substantially more mature seed capsules in the presence of *Cuscuta* (Fig. 1.6).

***Effect of* Cuscuta *on community structure* –** Plant species richness declined when the host community was released from *Cuscuta* parasitism (repeated measures ANOVA, $F = 8.13_{1,58}$, $p = 0.006$, Fig. 1.7). The change in species richness was significant across time ($F = 6.86_{1,58}$, $p = 0.011$), and the removal effect was more pronounced by the end of the second year. Over the two years of the experiment, removal of *Cuscuta* did not result in a closed canopy, and gaps persisted in both experimental treatments (Fig. 1.8). However, the proportion of bare ground intercepted through canopy gaps increased with *Cuscuta* infection ($F_{1,58} = 33.92$, $p \leq 0.0001$). *Cuscuta* strongly influenced species relative abundance in the host community by differentially impacting host species (Fig. 1.9). Removal of *Cuscuta* led to a significant shift in the relative abundance of plant species (MANOVA, Wilks' $\lambda = 0.154$; $F_{15,104} = 38.08$; $p \leq 0.0001$). Preferential parasitism of *Plantago* resulted in the most significant effect, as the relative abundance of this host increased by approximately 25%

with *Cuscuta* removal. *Salicornia* and *Jaumea* responded positively after only one year of parasite release, but no further changes in relative abundance of these two halophytes were detected after a second year. The relative abundance of *Cordylanthus*, *Triglochin*, and *Distichlis* declined in the absence of *Cuscuta*, suggesting an indirect positive effect of the parasite on these rare species.

DISCUSSION

Experimental removal of the parasitic plant *Cuscuta salina* from a northern California salt marsh reveals the importance of this consumer to the maintenance salt marsh species diversity. As species assemblages and abiotic conditions vary among locations within a species range, the intensity and types of interactions among species also may change (Dunson and Travis 1991, Power et al. 1996, Pennings et al. 2003). Along the California coast, highly visible orange mats of heavy *Cuscuta* infections are associated with a *Salicornia* host. However, *Cuscuta* is a generalist parasite whose host choices and infection levels vary within and between marshes throughout its range. While these differences exist, experimental evidence from this study supports the hypothesis (Pennings and Callaway 1996) that the parasitic plant *Cuscuta salina* plays an important role in structuring salt marsh plant communities and suggests the effect holds over a range of infection levels and environmental conditions.

Negative consequences of preferential parasitism

In this experiment, the direct consumer effects of the parasitic plant on its primary host were strong even though *Cuscuta* occurs at low abundance relative to other community members. The interactions of *Cuscuta* are atypical because while the loss or removal of an individual species can cause dramatic changes in communities, experiments indicate that only a few species will have such strong effects, and most will have weak effects due to low abundance (Paine 1974, Estes and Palmisano 1974, Menge et al. 1994). Parasite virulence was high on *Plantago*, even at low to moderate infectivity. This is likely because *Cuscuta* species alter host physiology by acting as a stronger sink for photosynthate than any other host organ (see Press et al. 2001). The reductions in primary host biomass and reproductive output measured in this study are similar to measured effects of other *Cuscuta* species (Wolswinkel 1974 and Jeschke et al. 1994). Low soil nutrient resources and high soil salinity levels (Fig. 1.3) may explain why *Cuscuta* did not reach high infection levels and did not form extensive mats extending to many hosts in this marsh. *Plantago* synthesizes and accumulates stress proteins and other nitrogen- or carbon-based compounds that serve as osmoticants. These adaptations produce nutrient-rich tissue, but consequentially limit the proportion of acquired resources that can be allocated to growth or chemical defense. The significant reduction in parasitized *Plantago* biomass (Fig. 1.5) suggests that host photosynthesis was not able to meet the extra parasite demand for carbon under these environmental conditions.

The fact that a number of parasitic plants exploit multiple hosts, strongly suppress host plants, and may show host preferences is well documented, yet knowledge of variation in host preferences and parasitic plant impacts on natural plant communities is rudimentary (see Press et al. 1999). In this study, *Plantago* was identified as the primary *Cuscuta* host, although host preference for *Salicornia* was observed at Carpinteria Marsh (Pennings and Callaway 1996). In coastal sage-scrub and oak-sycamore riparian wetland communities, *Cuscuta subinclusa* Durand and Hilgard discriminates among potential hosts and shows preference for *Malosma laurina* (Nutt.) Abrams. Preferential selection of hosts by *Cuscuta* parallels observations of herbivore food choice studies in salt marshes. Grazing studies consistently document selective foraging for nutrient-rich *Plantago maritima* by spring-staging geese (Prins 1980, Olff et al. 1997, Van der Wal et al. 2000) and by cattle (Jerling and Andersson 1982). Results from this study suggest that *Cuscuta* actively exploits resource heterogeneity and selects for host quality, but the predominate use of *Plantago* resources may also be explained by the temporal pattern of parasite germination and host development.

The interactions of *Cuscuta* are dependent on the life history of potential host community members. Because *Plantago* was well established, and in an advanced life stage in early spring it was vulnerable to attack following germination of *Cuscuta* at BMR at a time prior to significant above-ground growth of other potential hosts in the community. At this site, *Cuscuta* clearly played a strong role in reducing initial host performance. The mechanism for the strength of this effect appears to be the complete initial dependence of the holoparasite on this host, due to the timing and interplay of life history characteristics of these entwined species. Experiments with *Cuscuta attenuata* in Texas grasslands showed that the effect of *Cuscuta* depended on the order in which the parasite encountered different host species (Kelly and Horning 1999). At BMR, most

Cuscuta seedlings were completely dependent on *Plantago* before other secondary hosts were available for exploitation, and before *Cuscuta* attained sufficient resources to parasitize multiple hosts. This resulted in a powerful, virulent effect on *Plantago* at the very time that the host was allocating resources to reproductive output. The fact that *Plantago* was beginning this high resource demand life stage synchronous with the onset of a holoparasitic attack may explain the strong suppression imposed by the parasite. In some cases, *Cuscuta* obtained enough resources from its first host to reach reproductive maturity, but did not have enough resources for growth to secondary hosts. Reduction in host biomass and demographic repercussions imposed by *Cuscuta* were strong in this environment, and while the parasite achieved reproductive maturity its infection success was low to moderate (Fig. 1.4). A different outcome might be expected along environmental gradients, i.e. in eutrophic wetlands at an urban or grazed interface. These results emphasize the importance of studying parasitic interactions over a range of environmental conditions, as priority effects and the degree of parasite impact may vary with abiotic conditions and life history characteristics of the local host community.

Plantago was not able to recover from the impact of *Cuscuta* through compensatory growth. This is likely due to the relatively long duration of the holoparasite life cycle, and the amount of host biomass removed to support *Cuscuta*. Another symbiont not evaluated in this study may play a role in this outcome. Prior to host senescence and after *Cuscuta* has reached reproductive maturity, *Plantago* is attacked by a leaf fungus. Like *Cuscuta*, this symbiont does not kill the *Plantago* host, but the timing of the interaction appears to preclude compensatory growth of *Plantago* following *Cuscuta* senescence.

The direct consumer effects of *Cuscuta* may mask a facilitative role of the parasite for its primary host. Experiments have demonstrated that *Plantago* are susceptible to competition for light, and eventually replaced by late-successional species (Dormann et al. 2000). Because *Cuscuta* helps keep this intertidal high marsh community open and thereby reduces competition for light (Fig. 1.8), the parasite may indirectly contribute to the long term persistence of *Plantago.* By doing so, *Cuscuta* may also precondition the community by maintaining gaps for parasite germination and nutritious hosts for the next generation.

Neutral consequences of preferential parasitism

The abundance of the majority of plant species in the community exhibited a neutral response to the direct consumer effect of *Cuscuta* at this experimental time scale. Following two years of *Cuscuta* manipulation, 64% of plants in the community were equally abundant with or without *Cuscuta* (Fig. 1.9).

Indirect positive effects of* Cuscuta *enhance rare plant fitness

An unexpected outcome of this experiment was the indirect positive response of the hemiparasite *Cordylanthus* to the presence of *Cuscuta* even though both parasites are competing for host carbon. Because both parasites are generalists that can exploit a number of host species, access to hosts may not be a limiting resource. This phenomenon helps explain how the parasites can co-exist, but does not explain why *Cordylanthus* benefits from the association. If not competing for the same host photosynthate, it is possible that the availability and greater exploitation of a higher quality partner *(Plantago)* makes soil resources more available to other hosts that may support the hemiparasite. The hemiparasite acquires host resources, but also competes for light in order to supply a proportion of its own fixed carbon needs. In this regard, *Cuscuta* may benefit the hemiparasite by keeping the intertidal high marsh community canopy more open. The interaction also has the potential to link to significant changes in nutrient cycling within the community.

Sub-arctic hemiparasites tap nutrients that are otherwise immobilized on longer time scales by their perennial hosts, concentrate nutrients in their tissue, and produce high quality litter that can accelerate nutrient turnover and regeneration within the community (Press 1998, Quested et al. 2002, 2003). At BMR, *Cordylanthus* accumulates twice as much tissue nitrogen and nearly 5 times more tissue phosphorous than its hosts (B. Grewell, unpublished data). Its annual death and decomposition also may provide the functional link between diversity and nutrient cycling. The actual role of preferential parasitism and its interaction with resource competition and nutrient cycling in salt marshes remains to be assessed in future field experiments.

Cuscuta *improves salt marsh conservation status*

Ecologists now recognize that indirect interactions are often central to community dynamics (McCann 2000). In this study, preferential parasitism by *Cuscuta* resulted in complex cascading effects within the community. Because *Cuscuta* preferentially selects and forms physiological attachments with only a subset of potential hosts, its presence in the community may impede the development of competitive hierarchies and equilibria and ultimately enhance species diversity within and between plant communities. The indirect effects of this parasite appear to be of greatest importance relative to the overall conservation status of the wetland, and the identity of the species that benefit from the interactions can be linked to important community-level processes. *Distichlis* and *Cordylanthus* increased in relative abundance in *Cuscuta*- infected communities. *Distichlis* is a fugitive grass that pre-conditions harsh salt marsh bare patches for less stress tolerant species (Bertness 1991, Bertness et al. 1992). It is a common host choice of the rare *Cordylanthus* hemiparasite at BMR (B. Grewell, unpublished data). The physiological link between the *Cordylanthus* hemiparasite and its hosts further enhances this functional role in physical stress amelioration (Grewell 2004 and see Chapter 2). *Triglochin concinna* growth also was facilitated by *Cuscuta*. Restoration experiments in southern California hypothesize a keystone role for *Triglochin* because it sequesters high concentrations of nitrogen relative to its biomass, and potentially limits the growth of more robust perennials like *Salicornia virginica* (Zedler et al. 2001). The indirect interaction between *Cuscuta* and *Triglochin* may result in additive effects on nutrient cycling and the maintenance of species richness in the community that could be important and merit further attention. Manipulation of *Cuscuta* at BMR reveals important conservation implications as infection enhances species richness, and *Cuscuta* indirectly facilitates rare species that have been linked to ecologically important roles in other North American salt marshes, which may influence important ecosystem-level processes.

Parasitism and salt marsh plant community structure

A growing body of experimental work has unveiled the previously under-estimated importance of positive interactions in communities (Bruno et al. 2003). Given recent attention on the role of direct positive interactions in structuring salt marsh communities, this study suggests that a fuller range of symbiotic interactions including parasitism should be considered. The experimental removal of the parasitic plant *Cuscuta* reported here included a pairwise interaction approach. The evaluation of parasite effects on community-level plant species richness and abundance revealed a continuum of negative to neutral to positive effects of the parasite. Within this community, the net effect of the *Cuscuta* parasite load appears to be positive as it contributes to the persistence of rare plants and the maintenance of species richness and diversity. Additional studies are needed to understand fully the interactive nature of the complex multispecies associations in this parasitic interaction web, and how their balance might shift with changing environments. The results of this study also raise questions regarding the current model of plant community structure that suggests competition and consumer pressure prevail in benign conditions, while positive species interactions should increase with physical stress (Bertness and Callaway 1994). In this study, intense consumer pressure from a parasitic plant occurred in the zone of highest physical stress at BMR. It also was linked to indirect positive interactions within the community. *Cuscuta* appears to create spatial and temporal niche opportunites for coexistence within this harsh environment, echoing the view of Chesson and Huntly (1997) that consideration of these factors may complement a robust model of plant community structure.

Previous work has assumed that *Cuscuta* facilitates recruitment of subordinate species in gaps created by dominant host suppression in otherwise closed communities (Pennings & Callaway 1996, Callaway & Pennings 1998), but the exclusive assumption of a competitive release mechanism for species diversity can limit our understanding of community dynamics (Hacker and Gaines 1997). Competitive release does not fully explain the *Cuscuta* effect on community composition and species abundance in this study. At this site, potential recruitment gaps are greater when *Cuscuta* is present, but the community remains relatively open when the parasite is removed. This may be an artifact of the timescale of this experiment, but sand deposition and other natural disturbance processes also contribute to gap creation at this salt marsh site. My results suggest multiple mechanisms resulting from a continuum of mulitspecies interactions are at work. For example, a greater proportion of canopy gaps with *Cuscuta* expose more of the sediment surface to light and greater temperature fluctuations that may increase nitrogen mineralization. Because *Cuscuta* accumulates considerably more nitrogen than its hosts, facilitates a second parasite that does the same, and both return this nutrient to the system upon decomposition, the increase in gaps may make more nitrogen available to community associates. If the effects of *Cuscuta* go beyond direct consumption and also indirectly facilitate nutrient cycling, interplant parasitism can be an important modifier of competitive interactions during succession where light may not be the limiting resource.

Evidence from my study complements the work of Pennings and Callaway (1996), and expands our view of the complex interactions of *Cuscuta*. While physical and biological conditions vary considerably between southern and northern California salt marshes, the overall positive effect of *Cuscuta* on community diversity appears to persist across levels of infection, and in closed to open successional communities. *Cuscuta* appears to play a strong functional role in salt marsh community structure, but the mechanism for the overall effect varies. Understanding the role *Cuscuta* might play in changing processes that influence the course of succession has applied significance in restoration ecology, and may be useful in the prediction and management of restoration trajectories. Parasites play a key role in wetland species diversity. Successful conservation and restoration of wetlands may be contingent on our ability to understand the context and relative role of a broad range of symbiotic interactions that begin as a direct interplay between species, and may ultimately alter population dynamics and shape community structure.

ACKNOWLEDGEMENTS

I thank Eliška Rejmánková, Kevin Rice, Ted Grosholz, and Peggy Fiedler for comments that improved the manuscript. I also thank Peter Connors for facilitating this work at Bodega Marine Reserve, Rick Karban and Anurag Agrawal for encouragement and advice regarding the removal experiment, and

Kevin Rice and his lab for thoughtful discussions and countless equipment loans. This research was supported by a Bodega Marine Laboratory Research & Travel Grant, University of California Jastro-Shields Graduate Research Award, and a William & Patricia Switzer Foundation Research Fellowship.

LITERATURE CITED

Adams, D.A. 1963. Factors influencing vascular plant zonation in North Carolina salt marshes. Ecology 44:445-456.

Atsatt, P.R. and D.R. Strong. 1970. The population biology of annual grassland hemiparasites. I. The host environment. Evolution 24:278-291.

Barbour, M.G., R.B. Craig, F.R. Drysdale, and M.T. Ghiselin. 1973. Coastal Ecology: Bodega Head. University of California Press, Berkeley, California.

Bertness, M.D. 1991a. Zonation of Spartina patens and Spartina alterniflora in a New England salt marsh. Ecology 72:138-148.

Bertness, M.D. 1991b. Interspecific interactions among high marsh perennials in a New England salt marsh. Ecology 72:125-137.

Bertness, M.D. and R. Callaway 1994. Positive interactions in communities: a post cold war perspective. Trends in Ecol. and Evol. 9:191-193.

Bertness, M.D. and A.M.Ellison. 1987. Determinants of pattern in a New England salt marsh community. Ecological Monographs 57:129-147.

Bertness, M.D., L. Gough, and S.W. Shumway. 1992. Salt tolerances and the distribution of vascular plants in a New England salt marsh. Ecology 73:1842-1851.

Bertness and Leonard. 1997. The role of positive interactions in communities: lessons from intertidal habitats. Ecology 78:1976-1989.

Bronstein, J.L. 1994. Our current understanding of mutualism. Qtrly.Review of Biology 69:31-51.

Bruno, J.F., J.J. Stachowicz, and M.D. Bertness. 2003. Inclusion of facilitation into ecological theory. TREE 18:119-125.

Callaway, R.M. and S.C. Pennings. 1998. Impact of a parasitic plant on the zonation of two salt marsh perennials. Oecologia 114:100-105.

Chesson, P. and N. Huntly. 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. Am. Nat. 150:519-553.

Clay, K. 1990. Impact of fungi on competitive interactions. pp. 391-411 in: J.B. Grace and D. Tilman, eds. Perspectives on Plant Competition. Academic Press, Inc. San Diego, CA. USA.

CNPS 2001. Inventory of rare and endangered plants of California. Spec Publ 1, 6th edit. Rare Plant Scientific Advisory Committee, D.P. Tibor, convening ed. Calif Native Plant Soc, Sacramento, CA. 387 pp.

Cooper, W.S. 1926. Vegetational development upon alluvial fans in the vicinity of Palo Alto, California. Ecology 7:1-30.

Dormann, C. F., R.Van Der Wal, and J.P. Baker. 2000. Competition and herbivory during salt marsh succession: the importance of forb growth stategy. J. Ecology 88:571-583.

Dunson, W.A. and J. Travis. 1991. The role of abiotic factors in community organization. American Naturalist 138:1067-1091.

Dybdahl, M.F. and A. Storfer. 2003. Parasite local adaptation: red queen versus suicide king. TREE 18:523-530.

Estes, J.A. and J.F. Palmisano. 1974. Sea otters: their role in structuring nearshore communities. Science 185:1058-1060.

Flanagan, L.B. & R.L. Jefferies. 1989. Photosynthetic and stomatal responses of the halophyte, *Plantago maritima* L. to fluctuations in salinity. Plant and Cell Environ. 12:559-568.

Gibson, C.C. and A.R. Watkinson. 1992. The role of the hemiparasite annual *Rhinanthus minor* in determining grassland community structure. Oecologia 89:62-68.

Gibson, C.C. and A.R. Watkinson. 1991. Host selectivity and the mediation of competition by the root hemiparasite *Rhinanthus minor*. Oecologia 86:81- 87.

Gomez, J.M. 1994. Importance of direct and indirect effects in the interaction between a parasitic angiosperm (*Cuscuta epithymum*) and its host plant (*Hormathorophylla spinosa*). Oikos 71:97-106.

Grewell, B. J. 2004. Functional roles of endangered parasitic plants in northern California salt marshes. Proceedings of the 2002 California Native Plant Society North Coast Rare Plant Symposium. CNPS & University of California Press (In Press).

Grime, J.P. 1997. Biodiversity and ecosystem function: the debate deepens. Science277:1260-1261.

Hacker, S.D. and S.D. Gaines 1997. Some implications of direct positive interactions for community species diversity. Ecology 78:1990-2003.

Hooper, D.U. and P.M. Vitousek. 1997.The effects of plant composition and diversity on ecosystem processes. Science 277:1302-1305.

Jefferies, R.L., T.Rudmik, & E.M. Dillon. 1979. Responses of halophytes to high salinities and low water potentials. Plant Physiology 64:889-994.

Jerling, L. 1983. Composition and viability of the seed bank along a successional gradient on a Baltic sea shore meadow. Holarct. Ecol. 6:150-156.

Jerling, L. and M. Andersson. 1982. Effects of selective grazing by cattle on the reproduction of *Plantago maritima.* Holarct. Ecol. 5:405-411.

Jeschke, WD, & Hilpert, A. 1997. Sink-stimulated photosynthesis and sink dependent increase in nitrate uptake: Nitrogen and carbon relations of the parasitic association *Cuscuta reflexa-Ricinus communis.*Plant Cell and Enivron. 20(1): 47-56.

Jeschke, WD, P. Bäumel, F.C. Czygan & P. Proksch. 1994. Modelling the flows and partitioning of carbon and nitrogen in the holoparasite *Cuscuta reflexa* Roxb.and its host *Lupinus albus* L. II. Flows between host and parasite and within the parasitized host. J. Exp. Botanty 45:801-812.

Johnson, D.S. and H.H. York. 1915. The relation of plants to tide-levels. Carnegie Inst. Wash. Publ. 206:1-162.

Kareiva, P. and S.A. Levin (eds.) 2003. The importance of species: perspectives on expendability and triage. Princeton University Press, Princeton N.J. USA.

Kelly, C.K. 1990. Plant foraging: a marginal vaule model and coiling response in *Cuscuta subinclusa*. Ecology 71(5):1916-1925.

Kelly, C.L. and K. Horning. 1999. Acquisition order and resource value in *Cuscuta attenuata*. PNAS 96:13219-13222.

Kuijt, J. 1969. The biology of parasitic flowering plants. Universtiy of California Press. Berkeley.

Lawler, S.P., J.J. Armesto, and P. Kareiva. 2002. How relevant to conservation are studies linking biodiversity and ecosystem functioning? pp. 294-313 in: A.P. Kinzig, S.W. Pacala, and D. Tilman (eds.) The functional consequences of biodiversity. Princeton Monographs in Population Biology 33. Princeton U. Press, Princeton, NJ. USA.

Maschinski, J. and T.G. Whitham. 1989. The continuum of plant responses to herbivory: the influence of plant association, nutrient availability and timing. Am. Nat. 134:1-19.

Marvier, M.A. 1998. Parasitic impacts on host communities: plant parasitism in a California coastal prairie. Ecology 79:2616-2623.

Marvier, M.A. 1996. Parasitic plant-host interactions: plant performance and indirect effects on parasite-feeding herbivores. Ecology 77:1398-1409.

McCann, K.S. 2000. The diversity-stability debate. Nature 405:228-233.

McCallum, H. & A. Dobson 1995. Detecting disease and parasite threats to endangered species and ecosystems. Trends in Ecol and Evol. 10:190-193.

Menge, B.A., E.L. Berlow, C.A. Blanchette, S.A. Navarrete, and S.B. Yamada. 1994. The keystone species concept: variation in interaction strength in rocky intertidal habitat. Ecol. Monogr. 64:249-286.

Naeem, S.L., J. Thompson, S.P. Lawler, J.H. Lawton, and R.M. Woodfin. 1994. Declining biodiversity can alter the performance of ecosystems. Nature 386:734-737.

Olff, H.J., de Leeuw, J.P. Bakker, R.J. Platerink, H.J. van Wijnen, and W. de Munch. 1997. Vegetation succession and herbivory in a salt marsh: changes induced by sea level rise and silt deposition along an elevational gradient. J. Ecology 85:799-814.

Paine, R.T. 1974. Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. Oecologia 15:93-120.

Pennings, S.C. & R.M. Callaway. 2002. Parasitic plants: parallels and contrasts with herbivores. Oecologia 131:479-489.

Pennings, S.C. & R.M. Callaway. 1996. Impact of a parasitic plant on the structure and dynamics of salt marsh vegetation. Ecology 77:1410-1419.

Pennings, S.C., E.R. Selig, L.T. Houser, & M.D. Bertness. 2003. Geographic variation in positive and negative interactions among salt marsh plants. Ecology 84:1527-1538.

PERL 1990. A manual for assessing restored and natural coastal wetlands with examples from southern California. Pacific Estuarine Research Laboratory. California Sea Grant Report No. T-CSGCP-021, La Jolla, California.

Power, M.E., D.Tilman, L.A. Estes, B.A. Menges, W.J. Bond, L.S. Mills, G. Daily, L.C. Castilla, J.Lubchenco, and R.T. Paine. 1996. Challenges in the quest for keystones. Bioscience 46:609-620.

Press, M.C. 1998. Dracula or Robin Hood? A functional role for root hemiparasites in nutrient poor ecosystems. Oikos 82:609-611.

Press, M.C., J.D. Graves, & G.R. Stewart. 1988. Transpiration and carbon acquisition in root hemiparasitic angiosperms. J. Exp. Botany 39:1009 1014.

Press, M.C., J.D. Scholes, and J.R. Watling. 1999. Parasitic plants: physiological and ecological interactions with their hosts. pp. 175-197 in: Press, M.C., Scholes, J.D. and Barker, M.G.(eds.) Physiological Plant Ecology. British Ecological Society. Blackwell Scientific, Oxford, U.K.

Prins, H.H.Th., R.C. Ydenberg and R.H. Drent. 1980. The interaction of brent geese *Branta bernicla* and sea plantain *Plantago maritima* during spring staging: field observations and experiments. Acta Bot. Neerl. 29: 585-596.

Quested, J.M., C. Cornelissen, M.C. Press, T.V. Callaghan, R. Aerts, F. Trosien, P. Riemann, D. Gwynn-Jones, A. Kondratchuk, and S.E. Jonasson. 2003. Decomposition of sub-arctic plants with differing nitrogen economies: a functional role for hemiparasites. Ecology 84:3209-3221.

Quested, J.M., M.C. Press, T.V. Callaghan, J. Hans, and C. Cornelissen. 2002. The hemiparasitic angiosperm Bartsia alpina has the potential to accelerate decomposition in sub-arctic communities. Oecologia 130:88-95.

Rhoades, J.D. 1982. Soluble salts. Chapter 10 in: Dinauer, R.C. (ed.) Methods of soil analysis, part 2: chemical and microbiological properties. Second edition. Am. Soc. of Agronomy & Soil Sci. Soc. of Am. Madison, Wisconsin USA.

Seel, W.E., I.Cechin, C.A. Vincent, and M.C. Press. 1992. Carbon partitioning and transport in parasitic angiosperms and their hosts. pp. 199-223 In: C. J. Pollack, J.F. Farrar, and A.J. Gordon (eds.). Carbon Partitioning Within and Between Organisms. BIOS Scientific Publishers, Oxford, UK.

SYSTAT. 1999. SYSTAT Version 9.0 for Windows. SPSS, Inc. Chicago, Illinois.

ter Borg, S.J. and J.C. Bastiaans. 1973. Host parasite relations in *Rhinanthus serotinus* I. The effects of growth conditions and host; a preliminary review. pp. 236-246 in: Symposium on Parasitic Weeds, April 1973, Royal U. of Malta. European Weed Research Council and Malta University Press, Malta.

ter Braak, Cajo J.F. & P.Šmilauer. 2002. CANOCO 4.5 Software and reference manual for canonical community ordination (version 4.5). Biometris. Wageningen Netherlands and České Budějovice, Czech Republic.

Thomas, F., F. Cezilly, T. de Meeus, A. Crivelli, and F. Renaud. 1997. Parasitism and Ecology of Wetlands: A Review. Estuaries 20:646-654.

Thompson, J.N. 1999. The evolution of species interactions. Science 284:2116 2118.

Tilman, D. and J.A.Downing. 1994. Biodiversity and stability in grasslands. Nature 367:363-365.

Toft, C.A. 1991. An ecological perspective: the population and community consequences of parasitism. Chapter 16 in: C.A. Toft, Andre Aeschlimann, and L. Bolis (eds.) Parasite-Host Associations: Coexistence or Conflict? Oxford Science Publications, Oxford U. Press, Oxford.

Ungar, I.A. 1998. Are biotic factors significant in influencing the distribution of halophytes? Botanical Review 64:176-199.

van Damme, J. M.M. 1992. Selection for the maintenance of sex polymorphism in *Plantago*. - pp. 204-222 in: Kuiper, P.J.C. and M. Bos (eds). *Plantago*: a multidisciplinary study. Springer-Verlag, Berlin.

van der Wal, R., H. van Wijnen, S. van Wieren, O. Beucher, and D. Bos. 2000. On facilitation between herbivores: how brent geese profit from brown hares. Ecology 81:969-980.

Wolswinkel, P. 1974. Complete inhibition of setting and growth of fruits of *Vicia faba* L. resulting from the draining of the phloem system by *Cuscuta* species. Acta Botanica Neerlandica 23:48-60.

Zedler, J.B., J.C. Callaway, and G. Sullivan. 2001. Declining biodiversity: why species matter and how their functions might be restored in Californian tidal marshes. BioScience 51:1005-1017.

Table 1.1. Results of MANOVA and "protected" univariate F test results on the effect of *Cuscuta* removal on log-transformed fitness indicators of the dominant host *Plantago maritima* following 16 weeks of parasitism. Host fitness metrics include rosette growth (increase in rosette diameter), total dry biomass, increase in number of inflorescences, and total aggregated inflorescence spike length per plant.

MANOVA	Wilks' Lambda	F	df (effect)	df (error)	PR>F
(GLM)	0.60	9.01	4	55	≤ 0.0001
ANOVA					
Variation	SS	df	MS	F	PR>F
Rosette Growth	13.82	1	13.82	37.17	≤ 0.0001
Total Biomass	22.09	1	22.09	22.53	≤ 0.0001
Inflorescence Count	44.98	1	44.98	16.57	≤ 0.0001
Inflorescence Length	67.97	1	67.97	16.87	≤ 0.0001
Error	470.89	232	2.03		

Table 1.2. Results of MANOVA and "protected" univariate F test results on the effect of *Cuscuta* removal on log-transformed fitness indicators of *Cordylanthus maritimus* ssp. *palustris*. Hemiparasite fitness indicators measured at reproductive maturity include height, number of branches, flower production, seed capsules set, seed capsules matured, and total plant biomass.

MANOVA	Wilks' Lambda	F	df (effect)	df (error)	PR>F
(GLM)	0.39	67.97	6	255	≤ 0.0001
ANOVA					
Variation	SS	df	MS	F	PR>F
Hemiparasite Height	10.80	1	10.80	359.53	≤ 0.0001
Branches	571.71	1	571.71	147.83	≤ 0.0001
Flower Production	77.33	1	77.33	281.37	≤ 0.0001
Seed Capsules Set	71.46	1	71.46	160.90	≤ 0.0001
Seed Capsules Mature	80.27	1	80.27	90.65	≤ 0.0001
Total Biomass	99.63	1	99.63	296.41	≤ 0.0001
Error	1807.37	1560	1.16		

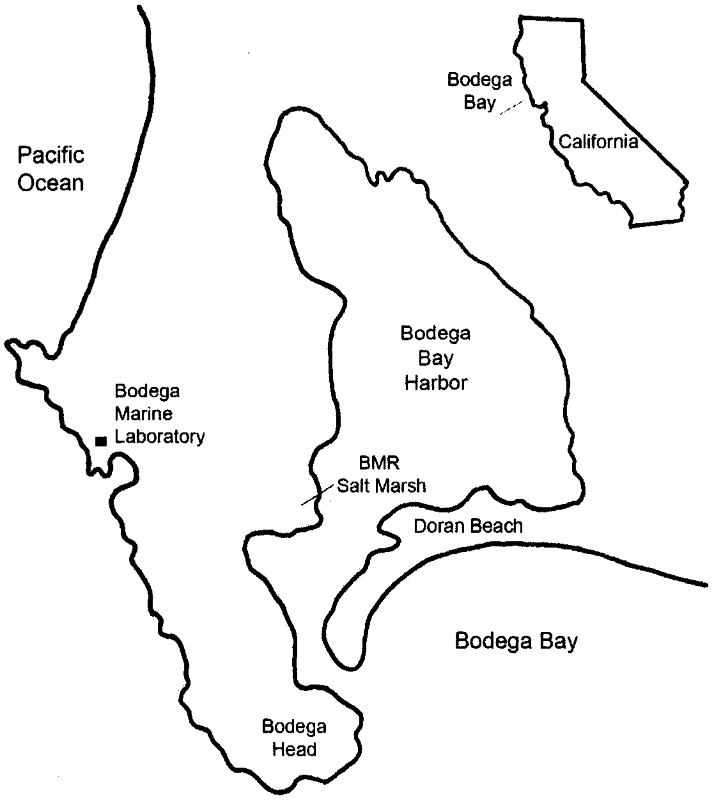


Figure 1.1. Map of the Bodega Marine Reserve (BMR) salt marsh study site within the Bodega Bay Harbor at Bodega Bay, California (38°19'N 123°04'W). The inset map of the state of California shows the location of Bodega Bay ~ 100 km north of San Francisco.

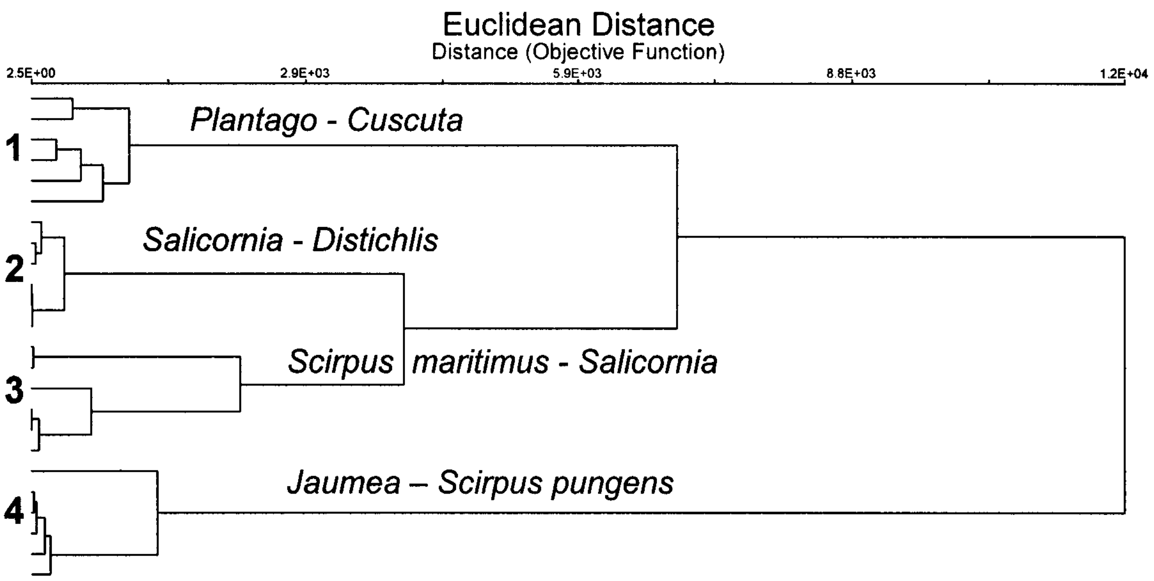


Figure 1.2. Hierarchical classification of Bodega Marine Reserve salt marsh vegetation based on species abundance by Euclidean distance-based cluster analysis using the average group linkage method. Plant species present in each cluster are as follows: **1** *Plantago – Cuscuta*: *Atriplex californicus, Atriplex triangularis, Cordylanthus maritimus ssp. palustris, Cuscuta salina, Distichlis spicata, Frankenia salina, Jaumea carnosa, Limonium californicum, Parapholis incurva, Plantago maritima, Polygonum marinense, Puccinellia nutkaensis, Salicornia virginica, Scirpus cernuus, Spergularia macrotheca*, and *Triglochin concinna*; **2** *Salicornia – Distichlis*: *Distichlis spicata, Jaumea carnosa,* and *Salicornia virginica; **3** Scirpus maritimus – Salicornia virginica: Distichlis spicata, Jaumea carnosa, Salicornia virginica,* and *Scirpus maritimus; and **4** Jaumea – Scirpus pungens: Distichlis spicata, Jaumea carnosa, Limonium californicum, Salicornia virginica, Scirpus cernuus, Scirpus pungens, Triglochin concinna*, and *Triglochin maritima.*

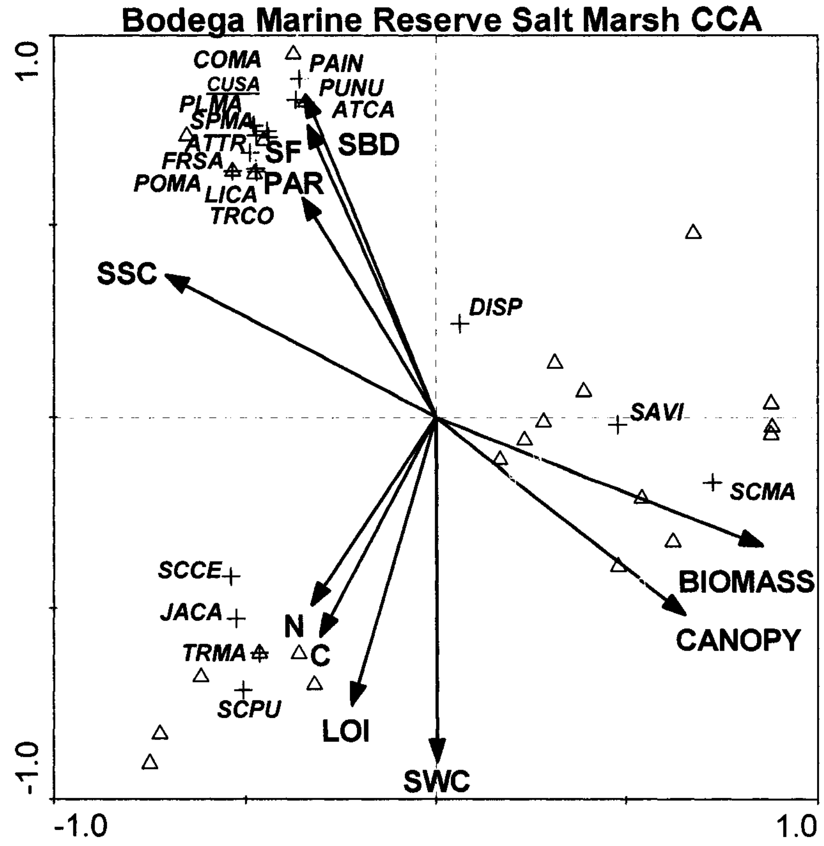


Figure 1.3. Canonical correspondence analysis ordination diagram relating plant community structure to environmental variables along the intertidal gradient in the Bodega Marine Reserve salt marsh. Symbols indicate plant species (+), releves (Δ), and environmental variables (arrows), first axis is horizontal and second axis is vertical. Four letter code abbreviations for species are ATCA = *Atriplex californicus*, ATTR = *Atriplex triangularis*; COMA = *Cordylanthus maritimus* ssp. *palustris*; CUSA = *Cuscuta salina*; DISP= *Distichlis spicata;* FRSA = *Frankenia salina*; JACA= *Jaumea carnosa*; LICA = *Limonium californicum*; PAIN = *Parapholis incurva*; PLMA = *Plantago maritima*, POMA = *Polygonum marinense* , PUNU = *Puccinellia nutkaensis* ;SAVI = *Salicornia virginica*; SCCE = *Scirpus cernuus*; SCMA = *Scirpus maritimus*; SCPU = *Scirpus pungens*; SPMA = *Spergularia macrotheca*; TRCO = *Triglochin concinna*; and TRMA = *Triglochin maritima.* Environmental variables are BIOMASS = Above ground plant biomass, CANOPY = maximum plant canopy height, C = total soil carbon, N = total soil nitrogen; LOI = soil organic matter by loss on ignition, SBD = soil bulk density, SSC = soil saturated conductivity, SWC = soil water content, SF = sunfleck fraction (community gaps); and PAR = below canopy photosynthetically active radiation. Soil phosphorus was measured but is not shown as it was eliminated during forward selection of significant variables ($p \leq 0.5$).

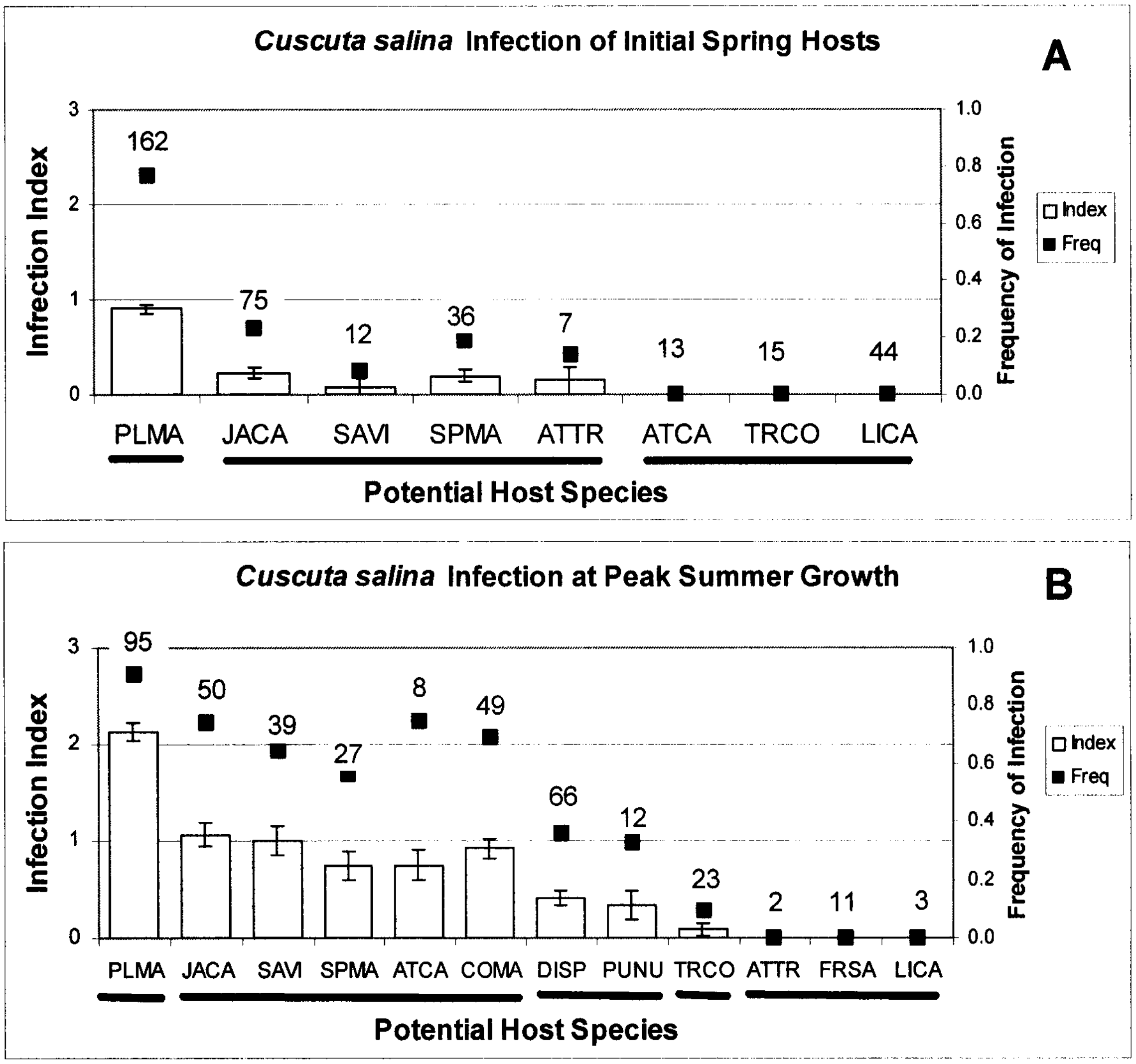


Figure 1.4. Relative levels of infection by *Cuscuta* of different host plants in April (A) following *Cuscuta* emergence and in July (B) at peak *Cuscuta* infection. Data are means + 1 SE. Infection levels range from 0 (no infection), 2 (moderate), to 3 (heavy infection). (A) Kruskall-Wallis = 162.59, df = 7, p = <0.0001; (B) Kruskall - Wallis = 204.75; df = 11, p = <0.0001. Species connected by a horizontal line do not differ in infection level (rank-sum tests at $p < 0.05$). Frequency of infection is the proportion of potential hosts parasitized of those encountered. Sample sizes are shown above frequency proportions. Species codes include PLMA (*Plantago maritima* var. *juncoides*), JACA (*Jaumea carnosa*), SAVI (*Salicornia virginica*), SPMA (*Spergularia macrotheca*), ATTR (*Atriplex triangularis*), ATCA (*Atriplex californicus*), COMA (*Cordylanthus maritimus* ssp. *palustris*), DISP (*Distichlis spicata*), PUNU (*Puccinellia nutkaensis*), TRCO (*Triglochin concinna*). FRSA (*Frankenia salina*), and LICA (*Limonium californicum*).

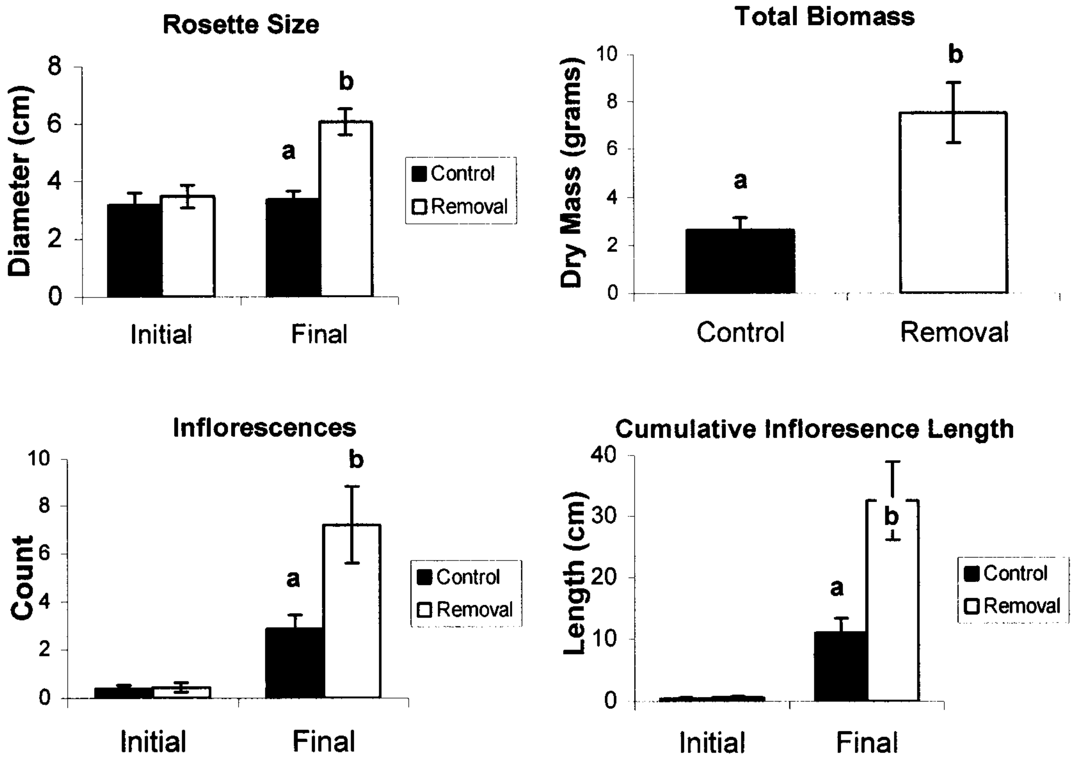


Figure 1.5. The effects of *Cuscuta* on growth and reproductive fitness of *Plantago maritima* var. *juncoides* at the end of a 16 week period in field conditions at Bodega Marine Reserve. Sample size included 30 hosts with *Cuscuta* infection, and 30 with *Cuscuta* removed. Data are means ± 1 SE. Treatments different at $p = 0.001$ based on Bonferroni-adjusted post hoc tests, are marked by different lowercase letters.

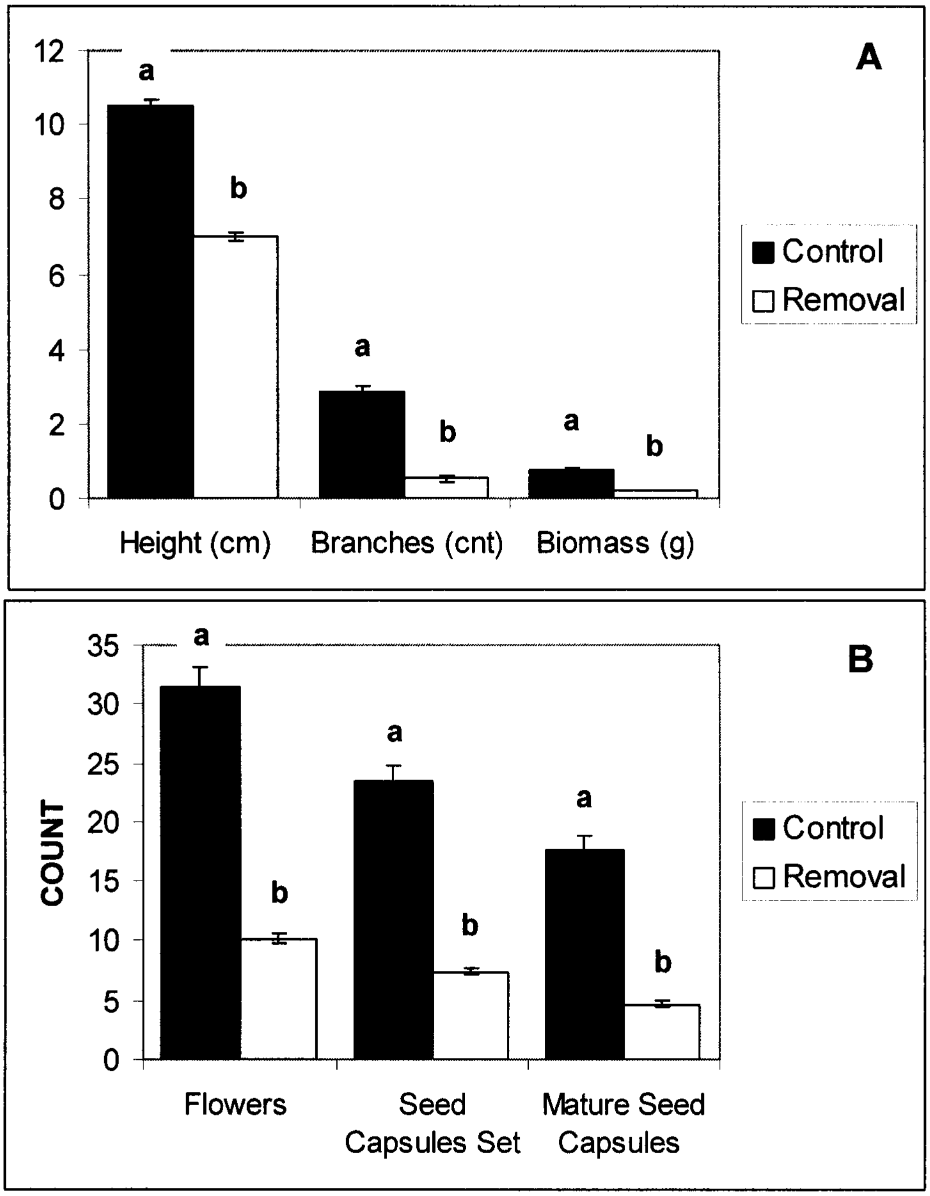


Figure 1.6. Indirect positive effects of *Cuscuta* on growth (A) and reproduction (B) of the rare hemiparasite *Cordylanthus maritimus* ssp. *palustris*. Controls (n = 115) are hemiparasite samples from plots with *Cuscuta*, while removals (n = 147) indicate *Cordylanthus* from plots without *Cuscuta*. Data are means ± 1 SE of pooled measurements over two years. Treatments different at p = 0.001 based on Bonferroni-adjusted post hoc tests, are marked by different lowercase letters.

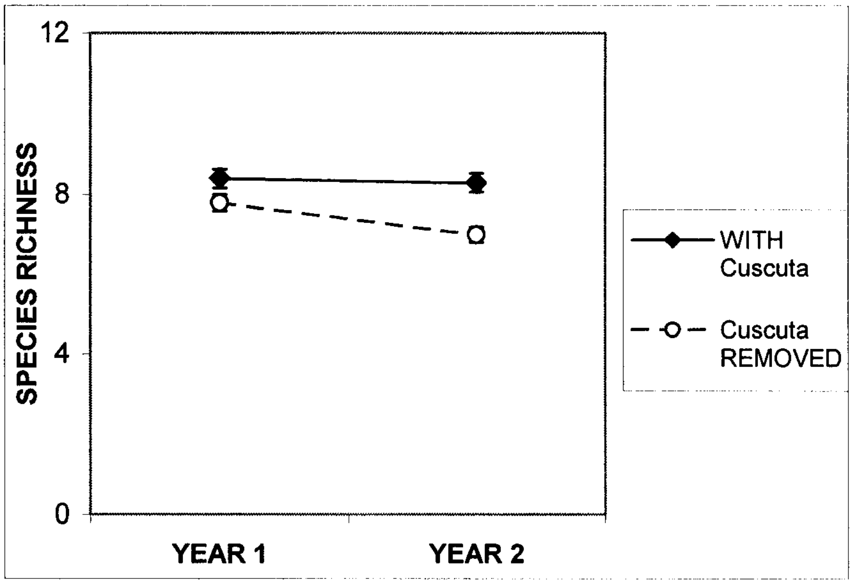


Figure 1.7. Plant community species richness in response to *Cuscuta* removal. Data are means ± 1 SE, with repeated measures ANOVA between subject effects $F_{1,58} = 8.13$, $P \leq 0.006$, and within subject effects $F_{1,58} = 6.86$, $P = 0.011$.

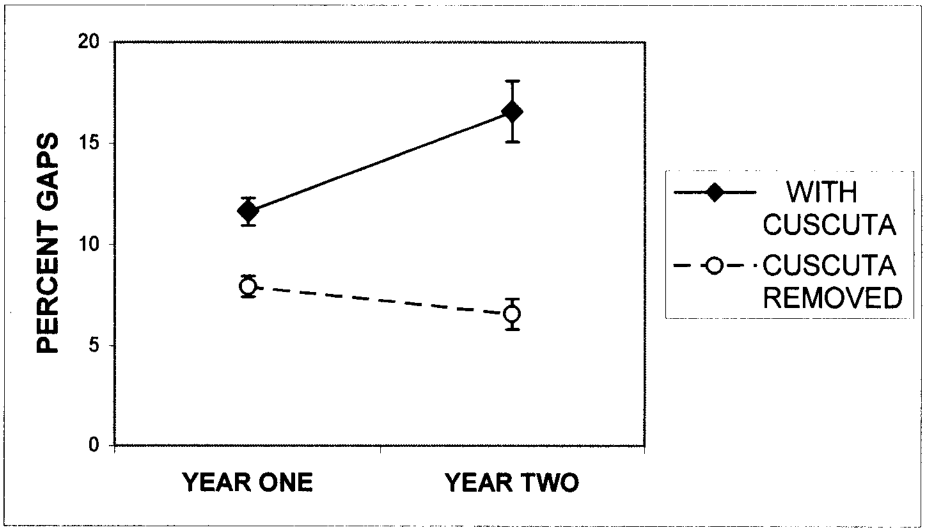


Figure 1.8. Canopy gap dynamics in response to *Cuscuta* removal. Data are means ± 1 SE. Treatment effect sizes are n=30 with *Cuscuta* and n=30 *Cuscuta* removed, with repeated measures between subject effects $F_{1,58} = 33.92$, $P \leq 0.0001$, and within subject effects $F_{1,58} = 17.78$, $P \leq 0.0001$.

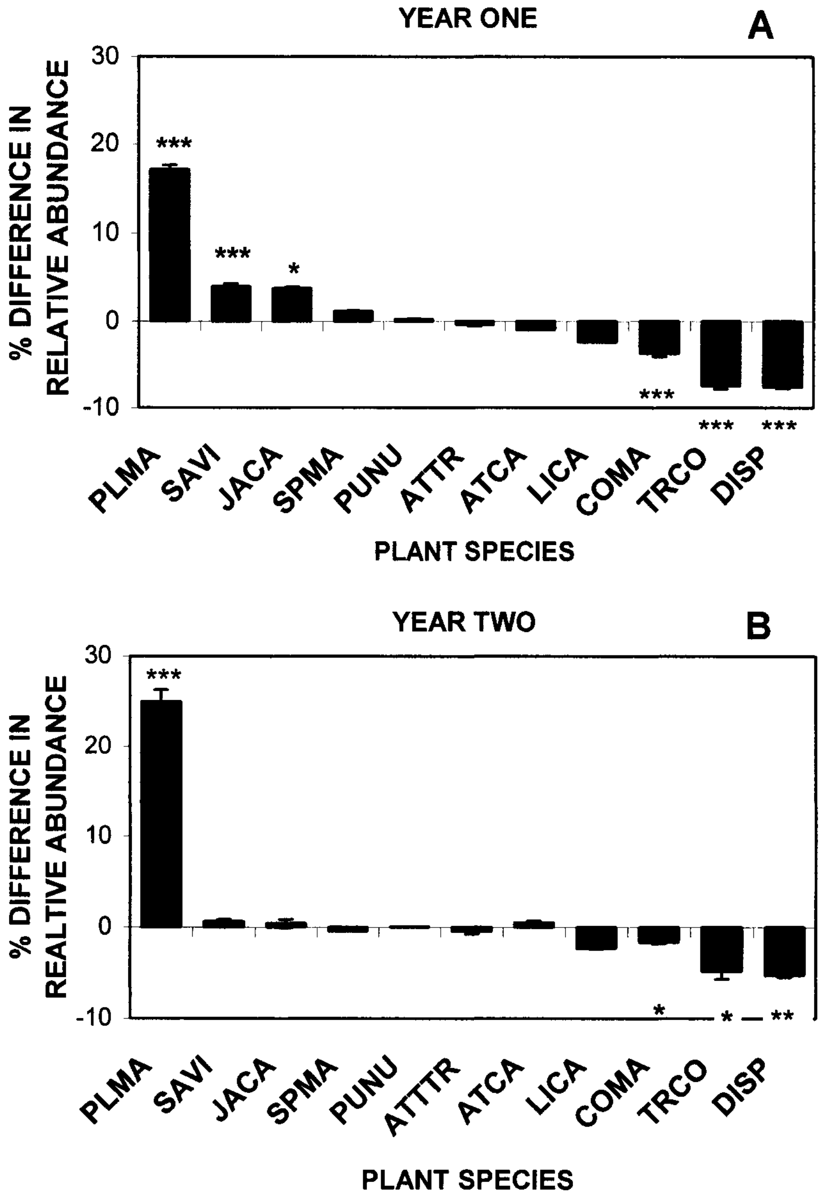


Figure 1.9. Variation in salt marsh plant community structure in response to *Cuscuta* removal. Each bar represents the mean difference (± 1 SE) in relative abundance of plant species resulting from one year (A) and two years (B) of release from *Cuscuta* parasitism. MANOVA results for overall comparisons of relative species abundance (% cover, arcsin square-root transformed) with and without Cuscuta parasitism:N = 30 for each treatment. Wilks' $\lambda = 0.154$; $F_{15,104} = 38.08$; $p \leq 0.0001$). Paired t-tests were used to compare species abundance between controls and parasite removal plots. Asterisks indicate significant variation in species response to *Cuscuta* removal (*** $p < 0.0001$, ** $p < 0.001$, *$p < 0.01$).

CHAPTER 2

HEMIPARASITE-GENERATED ENVIRONMENTAL HETEROGENEITY ENHANCES SPECIES COEXISTENCE IN NORTHERN CALIFORNIA SALT MARSHES

ABSTRACT

Tidal inundation and salinity are considered to be controlling factors in salt marsh species distributions. Parasitic plants may also influence community organization as parasite – host interactions may play a functional role in stress amelioration due to physiological mechanisms for salinity tolerance and resource acquisition. Parasitic angiosperms can be locally abundant, but 56 species are threatened or endangered in the United States due to habitat loss. Endangered root hemiparasites (*Cordylanthus maritimus* ssp. *palustris*; *Cordylanthus mollis* ssp. *mollis*) occupy unique habitat within fragmented northern California tidal wetlands. My objective was to examine the effects of root hemiparasites on soil salinity, aeration, and community composition. Experimental bare patches, artificially shaded bare patches, and parasite removal patches across intertidal zones were compared to controls with hemiparasites. Plant community composition, soil salinity, and redox potential were measured as response variables. Results suggest the hemiparasite – host association modifies sediment physico-chemical conditions improving both aeration and salinity, and enhances plant species richness. Greater understanding of biological interactions coupled with abiotic factors may improve rare hemiparasite conservation and restoration success.

INTRODUCTION

The ecological consequences of accelerated losses of biodiversity are of growing concern. Ecologists have long argued that species are not interchangeable (Ehrlich & Ehrlich 1981, Lawton 1994, Vitousek & Hooper 1994). Understanding the underlying processes and mechanisms responsible for community species diversity patterns has challenged ecologists for decades, but the urgency for this understanding has increased with human population pressure on sensitive ecosystems. Substantial evidence that some plants are a powerful community organizing force makes the potential loss of species a serious concern (Grime 1997, Hooper & Vitousek 1997). There is also growing evidence of a relationship between species diversity and community function that is compromised when community diversity is experimentally reduced (see Schläpfer and Schmid 1999 and Kinzig et al. 2001). Knowing which species are important in maintaining community-level diversity, understanding the breadth of their effects, and how their effects may vary with environmental conditions appear to be vital to conservation management. This understanding is also imperative if we hope to achieve success in ecological restoration and endangered species recovery.

The idea that individual plant species may modify habitat conditions that, in turn, benefit interspecific coexistence has long been considered as an important mechanism of plant community succession (Clements 1916, 1920). Plants respond to and change their environments, and can actively modify factors such as water and nutrient availability. Experimental research in coastal plant communities reveals that individual species can regulate ecosystem functions through habitat modification and facilitation, and the functional role of these species is particularly significant in harsh conditions typical of salt marshes

(Bertness & Callaway 1994, Bertness & Hacker 1994, Bruno 2000). Species that modify the environment in a way that reduces physical stress or disturbance and facilitate less stress tolerant species have been called “ecosystem engineers” due to their potential to influence species abundance and interspecific interactions (Jones et al. 1994,1997, Lawton 1994), yet the physical alteration of habitat by organisms has not been fully considered (Brown 1995, Alper 1998). Recent research illustrates how species functioning as ecosystem engineers that increase habitat complexity or heterogeneity tend to cause species richness to rise, while those that decrease complexity tend to have the reverse effect (Crooks 2002).

A better understanding of environmental and biological factors that determine plant community structure is a major goal of plant ecologists. Tidal inundation and salinity are considered to be controlling factors in salt marsh species distributions and physico-chemical factors can affect the outcome of biological interactions (Pennings & Callaway 1992, Callaway & Pennings 2000). Halophytes may passively ameliorate soil salinity through canopy shading that reduces evaporative salt accumulation. Plants can also actively create acceptable environments for neighboring plants that may be unable to adjust to harsh physical conditions on their own. Aerenchyma tissue is a wetland plant anatomical adaptation to flooding that enables some species to maintain oxygen concentrations in root tissue. Release of oxygen from aerenchyma into the substrate may improve rhizosphere oxygen limitation and provide a more hospitable environment for neighboring plants (Hacker & Bertness 1995). Salt marsh plants can also influence soil chemistry through salinity tolerance mechanisms as they actively reduce soil salinity through uptake of inorganic salts in soil solution, active secretion through salt glands, and salt dilution by the development of succulence or synthesis of organic compounds (Queen 1974, Adam 1993). Active plant response to environmental stress conditions is energy consumptive, and may limit the growth or exclude poorly adapted species from the salt marsh.

Parasite – host interactions are considered to play a major role in community structure and the generation of biological diversity (Dobson and Crawley 1994, Thompson 1999). Native parasitic plants are particularly conspicuous, and ecologically important members of coastal salt marsh communities. Research in southern California suggests the holoparasitic vine *Cuscuta salina* (dodder) can exert keystone effects on community structure because depression of *Salicornia* host growth enhances community diversity and alters salt marsh ecotones (Pennings and Callaway 1996, Callaway and Pennings 1998). Hemiparasites may have equally important functions, but their effects are poorly understood. Studies that have examined the community level effects of hemiparasites have been few, and limited to grassland communities (ter Borg and Bastiaans 1973, Gibson and Watkinson 1992, Matthies 1996, Davies et. al 1997, Marvier 1998, and Joshi et al. 2000). Results provide evidence that parasitic plants may fundamentally alter ecosystem processes and typically enhance community diversity through their impact on competitive interactions. The ability of hemiparasites to create spatial heterogeneity through physical stress modification and resultant community level effects has not been explored.

In this paper, I investigate the potential habitat-modifying role of two congeneric parasitic plant species endemic to northern California and Oregon salt marshes. I begin with a general introduction to plant parasitism, and the conservation status of rare parasitic plants. I review the adaptation and response of plants to the salt marsh environment, and a potential mechanism for parasitic plants as a community organizing force. Next I present results from a removal experiment to examine the effects of root hemiparasites on soil salinity, aeration, and plant community structure. I conclude with a discussion of conservation and restoration implications.

Parasitic angiosperms are important members of plant communities with approximately 4,000 species worldwide. Parasitic angiosperms form physiological links with host plants and depend on them for water, carbon, and nutrients. They are functionally classified by their point of attachment to hosts (root or shoot), depending on whether the vascular connection is below or above ground. They are further classified as either hemi- or holoparasites, depending on the presence or absence of chlorophyll, respectively. Holoparasites are considered to be heterotrophic, while hemiparasites are capable of fixing a portion of their carbon through photosynthesis (Press 1995). Plant parasites can be locally abundant in nutrient poor habitats, but 56 species from 6 plant families are threatened or endangered in the United States due to habitat degradation or human exploitation (Press et al. 1999, Marvier & Smith 1997). Within California, 30% of the 165 native species and subspecies of parasitic plants are of conservation concern (CNPS 2001).

Endangered root hemiparasites from the *Cordylanthus* genus occupy unique habitat within fragmented Pacific Coast tidal marshes, and two species are known from northern California and Oregon. *Cordylanthus maritimus* ssp. *palustris* (Pt. Reyes bird's-beak) occurs along the Pacific Coast from northern Oregon to the San Francisco Estuary, California though several populations within this historic range are extirpated (Chuang & Heckard 1973, CNPS 2001). *Cordylanthus mollis* ssp. *mollis* (soft bird's beak), a San Francisco Estuary endemic known only to Suisun and North Bay tidal wetlands, has also suffered range reductions due to habitat loss (CNPS 2001). Salt marsh *Cordylanthus* species can be facultative hemiparasites in greenhouse conditions, but host plants are necessary for survival in the field (Chuang & Heckard 1971). These rare hemiparasites occur in a patchy distribution within high tidal marsh, and are consistently members of diverse plant assemblages relative to those found in other salt marsh elevation zones (Grewell et al. 2003, Kelly and Fletcher 1994).

Hemiparasite – host plant interactions may play a functional role in habitat amelioration due to physiological mechanisms for salinity tolerance and resource acquisition. Hemiparasites must achieve a low water potential to extract subsidies of water and carbon compounds from hosts. Consequently, hemiparasites maintain high transpiration rates, keeping stomata open even through the night to maximize water loss for a continuous supply of host resources (Press 1989). This process may result in greater host uptake of water and salts from the rhizosphere. *Cordylanthus* hemiparasites expel excess sodium through salt excretion glands, and on hot summer afternoons salt crystals are visible on floral bracts. These physiological aspects of parasite – host water relations provide a potential mechanism for rootzone anoxia and salinity stress amelioration.

I present results of a three year removal experiment designed to test the hypothesis that hemiparasitic plants can ameliorate salt marsh physical stress conditions, and that these effects can lead to changes in plant community structure. Specifically, the objectives of the study were: (1) to examine salt marsh vegetation and abiotic stress gradients, (2) to test the role of hemiparasites as salt marsh habitat modifiers, and (3) to evaluate plant community response to interplant parasitism. Because species functions may be context dependent at the community level and may change in different parts of the environmental ranges where they occur (Power et al. 1996, Pennings et al. 2003), I examined the effects of two rare but locally abundant root hemiparasites on soil salinity and aeration (redox potential)at extreme ends of regional environmental gradients to test the relative role of parasitic plants as habitat modifiers.

METHODS

Study areas

To compare parasite and salt marsh plant influence on intertidal stress gradients, parallel experiments were conducted at two estuary sites chosen to represent extremes in climate, tidal range, and aqueous salinity present in northern California tidal wetlands (Fig. 2.1). The first site, at Tom's Point Preserve, a private nature preserve near the seaward end of the Tomales Bay Estuary (TBE) is 0.5 km from the Pacific Ocean in Marin County (38° 13'N 122° 57'W) and 80 km north of San Francisco, California USA. The tidal wetland is typical of high tidal elevation back-barrier salt marshes of the northern California and Oregon coasts. The second site was the Hill Slough Wildlife Area tidal wetland in the Suisun Marsh reach of the San Francisco Estuary (SFE), 70 km upstream of the Golden Gate tidal inlet in Solano County (38° 13'N 121° 59'W). The Hill Slough tidal wetlands grade to the low elevation Potrero Hills flanking Suisun Marsh, and are subject to typical estuarine hydrology within the upper reach of a large drowned river valley estuary (Conomos et al. 1985).

Both sites experience a Mediterranean-type climate, with most rain falling from November through April (Fig 2.2). Hot, dry summers prevail at the upper SFE site, while coastal fog moderates air temperature and humidity at TBE (Fig. 2.2 and see Corbin and D'Antonio 2004). During the summer growing season, there is a steep environmental gradient between the coastal and inland estuary sites. Salinity of flood tides in the back-barrier salt marsh at TBE equals or slightly exceeds that of seawater (approximately 35 ppt or 52 mS cm^{-1}) during summer, maximum tidal range is 2 meters, average maximum daily temperature (July – September) is 17.5°C with 90% relative humidity and prevalent fog. By contrast, salinity of summer flood tides at the upper SFE site is about 20% of seawater, maximum tidal range is 1.2 meters, average maximum daily temperature (July – September) is 30.9°C with 60% relative humidity, and summer fog is rare. Both sites experience mixed semi-diurnal tidal flooding cycles. Substrate salinity increases with elevation and elevational variation in physical conditions corresponds to a distinct plant species zonation pattern with a unimodal pattern of species diversity (Figs. 2.3 – 2.4). Plant community composition varies between sites, but in both locations the highest number of species are observed in the high intertidal zone that supports parasitic plants.

Experimental design

To study the effect of salt marsh vegetation on intertidal stress gradients within and between marshes, five experimental blocks were randomly dispersed in each of three distinct intertidal vegetation zones at low, medium, and high elevations within the marsh. Each block included three experimental treatments established in June 1999. To examine the active role of plant growth and physiological processes on intertidal stress gradients, 1-m^2 control plots with the natural plant community intact were identified. Experimental bare patches (1-m^2) were established to examine intertidal stress gradients independent of vegetation. Following Bertness 1991, Shumway and Bertness 1994, and Pennings et al. 2003, bare patches were generated by severing rhizome connections to a depth of 25 cm between each patch area and the surrounding vegetation. Plots were treated with a short-lived systemic aquatic herbicide (glyphosate, Monsanto, St. Louis, Missouri USA) to kill above and below-ground vegetation. Standing dead material was removed by manual trimming, and plots were subsequently maintained free of vegetation by trimming back invading plants as needed through the growing season.

Because marsh plants may reduce physical stress by passively shading the soil and preventing or reducing the evaporative accumulation of salts and the amelioration of rhizosphere hypoxia, shade treatments were installed over half (0.5 X 1 m) of each bare patch within experimental blocks. Shade frames were constructed of PVC pipe, fitted with water-permeable shade cloth, and installed at the height of surrounding vegetation canopy in each elevation zone. Photosynthetically active radiation (PAR) was measured 5 centimeters above the soil surface under the natural plant canopy and 5 cm above the canopy at 10 random sites in each zone within 90 minutes of solar noon with a Decagon SF-80 sunfleck ceptometer. Calculations from these measurements were used to determine the level of shade reduction required to mimic passive shading of the natural plant community adjacent to experimental plots. Low intertidal shade treatments (90% incident PAR) and mid-intertidal shade treatments (70% incident PAR) were installed at both sites. The lower- high elevation zone shade treatments were 70% incident PAR at SFE, while the more open high intertidal community at TBE received a 45% incident PAR shade treatment.

Cordylanthus hemiparasites were restricted to the high intertidal zone at both sites. To explicitly test the hypothesis that parasitic plant – host interactions ameliorate salinity and hypoxia stress conditions in the rhizosphere to a greater degree than we would expect from active plant processes in un-infected communities, a 1 m^2 hemiparasite removal treatment was added to all blocks within the high zone to examine the influence of the parasitic plants on salinity and hypoxia stress. The parasitic vine *Cuscuta salina* was rare at TBE and did not emerge in experimental plots. However, *Cuscuta* emerged in some plots at SFE. Because *Cuscuta* effects could potentially confound the effects of the hemiparasites, the parasitic vine was removed to maintain treatments.

Beginning in July 1999, pore water salinity (soil saturation extract) and sediment redox potential were measured bimonthly in weeks following the highest tides to increase the probability of detecting zonal differences in salt accumulation. Soils in some plots were too dry to extract interstitial water in the field, and soil texture varies considerably over the intertidal gradient (B. Grewell, unpublished data). Therefore, three soil cores were randomly sampled (5 cm depth) and combined for a composite from each plot and standard soil saturation pastes were prepared and vacuum-extracted through a Büchner funnel (Rhoades 1982). Saturation extract salinity was determined with a YSI Model 30 Conductivity-Salinity-Temperature Meter (YSI Inc. Yellow Springs, Ohio USA). Saturated soil paste extracts underestimate field soil salinity concentrations, except when field soils are wet, but control for the different moisture retention capacities of soils with different textures (Richards 1954). Substrate redox potential was measured in situ at a depth of 5 cm with a sealed platinum OPR electrode (filled with KCl solution saturated with Ag/AgCl reference solution) connected to an Oakton 300 series portable waterproof pH/mV meter (Oakton Instruments, Vernon Hills, Illinois USA). Accuracy of redox electrodes was verified before each use with Hanna HI7020 potassium hydrogen phthalate - quinhydrone redox solution (Hanna Instruments Inc., Ann Arbor, Michigan USA).

Log-transformed data from salinity and redox measurements were analyzed with repeated measures analysis of variance (ANOVA) tests using the general linear modeling procedure (GLM) in Systat 9.0 (SPSS, Inc). When time was not significant, data were pooled for ANOVA, and post hoc treatment comparisons were made with Bonferroni adjusted probabilities.

At peak summer growth, I evaluated the plant community composition of 1-m^2 control and parasite removal plots for three years. The number and identity of plant species present were recorded. Grids with 100 subdivisions were placed over plots and percent cover by plant species was determined by the point intercept method. In the high intertidal zone, parasite removal and control plots were maintained for three years to evaluate plant community response to parasite removal over time. To test for community level effects of interplant parasitism, I compared the number of plant species in parasite removal vs. control plots. I used repeated measures ANOVA with treatment (control or removal) as the main effect to examine the effect of parasite removal on species richness. To test for the effects of parasitism on the relative abundance of individual plant community associates, I used repeated measures ANOVA with treatment (control vs. removal) as the main effect for each species with a sufficient number of detections for the statistical test.

RESULTS

Plant community pattern varied with intertidal zone; the greatest plant species richness was in the high intertidal zone at both inland and outer coastal sites (Figs. 2.3-2.4). Distinctive changes in physical stress were observed across the elevation gradient of the regularly flooded tidal marshes (Fig. 2.5). Stress gradients were steepest in bare and shaded treatments void of vegetation where sediment salinity and redox potential increased with intertidal elevation. Natural plant cover reduced soil salinity at both sites. Sediments were most reduced in the low zone where depth and duration of tidal flooding is greatest, but the presence of a plant community increased root zone redox potential. The degree of abiotic stress varied between sites at a regional scale (Fig. 2.5). At TBE, pore water salinity and hypoxia stress were much greater than conditions measured at SFE.

Experimental removal plots revealed the effect of parasitic plants on high marsh abiotic stress gradients (Fig. 2.6). There was a significant difference in pore water salinity among experimental treatments in the high zone at SFE ($F_{3,76} = 9.22$, $p \leq 0.0001$). Salinity was highest in bare plots, and passive shading did not ameliorate this effect. Salinity was lowest in plots with natural plant cover, and the presence of hemiparasites resulted in further reductions of pore water salinity. At TBE, pore water salinity also varied among high zone treatments ($F_{3,56} = 40.229$, $p \leq 0.0001$), and mean pore water salinity was 41% lower in control plots with hemiparasites compared to removal plots. The presence or absence of parasitic plants did not result in a detectable difference in sediment redox conditions in the high zone at Suisun where the root zone was oxidized in weeks following the highest tides ($F_{3,76} = 0.77$, $p = 0.516$). A different response was observed at TBE near the ocean entrance to Tomales Bay, where reducing conditions prevailed across the entire intertidal gradient. Redox potential in the iron reducing range was recorded in high marsh (Fig. 2.6), and redox conditions improved in the presence of parasitic plants ($F_{3,56} = 10.64$, $p \leq 0.0001$).

Plant species richness in the salt marsh is enhanced when hemiparasites interact with host plants in the community (Fig. 2.7). Species richness decreased in the absence of parasitic plants (F = 61.54, p = <0.0001) and the effect was consistent over three years in the SFE. At TBE, species richness also declined with parasitic plant removal (F=28.474, p = 0.001), and the observed effect was consistent over three years of repeated measures. The relative abundance of hemiparasites in control plots did not vary among years at the SFE site (Fig. 2.8, GLM - ANOVA_{rm}, $F_{2,12} = 0.418$, p = 0.67). The *Cordylanthus* parasite was a common member of the community at this inland site where its relative abundance (23% mean cover ± 3% SE) was exceeded only by *Salicornia* and *Distichlis*. At TBE, hemiparasites were also conspicuous high marsh community members (17% mean cover ± 1.5% SE), but there was some variation in relative abundance as hemiparasite cover declined slightly over the three year study (Fig. 2.8, GLM - ANOVA_{rm}, $F_{2,12} = 3.82$, p = 0.05).

The effect of parasitic plants on individual host community species varied within and between marshes (Table 1, Figs. 2.9-2.10). The *Cordylanthus* parasite was a common member of the high intertidal zone community at the SFE site where its abundance was exceeded only by *Salicornia* and *Distichlis*. The effect of *Cordylanthus* on *Salicornia virginica* was strongly negative at SFE, and relative abundance of this host (confirmed through examination of haustoria, personal observation) increased by 30% with hemiparasite removal. The spread of *Salicornia* following parasite release displaced other members of the community by the third year. The overall effect of parasite removal on *Distichlis* was positive (Table 1), but in the third year a sharp decline was recorded as *Salicornia* became more dominant in uninfected plots. Rare members of the SFE high marsh community whose abundance improved with *Cordylanthus* parasite presence included *Atriplex triangularis* and *Triglochin maritima* (Table 1, Fig. 2.9). While sample size may not have been sufficient to statistically detect an effect on other rare species, data trends suggest *Aster subulatus* and *Frankenia salina* may also increase in abundance in the presence of the hemiparasites (Fig. 2.9).

Although hemiparasites were less abundant on the outer coast at TBE, their effects on the relative abundance of community members were strong. When hemiparasites were removed from the community, *Salicornia virginica* and *Jaumea carnosa* quickly became more dominant and their absolute cover increased by an average of 17.3% and 21.1% respectively by the third year (Table 1, Fig. 2.10). *Cordylanthus* establishes haustorial connections with both of these host species (B. Grewell, unpublished data). A neutral effect on *Distichlis* was observed, as the abundance of this dominant community member did not respond to parasite removal. The hemiparasite effect was strongly facilitative for several rare community members at TBE. *Frankenia salina*, *Scirpus cernuus*, *Spergularia macrotheca*, and *Triglochin concinna* are all less common species in the community that decreased in abundance when hemiparasites were removed (Table 1, Fig. 2.10). *Triglochin concinna was* driven to extinction by the third year of experimental removal, adding to evidence that this species is strongly facilitated by the indirect effects of parasitism (see Chapter 1, this thesis). Limitations on experimental replication at these sensitive sites may have precluded my ability to statistically detect effects on all rare species. Abundance data and field observations suggest *Limonium californicum* and other rare species may also benefit from hemiparasites.

In summary, hemiparasites reduce the abundance of competitive dominants and increase the abundance of less common species resulting in an overall increase in plant species diversity (Figs. 2.6 and 2.9 – 2.10). The positive community-level effect of the hemiparasite is most pronounced at the site with the highest salinity and hypoxia stress conditions (TBE) where a greater number of rare plant species are facilitated (Fig. 2.10).

DISCUSSION

In a field removal experiment, I have demonstrated that hemiparasite – halophyte host associations can enhance the amelioration of physical stress conditions in the salt marsh that exceed the passive role of shading by vegetation. The stress-ameliorating effect of the hemiparasites is associated with increased plant species richness in the community, and the effect is most pronounced with elevated salinity and hypoxia stress.

Hemiparasite influence on stress gradients

Distinctive salt marsh plant zonation reflects physical stress gradients associated with depth and duration of tidal flooding, but in recent years there has been an increasing awareness that these patterns are modified by interactions among species (reviewed in Unger 1998). Studies suggest that competitive subordinate species with physiological tolerance are displaced to the most physically stressful habitats, and the importance of facilitation increases with environmental stress (Bertness & Callaway 1994, Bertness & Hacker 1994, Brewer et al. 1997). The results of this experiment add support to the idea that abiotic stress may limit species richness at lower elevations of the marsh, the presence of vegetation ameliorates this physical stress, and positive interactions among species are prevalent in stressful conditions. Results also complement other studies that have demonstrated that facilitation and interference may operate simultaneously, and that the overall effect of one species on another may vary with environmental conditions (see Greenlee and Callaway 1996).

The presence of parasitic plants ameliorated abiotic stress in north coast salt marshes, resulting in an increase in species richness. This is not the first evidence of species richness enhancement following stress amelioration involving a consumer. Grazing by snow geese produced bare areas with elevated soil salinity and lower soil moisture than vegetation areas of subarctic salt marshes. Excluding herbivorous geese caused an increase in species richness due to reduction in abiotic stress (Bazeley & Jefferies 1986). In this study, the opposite effect was observed as indirect effects of hemiparasite consumers resulted in an increase in plant species diversity. Parasite – host interactions open gaps in the community due to dominant host suppression, but the physical stress ameliorating actions of the hemiparasites may facilitate colonization by rare species. Previous research has demonstrated that consumer effects on community diversity are greater with more benign environmental conditions (Menge and Sutherland 1987). My results may be the first to demonstrate an indirect positive consumer effect on community diversity along an environmental stress gradient. Parasitic interactions appear to ameliorate root zone salinity stress at landscape scales, but amelioration of hypoxia appears to be context dependent and not as influential at sites with reduced tidal range, and at upper estuary sites where evaporative demand is high due to reduced coastal climate effects. The hemiparasites may have played a larger role as habitat modifiers in Suisun under historic tidal regimes prior to extensive diking of wetlands and water diversions.

Hemiparasite influence on ecosystem processes

Root hemiparasites represent a distinct plant functional group, and they appear to influence both host plant community diversity and nutrient cycling (Press 1998). The magnitude of species influence on ecosystem processes is thought to vary among taxa and functional groups (Symenstad et al. 1998, Symstad 2000). It is also recognized that the contributions made by influential species to overall ecosystem function can be conditioned by variation in ecological performance across natural gradients (Wellnitz and Poff 2001). In this study, congeneric hemiparasites perform as a functional group and species richness was enhanced across the regional climatic and estuarine gradient when hemiparasites were present. In southern California, correlative studies suggest that *Cuscuta salina*, a holoparasite, indirectly facilitates *Limonium californicum* and *Frankenia salina* by suppressing otherwise dominant *Salicornia virginica* (Pennings & Callaway 1996). In northern California, under very different environmental conditions, these salt marsh plants and other rare members of the community also indirectly benefited from suppression of dominant hosts, the effect may be enhanced by the habitat modifying ability of the parasites. The contribution of a species to ecosystem processes can outweigh species abundance (Power et al. 1996) and relative abundance measures may not represent full effects. Thus, the use of relative abundance measures to assess community response in this experiment should be regarded as a conservative estimate. Species density measurements are not practical in this community, as fragile hemiparasite – host root connections can be dislodged with the disturbance of the canopy required for accurate counts (personal observation). Biomass measurements preclude the evaluation of long-term effects in permanent plots, and destructive sampling must be limited in endangered species habitats. The contracted spatial and temporal scale of removal experiments may also limit our understanding of the long term effects of species loss, but the detection of an effect under these constraints provides evidence for concern about the extinction of the species (Schoener and Spiller 2003). Despite these limitations, this experiment has yielded significant information that improves our understanding of processes underlying salt marsh community structure. This study presents evidence that while parasitic plants may convey direct negative effects on their hosts, they are also linked to positive community level effects. These results also provide support for the functional significance of species interdependence.

Evolutionary implications

Important evolutionary consequences of active niche construction by organisms have been largely neglected in evolutionary biology (Odling-Smee et al. 2003). The modification of environmental conditions by hemiparasites has the potential to modify natural selection pressures in the local environment. This paper provides evidence that hemiparasites modify the physical environment of their host community, and by doing so facilitate species coexistence. The amelioration of rhizosphere stress also has the potential to accelerate nutrient cycling. Subarctic hemiparasites exploit host nutrients that are otherwise locked up on longer time scales by their perennial hosts, concentrate nutrients in their tissue, and produce high quality litter which can accelerate nutrient turnover and regeneration within the community (Press 1998, Quested et al. 2002,2003). If salt marsh hemiparasites modify their environment and also influence nutrient cycling, and if these processes operate over evolutionarily significant time scales, the parasitic plants may be an important agent of natural selection within their host community.

Conservation and restoration implications

My results suggest that recovery of endangered parasitic plant populations may contribute to the conservation of biological diversity. The loss of an endangered parasitic plant has the potential to reduce habitat heterogeneity and change the distribution and abundance of other species in the salt marsh. The restoration of ecosystem processes is integral to preserving functional natural communities. Reintroduction of rare hemiparsites within their historic range may enhance ecological functions in tidal wetland restoration efforts. Endangered parasitic plants present unique conservation challenges that require careful consideration of appropriate host communities (Zedler 1996, Marvier & Smith 1997). If a suitable host community is in place, the ability of hemiparasites to generate spatial heterogeneity by ameliorating physical stress throughout their patchy distribution within the high intertidal zone could be of practical use in the restoration of species-rich wetlands.

ACKNOWLEDGMENTS

I thank Eliška Rejmánková, Ted Grosholz, and Kevin Rice for useful comments on an earlier version of this paper. I thank John Kelly and Audubon Canyon Ranch for access to Tom's Point Preserve, and the California Dept. of Fish and Game for rare plant research permits and access to the Hill Slough Wildlife Area. I thank Mark Bertness for suggestions on the experimental design, and for research contributions from his lab that inspired this work. I am grateful to Steve Kidner and Michele Lege for help in the field. This research was supported by the William and Patricia Switzer Foundation, University of California Jastro-Shields Graduate Research Awards, and a Society of Wetland Scientists Research Award.

LITERATURE CITED

Adam, P.A. 1993. Salt marsh ecology. Cambridge University Press, New York.

Alper, J. 1998. Ecosystem engineers shape habitats for other species. Science 280:1195-1196.

Bazeley, D.R. & R. L. Jefferies. 1986. Changes in the composition and standing crop of salt-marsh plant communities in response to the removal of a grazer. J.Ecol.74:693-706.

Bertness, M.D. 1991. Interspecific interactions among high marsh perennials in a New England salt marsh. Ecology 72:125-137.

Bertness, M.D. and R.M. Callaway. 1994. Positive interactions in communities. TREE 9:191-193.

Bertness, M.D. and S.D. Hacker. 1994. Physical stress and positive associations among marsh plants. American Naturalist 144:363-372.

Brewer, J.S., J.M. Levine, & M.D. Bertness. 1997. Effects of biomass removal and elevation on species richness in a New England salt marsh. Oikos 80: 333-341.

Brown, J.H. 1995. Organisms as engineers: a useful framework for studying effects on ecosystems? TREE 10:51-52.

Bruno, J.F. 2000. Facilitation of cobble beach plant communities through habitat modification by *Spartina alterniflora*. Ecology 81(5):1179-1192.

Callaway, R.M. & S.C. Pennings. 1998. Impact of a parasitic plant on the zonation of two salt marsh perennials. Oecologia 114:100-105.

Callaway, R.M. and S.C. Pennings. 2000. Facilitation may buffer competitive effects; indirect and diffuse interactions among salt marsh plants. American Naturalist 156:416-424.

Chuang, T. I., and L. R. Heckard. 1971. Observations of root-parasitism in *Cordylanthus* (Scrophulariaceae). American Journal of Botany 58: 218-228.

Chuang, T. I., and L. R. Heckard. 1973. Taxonomy of *Cordylanthus* subgenus Hemistegia (Scrophulariaceae) Brittonia 25: 135-158.

Clements, F.E. 1916. Plant Succession: an analysis of the development of vegetation. Carnegie Institution of Washington Publication 242.

Clements, F.E. 1920. Plant indicators: the relation of plant communities to process and practice. Carnegie Institution of Washington Publication 290.

CNPS. 2001. Tibor, D. P. (Convening Editor). California Native Plant Society's inventory of rare and endangered plants of California. 6th Edition. CNPS, Sacramento, California.

Conomos, T.J., R.E. Smith, and J.W. Garner. 1985. Environmental setting of the San Francisco Bay. Hydrobiologia 129:1-12.

Corbin, J.D. and C.M. D'Antonio. 2004. Competition between native perennial and exotic annual grasses: implications for an historical invasion. Ecology 85:1273-1283.

Crooks, J.A. 2002. Characterizing the ecosystem-level consequences of biological invasions: the role of ecosystem engineers. Oikos 97:153-166.

Davies, D.M., J.D. Graves, C.O. Elias, and P.J. Williams. 1997. The impact of *Rhinanthus* ssp. on sward productivity and composition: implications for the restoration of species-rich grasslands. Biol. Conservation 78:87-93.

Dobson, A. and M. Crawley. 1994. Pathogens and the structure of plant communities. TREE 9:393-398.

Ehrlich, P.R. & A.H. Ehrlich 1981. Extinction: the causes and consequences of the disappearance of species. Random House. New York, New York. USA.

Gibson, C.C. and A.R. Watkinson. 1989. The host range and selectivity of a parasitic plant: *Rhinanthus minor* L. Oecologia 78: 401-406.

Greenlee, J.T. and R.M. Callaway. 1996. Abiotic stress and the relative importance of interference and facilitation in montane bunchgrass communities in western Montana. Am. Naturalist 148:386-396.

Grewell. B.J., M.A. DaPrato, P.R. Hyde, & E. Rejmankova. 2003. Experimental reintroduction of endangered soft bird's beak to restored habitat in Suisun Marsh. Final report submitted to CALFED Ecosystem Restoration Project 99-N05.

Grime, J.P. 1997. Biodiversity and ecosystem function: the debate deepens. Science227:1260-1261.

Hooper, DU. and P.M. Vitousek 1997. The effects of plant composition and diversity on ecosystem processes. Science 277:1302-1305.

Hacker, S.D. and M.D. Bertness. 1995. Morphological and physiological consequences of a positive plant interaction. Ecology 76:2165-2175.

Jones, C.G., J.H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. Oikos 69:373-386.

Jones, C.G., J.H. Lawton, and M. Shachak. 1997. Positive and negative effects f organisms as physical ecosystem engineers. Ecology 78:1946-1957.

Joshi, J., D. Matthies, and B. Schmid. 2000. Root hemiparasites and plant diversity in experimental grassland communities. J. Ecology 88:634-644.

Kelly, J. P. and G. Fletcher. 1994. Habitat correlates and distribution of *Cordylanthus maritimus* (Scrophulariaceae) on Tomales Bay, California. Madrono 41:316-327.

Kinzig, A.P., S.W. Pacala, and D. Tilman. 2001. The Functional Consequences of Biodiversity. Monographs in Population Biology No. 33. Princeton University Press, Princeton, N.J. USA.

Lawton, J.H. 1994. What do species do in ecosystems? Oikos 71:1-8.

Marvier, M.A. 1998. Parasite impacts on host communities: plant parasitism in a California coastal prairie. Ecology 79:2616-2623.

Marvier M.A. and D.L. Smith. 1997. Conservation implications of host use for rare parasitic plants. Conservation Biology 11:839-848.

Matthies, D. 1996. Interactions between the root hemiparasite *Melampyrum arvense* and mixtures of host plants: heterotrophic benefit and parasite mediated competition. Oikos 75:118-194.

Menge, B.A. and J. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. American Naturalist 130:730-757.

Odling-Smee, F.G., K.N. Laland, and M. W. Feldman. 2003. Niche Construction: the Neglected Process in Evolution. Monographs in Population Biology No.37. Princeton University Press, Princeton, N.J. USA.

Power, M.E., Tilman, D., Esters, L.A., Menge, B.A., Bond, W.J., Mills, L.S., Daily, G., Castilla, L.C., Lubchenco, J. and Paine, R.T. 1996. Challenges in the quest for keystones. Bioscience 46:609-620.

Pennings, S.C. and R.M. Callaway. 1992. Salt marsh plant zonation: the relative importance of competition and physical factors. Ecology 73:681-690.

Pennings, S.C. and R.M. Callaway. 1996. Impact of a parasitic plant on the structure and dynamics of salt marsh vegetation. Ecology 77:1410-1419.

Pennings, S.C., E.R. Selig, L.T. Houser, and M.D.Bertness. 2003. Geographic variation in positive and negative interactions among salt marsh plants. Ecology 84:1527-1538.

Press, M.C., J.D. Scholes, and J.R. Watling. 1999. Parasitic plants: physiological and ecological interactions with their hosts. pp. 175-197 in: Press, M.C., Scholes, J.D. and Barker, M.G.(eds.) Physiological Plant Ecology. British Ecological Society. Blackwell Scientific, Oxford, U.K.

Press, M.C. 1998. Dracula or Robin Hood? A functional role for root hemiparasites in nutrient poor ecosystems. Oikos 82:609-611.

Press, M.C. 1995. Carbon and nitrogen relations. pp. 103-124 in: M.C. Press and J.D. Graves (eds.) Parasitic Plants. Chapman & Hall. London, U.K.

Press, M.C. 1989. Autotrophy and heterotrophy in root hemiparasites. Trends in Evolution and Ecology 4:258-263.

Queen, W.H. 1974. Physiology of coastal halophytes. Pp. 345-354 in: Reimold, R.J. and W.H. Queen. Ecology of Halophytes. Academic Press, New York, New York. USA.

Rhoades, J.D. 1982. Soluble salts. Chapter 10 in: Dinauer, R.C. (ed.) Methods of soil analysis, part 2: chemical and microbiological properties. 2nd edition. Am. Soc. of Agronomy & Soil Sci. Soc. of Am. Madison, Wisconsin USA.

Richards, L.A. (ed.). 1954. Diagnosis and improvement of saline and alkali soils. Agricultural Handbook No. 60. USDA, Washington, D.C. U.S.A.

Schläpfer, F. and B. Schmid. 1999. Ecosystem effects of biodiversity – a classification of hypotheses and cross-system exploration of empirical results. Ecological Applications 9:893-912.

Schoener, T. W and D.A. Spiller. 2003. Effects of removing a vertebrate versus an invertebrate predator on a food web, and what is their relative importance? pp. 69 – 84 in: P. Kareiva and S.A. Levin (eds.) The Importance of Species. Princeton University Press, Princeton, N.J. USA.

Shumway, S.W. and M.D. Bertness. 1994. Plant size effects on marsh plant secondary succession mechanisms. Ecology 75:564-568.

Symstad, A.J. 2000. A test of the effects of functional group richness and composition on grassland invasibility. Ecology 81:99-109.

Symstad, A.J., D. Tilman, J. Willson, and J.M.H. Knops. Species loss and ecosystem functioning: effects of species identity and community composition. Oikos 81:389-397.

ter Borg, S.J. and J.C. Bastiaans. 1973. Host parasite relations in *Rhinanthus serotinus* I. The effects of growth conditions and host; a preliminary review. pp. 236-246 in: Symposium on Parasitic Weeds, April 1973, Royal U. of Malta. European Weed Research Council and Malta University Press, Malta.

Thompson, J.N. 1999. The evolution of species interactions. Science 284:2116 - 2118.

Ungar, I.A. 1998. Are biotic factors significant in influencing the distribution of halophytes in saline habitats? Botanical Review 64:176-199.

Vitousek, P. M. & D.U. Hooper 1994. Biological diversity and terrestrial ecosystem biogeochemistry. P. 255-270 in: E.D. Schulze & H.A. Mooney (eds.). Biodiversity and Ecosystem Function. Springer-Verlag, Berlin.

Wellnitz, T. and N. L.Poff. 2001. Functional redundancy in heterogeneous environments: implications for conservation. Ecology Letters 4:177-179.

Zedler, JB. 1996. Ecological function and sustainability in created wetlands. In Restoring Diversity: strategies for reintroduction of endangered plants, eds. DA Falk, CI Millar & M Olwell. Washington, DC: Island Press.

Table 2.1. ANOVA table for the effects of parasitic plant removal on arcsine-transformed relative abundance of host plant community associates. Results are based on repeated measures analysis over three years of experimental removals from permanent plots. When a significant effect was detected, the direction of the response is indicated (positive response =+, negative response = -). Data for species in only a small fraction of plots are excluded.

HILL SLOUGH-SUISUN, SAN FRANCISCO ESTUARY:

	Parasite Removal		
Species	F	P	Direction
Aster subulatus var. ligulatus	2.58	0.147	
Atriplex triangularis	4.88	0.058	-
Distichlis spicata	7.83	0.023	+
Frankenia salina	0.63	0.548	
Limonium californicum	1.12	0.321	
Polypogon monspeliensis	1.482	0.258	
Salicornia virginica	27.79	0.001	+
Triglochin maritima	14.49	0.005	-

TOM'S POINT, TOMALES BAY ESTUARY:

	Parasite Removal		
Species	F	P	Direction
Distichlis spicata	2.19	0.177	
Frankenia salina	11.88	0.009	-
Jaumea carnosa	11.12	0.01	+
Limonium californicum	4.81	0.06	
Salicornia virginica	7.16	0.028	+
Scirpus cernuus	73.15	< 0.0001	-
Spergularia macrotheca	5.97	0.04	-
Triglochin concinna	17.28	0.003	-

Note: for all species, df = 1,8

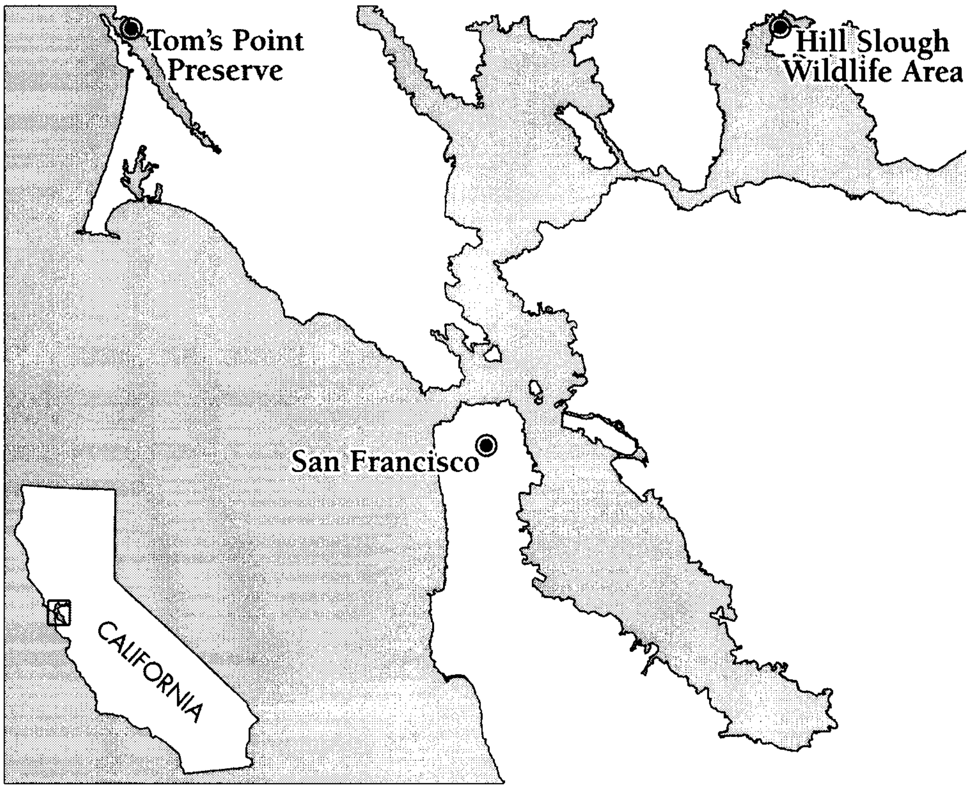


Figure 2.1. Map of the study sites at Tom's Point Preserve, Tomales Bay Estuary (TBE) and Hill Slough Wildlife Area - Suisun Marsh, San Francisco Estuary (SFE). The inset map of the state of California shows the location of Tomales Bay and the San Francisco Estuary.

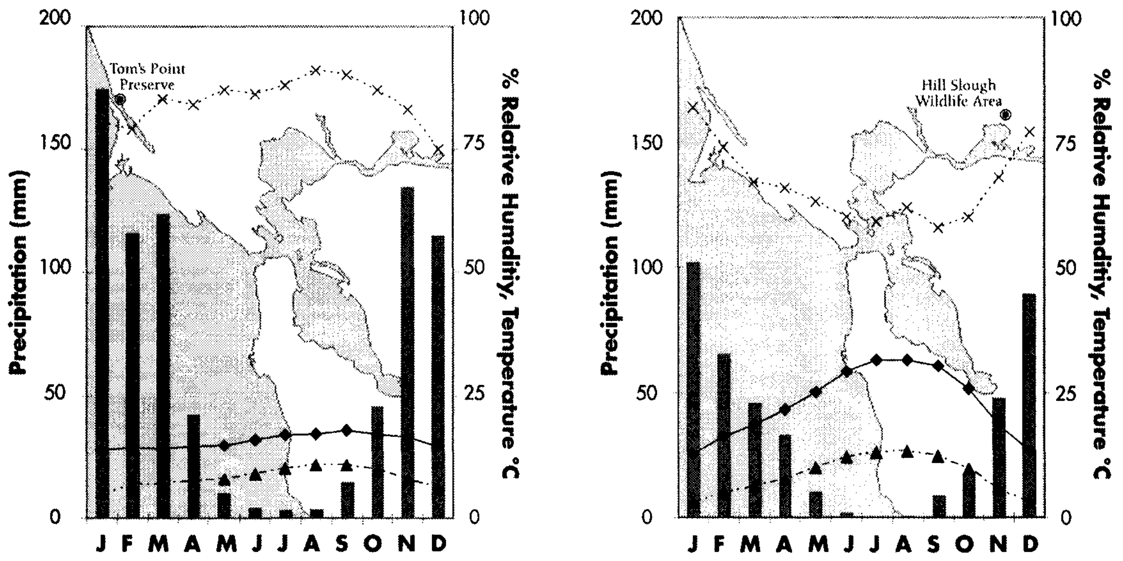
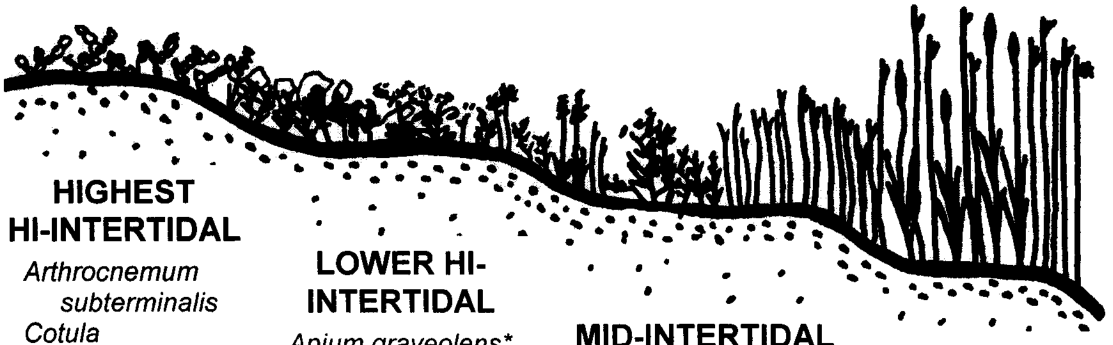


Figure 2.2. Climate diagrams for Tom's Point Preserve, Tomales Bay Estuary (TBE) and Hill Slough Wildlife Area - Suisun Marsh, San Francisco Estuary (SFE) study sites. Climate data for TBE is represented by data from Bodega Marine Laboratory, 20 km north of the study site while SFE data is from Travis Air Force Base, Fairfield 3 km northeast of Hill Slough. Diamond symbols connected by sold lines represent average maximum monthly air temperature, triangle symbols connected by broken lines represent average minimum monthly air temperature, X symbols connected by dashed lines represent mean monthly relative humidity, and bars are mean monthly precipitation.



HIGHEST HI-INTERTIDAL

Arthrocnemum subterminalis
*Cotula cornonipfolia**
Cressa truxillensis
Frankenia salinia
Juncus bufonius
Salicornia virginica

LOWER HI-INTERTIDAL

*Apium graveolens**
Aster subulatus var. ligulatus
Atriplex triangularis
Cordylanthus mollis
Cressa truxillensis
Cuscuta salina
Distichlis spicata
Frankenia salinia
Glaux maritima
*Hainardia cylindrica**
Hutchinsia procumbens
Jaumea carnosa
Juncus bufonius
*Lactuca saligna**
*Lepidium latifolium**
Limonium californicum
*Lotus corniculatus**
Plantago maritima
Plantago subnuda
Pluchea odorata
*Polygonum arenastrum**
*Polypogon monspeliensis**
Puccinellia simplex
Salicornia virginica
Scirpus koilolepis
*Sonchus oleraceous**
Spergularia marina
Trifolium workskijoldii
Triglochin concinna
Triglochin maritima

MID-INTERTIDAL

*Apium graveolens**
Aster lentus
Distichlis spicata
Euthamia occidentalis
Glaux maritima
Grindelia stricta var. angustifolia
Jaumea carnosa
Juncus balticus
*Lepidium latifolium**
Pontentilla anserina var pacifica
Pluchea odorata
Salicornia virginica
Scirpus americanus
Triglochin maritima

LOW INTERTIDAL

Hydrocotyle verticillata
Lathyrus jepsonii
Lilaeopsis masonii
Scirpus acutus
Scirpus californicus
Typha angustifolia
Typha domingensis

Increasing Depth, Duration, & Frequency of Tidal Inundation →

← **Increasing Soil Salinity**

Figure 2.3. Schematic diagram of the salt marsh intertidal gradient at Hill Slough, Suisun Marsh - San Francisco Estuary illustrating differences in plant species occurrence among major vegetation zones and physical conditions considered in this study. Exotic species indicated by * symbol.

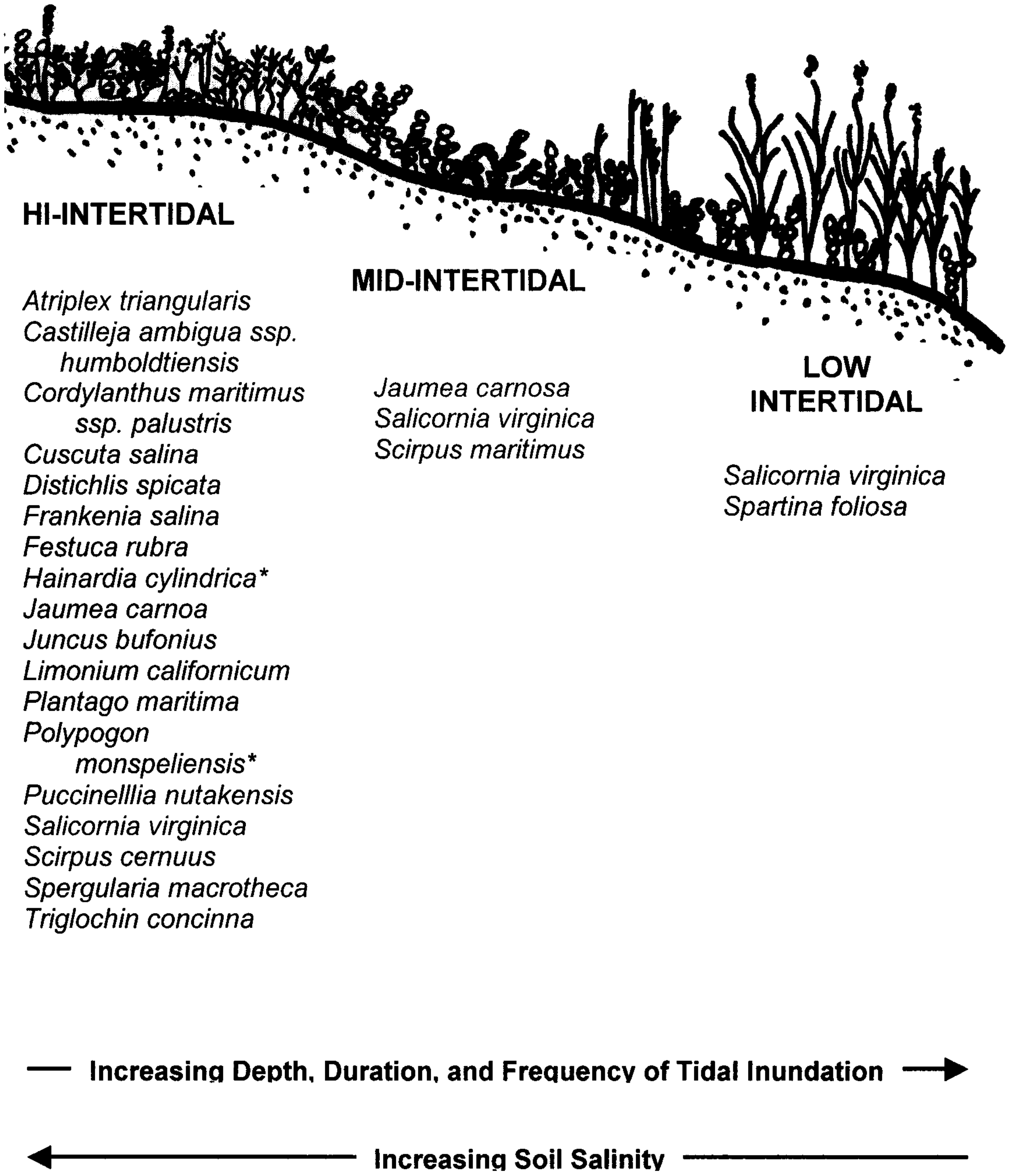


Figure 2.4. Schematic diagram of the salt marsh intertidal gradient at Tom's Point - Tomales Bay Estuary illustrating differences in plant species occurrence among major vegetation zones and physical conditions considered in this study. Exotic species indicated by * symbol.

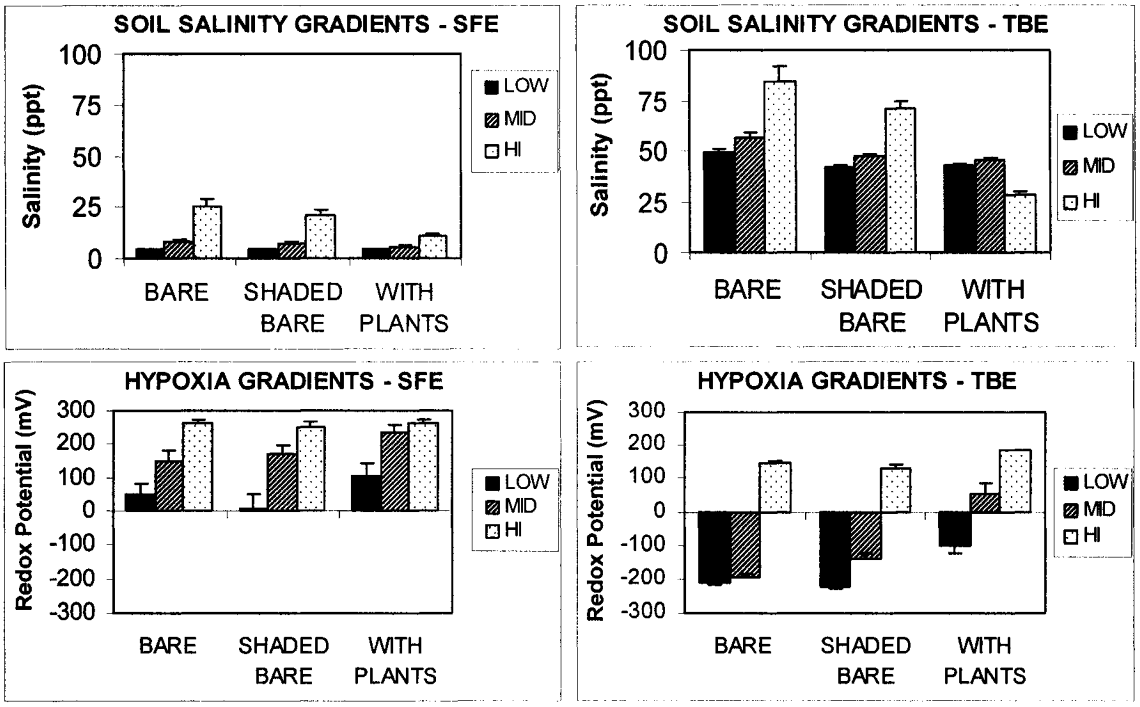


Figure 2.5. Intertidal pore water salinity and hypoxia (redox potential) gradients in bare plots, artificially shaded bare plots, and control plots with vegetation at Suisun Marsh, San Francisco Estuary (SFE) and Tom's Point, Tomales Bay Estuary (TBE) salt marshes. Bar shading represents low, middle, and high intertidal elevations as shown in legends. Data are means ± 1 SE of 15 replicates per intertidal zone from pooled biweekly measurements July – September 1999.

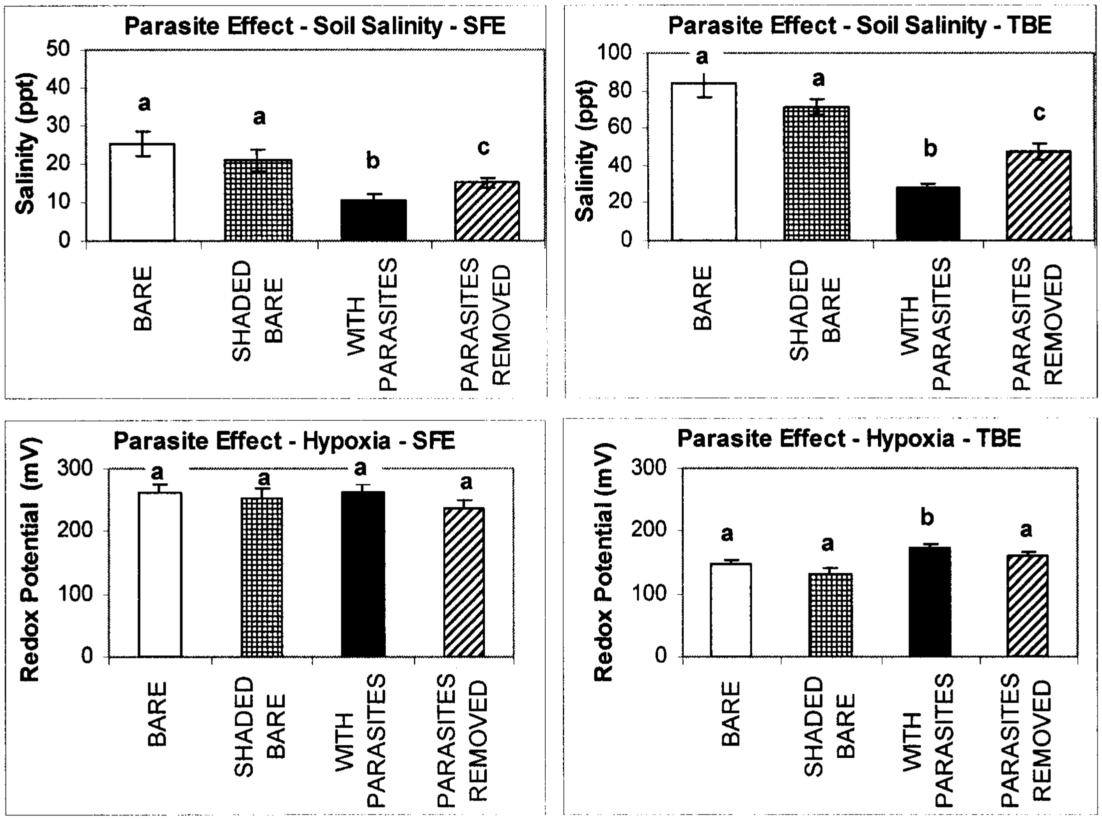


Figure 2.6. The effect of parasitic plants on rootzone pore water salinity and redox potential at brackish Suisun Marsh (SFE) and outer coastal Tomales Bay (TBE) sites. Note scale change between Suisun and Tomales salinity graphs. Data are means of pooled measurements + 1 SE. Treatments different at $p = 0.05$ are marked by different lower case letters.

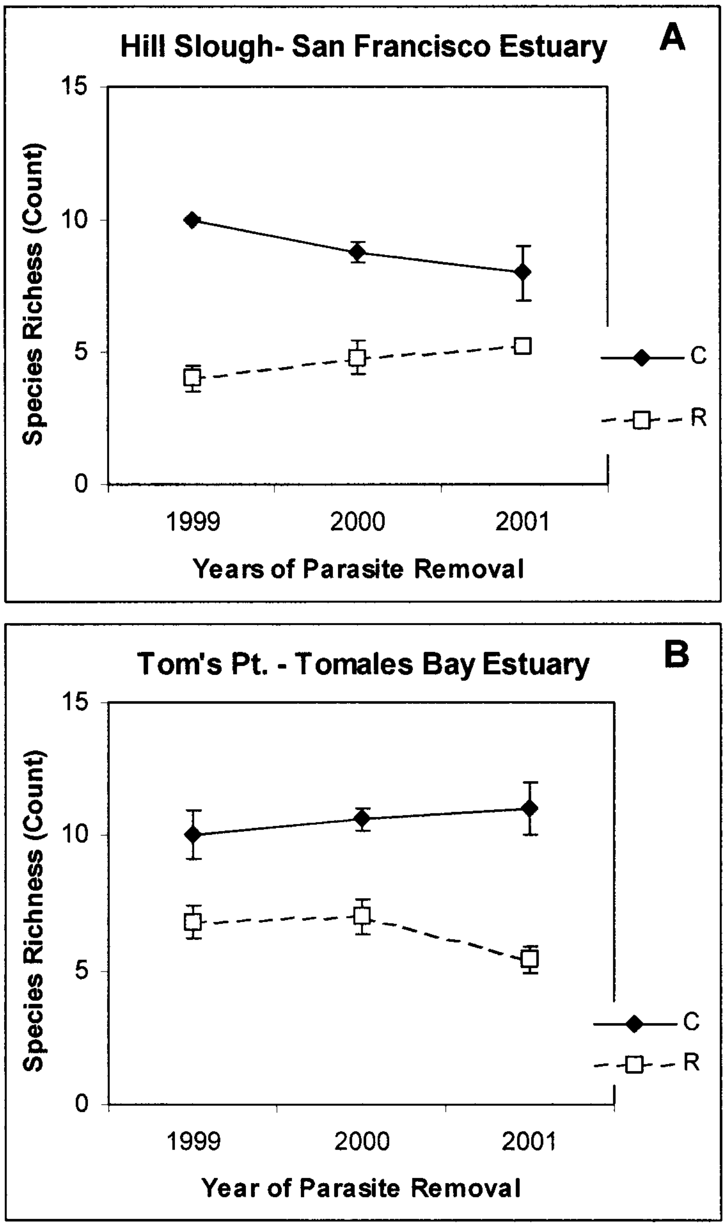


Figure 2.7. Plant community species richness response to three years of hemiparasite removal from two salt marshes at extreme ends of climatic and estuarine gradients (Plot A: Suisun Marsh; Plot B Tomales Bay). Treatment codes: C = control plots with hemiparasites present, R = hemiparasite removal plots.

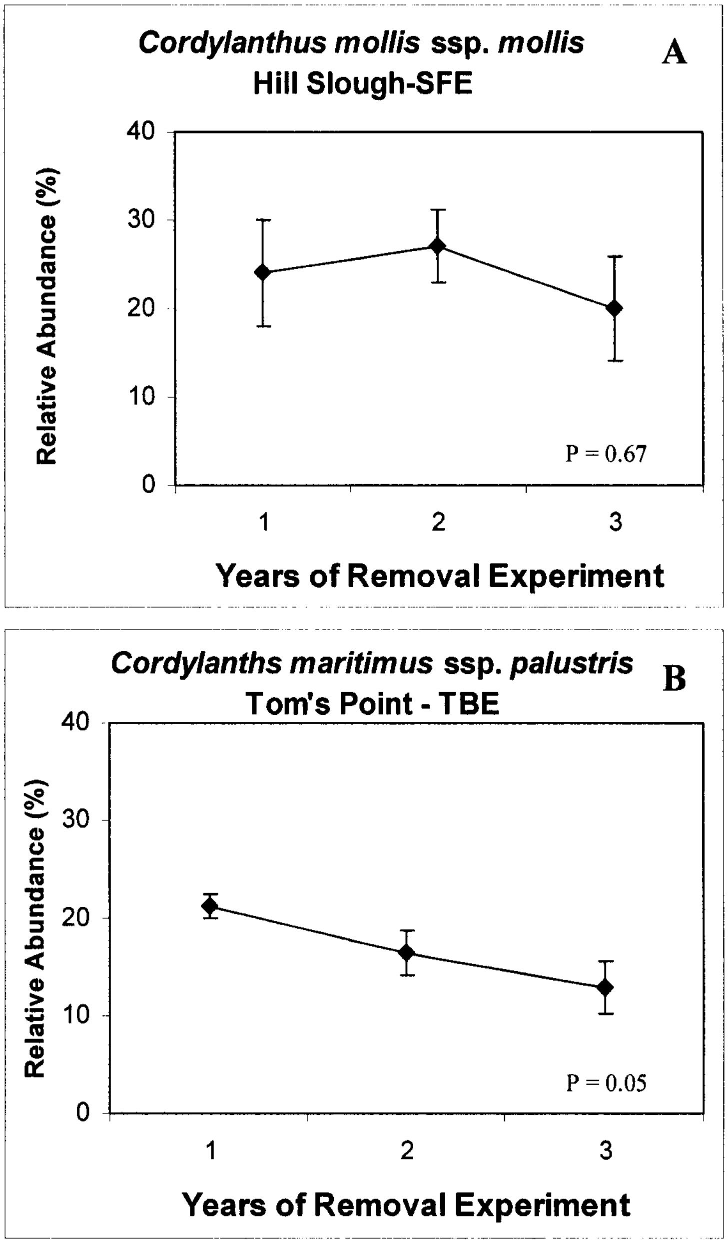


Figure 2.8. Relative abundance of hemiparasites in experimental control plots at study sites (Plot A: Suisun Marsh; Plot B Tomales Bay). Data are means ± 1SE from 5 replicate plots per site monitored for 3 years.

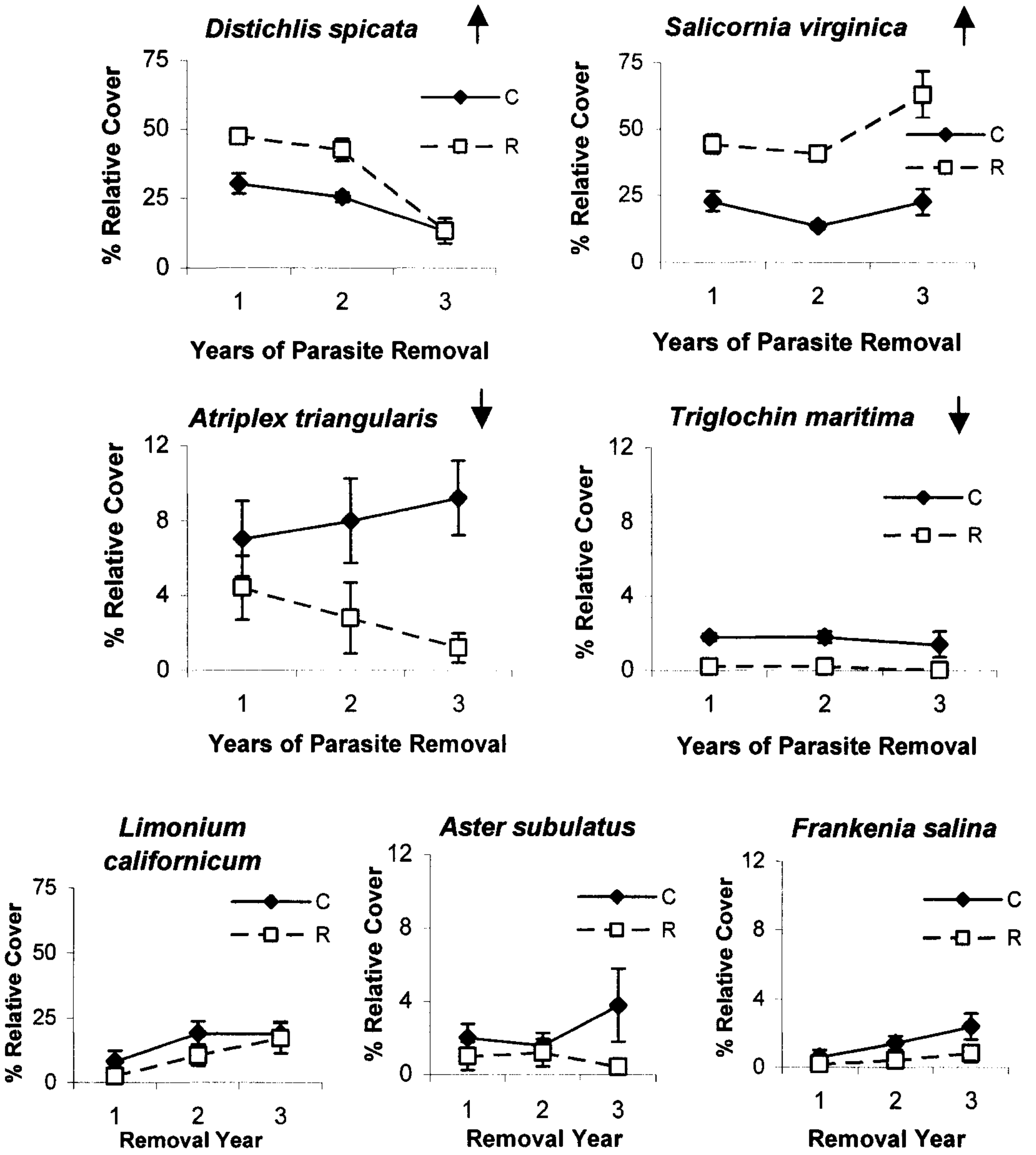


Figure 2.9. Change in relative abundance of plant species at SFE (Hill Slough, Suisun Marsh) following three years of parasitic plant removal. Note the change in relative abundance scale between graphs of dominant species and subordinate species. Rare species occurrences with insufficient sample sizes for statistical analyses have been excluded. Data are means ± 1 SE. The direction of the effect of parasite removal on species with significant responses is indicated by arrow symbols following the species name.

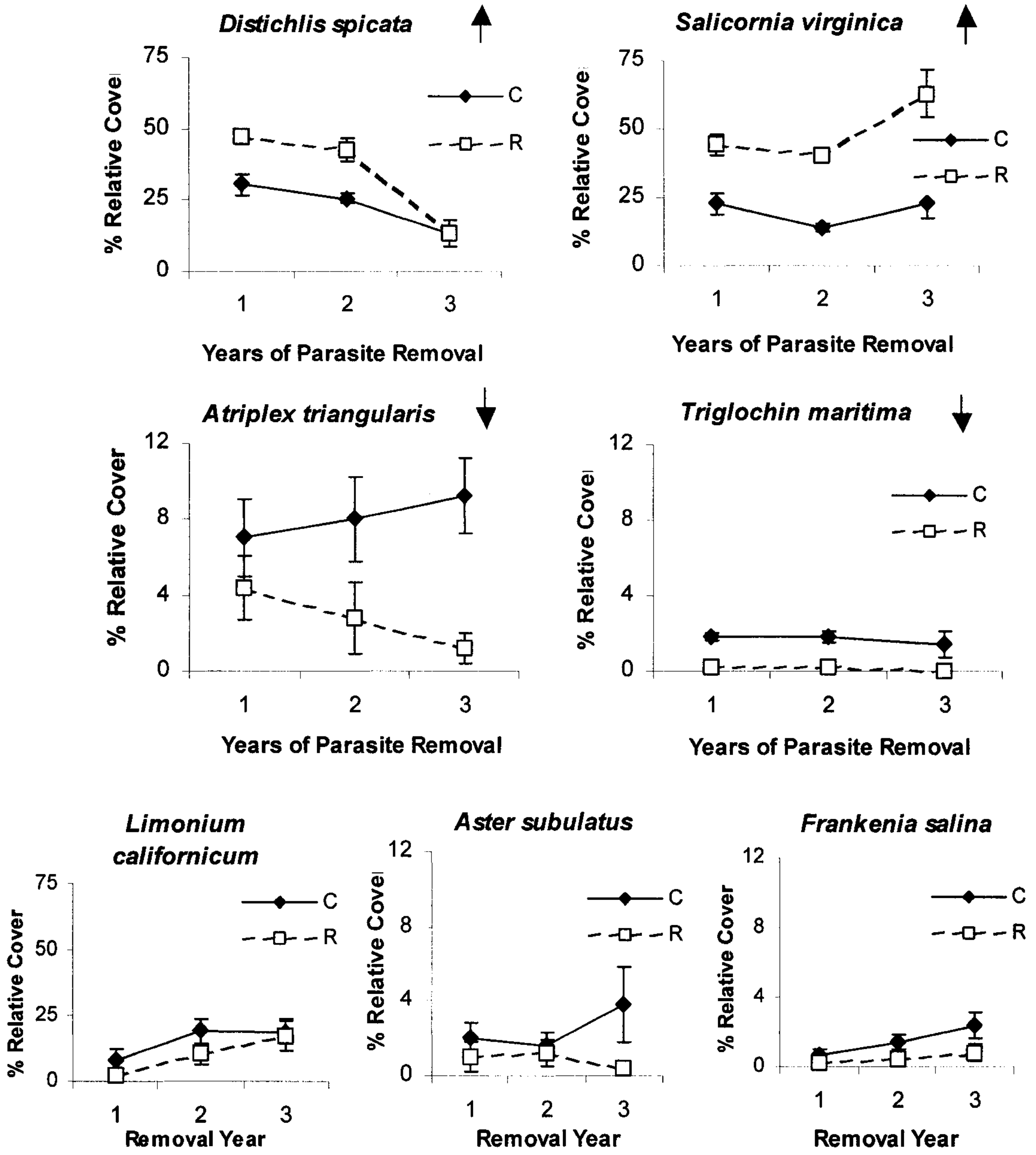


Figure 2.10. Change in relative abundance of dominant and subordinate plant species at TBE (Tom's Point Preserve, Tomales Bay Estuary) following three years of parasitic plant removal. Data are means ± 1SE. The direction of the effect of parasite removal on species with significant responses is indicated by arrow symbols following the species name. Note relative abundance scale change between graphs of dominant and subordinate species.

CHAPTER 3

DISTURBANCE RESTORATION FOR DEMOGRAPHIC ENHANCEMENT OF AN ENDANGERED PARASITIC PLANT INCREASES SALT MARSH INVASABILITY

ABSTRACT

I present results of an experimental reintroduction of an endangered parasitic plant to a restoration site in the San Francisco Estuary. In three years of field experiments, I tested disturbance management methods for enhancement of rare plant establishment and fitness. I identified critical life stages and used life table survival analysis and accelerated failure time models to compare restoration and reference populations, and restoration management actions. Experimental tests indicate vegetation gap creation is a successful restoration technique that will enhance rare plant establishment and fitness, but the benefits can be offset by exotic plant invasions. Demographic monitoring revealed seedling life stage vulnerability that can influence population growth and persistence. High seedling mortality was strongly correlated with the presence of exotic winter annual plant species that are unsuitable hosts for endangered root hemiparasites. Seedling survival and adult fecundity were also reduced under muted tidal regimes. Applied conservation significance of the study points to a critical need for regional invasive plant control and restoration of historic tidal regimes as important first steps in endangered plant recovery and restoration efforts in the San Francisco Estuary of California.

INTRODUCTION

Plants exist within dynamic ecosystems and have evolved with a variety of disturbance regimes. Disturbances can create small-scale gaps in communities that can be filled by colonizing species. It has long been recognized that plant population dynamics as well as plant community properties including diversity, competitive effects, and susceptibility to exotic species invasion may be influenced by disturbance (see Bazzaz 1983, 1986, Pickett and White 1985) and the characteristics of disturbance-generated gaps (McConnaughay and Bazzaz 1990). Many rare plant species occupy successional habitat and require disturbance for regeneration (Grubb 1977, Connell 1978, Denslow 1980, Petraitis et al. 1989, Menges 1991, Hobbs and Huenneke 1992, Menges and Hawkes 1998). Disturbance processes can also enhance the establishment of invasive plant species (D'Antonio et al. 1993, Hobbs and Mooney 1995, Lambrinos 2000, Gerlach and Rice 2003) that may ultimately offset initial benefits to fugitive rare species.

The recovery of endangered plants in human-altered landscapes may require creation of new populations in restoration efforts, but sufficient scientific information is often lacking (Boersma et al. 2001). Persistence of rare plants in disturbance-prone habitats is dependent on the successful transition of individual plants through critical life stages. In the establishment of a new population, survival and fertility of individual plants should be maximized to increase the population growth rate and ultimately reduce the chance of extinction. For this reason, it is essential to evaluate the demographic status of endangered species to identify and understand the life history stages that have the greatest impact on population growth so we can design and implement biologically relevant and effective recovery efforts (Schemske et al. 1994). Life stage specific vital rates can also be useful response variables for a retrospective analysis of conservation actions such as restoration management techniques (Caswell 2001).

Cordylanthus mollis A. Gray ssp. *mollis* (soft bird's-beak; Scrophulariaceae) (hereafter *Cordylanthus mollis*) is a federally endangered plant species endemic to high intertidal elevation zones of North Bay salt marshes within the San Francisco Estuary of California (CNPS 2001). Extant populations have been reduced to 50% of the historic range due to habitat loss and fragmentation, and human alteration of hydrologic regimes (Ruygt 1994). Restoration and recovery of endangered parasitic plants will require restoration of host community structure, composition, and host quality to sustain parasite populations (Marvier and Smith 1997). Like other rare root hemiparasites (Vanderweir and Newman 1984, ter Borg 1985, Menges 1990, Marvier and Smith 1997, Petrů and Lepš 2002), persistence of *Cordylanthus mollis* is dependent on disturbance-generated gaps within appropriate host plant communities.

To test the hypothesis that local disturbance can be a useful technique to establish rare plant populations and enhance individual plant fitness, I suppressed competition through creation of plant community gaps and experimentally reintroduced *Cordylanthus mollis* to a restoration site within the historic range of the species. The reintroduced population was compared to reference populations with demographic survival analyses. Significant seedling mortality was observed within some populations. Because seedling survival is essential to population establishment, I assessed potential host relations of near neighbors and environmental factors throughout the seedling life stage. Finally, I examined the influence of disturbance management on rare plant performance, plant community composition, and environmental conditions at the restoration site. Specifically, my objectives were to 1) test timing of seeding and gap creation as restoration management techniques; 2) compare the demographic status of the reintroduced population to natural reference populations; 3) identify life history stages that may limit population growth and identify causes of demographic variation at those stages, and 4) evaluate rare plant demographic and plant community response to manipulation of the restoration microenvironment.

METHODS

Study species

Cordylanthus mollis is an annual root hemiparasitic herb that relies on a host association for survival within the harsh environment of high intertidal salt marsh. Hemiparasites are heterotrophic plants capable of photosynthesis, but also receive crucial host subsidies of water, nitrogen, fixed carbon, and mineral compounds through haustorial organ connections to vascular tissues in host plant roots (Press 1989, Press et. al 1999). *Cordylanthus* hemiparasites acquire resources from a variety of available hosts and are not host specific (Chuang and Heckard 1971). *Cordylanthus mollis* typically emerges from the seed bank in March or April, but during extended drought cycles seedlings have been observed as early as December (B. Grewell, personal observation). Foliage is gray-green and often tinged with purple. Plants are often multi-branched above the base and may reach heights up to 50 cm tall, but most mature individuals range from 20 to 35 cm. Long soft hairs are present on stems and floral bracts. The plant has numerous salt secretion glands and salt crystals are often visible on floral bracts and leaves Sympetalous flowers are cream with yellow tips, and are closely arranged on elongated inflorescence spikes. Each flower is subtended by a single toothed bract and undivided calyx. The corolla is club-shaped with a beak that encloses the stigma and stamens. Seeds are formed in elongated capsules that are asymmetrically attached near the base. Seed production of up to 32,000 propagules per plant has been observed under ideal conditions (B. Grewell, unpublished data). The seed coat is deeply reticulate and a distinctive taxonomic factor within the subgenus *Hemistegia* (Chuang and Heckard 1972). Plants are out-crossing and floral visitors include *Bombus, Anthidium*, *Melissodes*, *Halictus*, and *Lassioglossum* bees. Developing seed capsules are parasitized by micro-lepidopteran seed predators (*Saphenista*, sp. Tortricidae and *Lipographis fenestrella*, Pyralidae) (Grewell et al. 2003). The abundance of seed-eating birds (*Passerculus sandwichensis*, *Sturnella neglecta*) and small mammals (*Reithrodontomys raviventris*) appear to increase in the rare plant patches after seed ripening (B. Grewell, personal observation), but their effects as post-dispersal seed predators are unknown.

Cordylanthus species are gap colonizers, and the endangered congener *Cordylanthus maritimus* Benth..ssp. *maritimus* does not establish or grow well when the host canopy casts too much shade (Fink and Zedler 1989). Extant populations of *Cordylanthus mollis* occupy host communities with unique community structure characteristics, while soil physico-chemical characteristics are highly variable across the occupied range (Grewell et al. 2003). The rare plants are most often found in mixed halophyte communities with intermediate canopy height, canopy-gaps, and intermediate levels of photosynthetically active radiation penetration through the canopy. Frequent plant associates of *Cordylanthus mollis* are *Cuscuta salina* Engelm. var. *major* Yunck., *Distichlis spicata* (L.), *Atriplex triangularis* Willd., *Limonium californicum* (Boiss.) A.A. Heller, *Salicornia virginica* L. and *Plantago subnuda* Pilger.

Study sites

A rare plant reintroduction experiment was established at Solano Land Trust's Spring Branch wetland restoration site at the Rush Ranch open space preserve (RUSH) in Solano County California (38° 12'N 122° 01'W; Fig. 3.1). Rush Ranch includes nearly 1000 acres of relict tidal wetlands within the brackish Suisun Marsh reach of the San Francisco Estuary (SFE). The Spring Branch watershed was isolated from tidal action in the early 20th century when the channel was filled for a farm road. Tidal hydrology was restored to the area in 1991. At the initiation of this study, a tidal wetland plant community was well established with plant species composition and structure typical of natural soft bird's beak population sites (Grewell et al. 2003). The area was monitored each year following reintroduction of tidal hydrology, but *Cordylanthus mollis* had not established through natural dispersal from fragmented extant populations (B. Grewell, unpublished data). Preliminary soil and vegetation sampling in 1999 - 2000 suggested plant community succession had progressed to the point where a small-scale experimental reintroduction could be tested to serve as a model for regional endangered plant recovery planning.

Demographic reference plots were established within historic *Cordylanthus mollis* populations at the Hill Slough Wildlife Area (HILL) in Suisun Marsh (SFE), Solano County approximately 70 km upstream of the Golden Gate tidal inlet (38° 13'N 121° 59'W; Fig. 3.1). During the second year of the study, additional reference population monitoring sites were established near Southampton Bay (BBAY; 38° 03'N 122° 11'W) and at an upper marsh site within the Benicia State Recreation Area (BSRA; 38° 04'N 122° 11'W) in the Carquinez Straits reach of the SFE (Fig. 3.1). Tidal wetland reference marshes grade to low elevation hills of the California Coast Range, and are subject to typical estuarine hydrology within the upper reach of a large drowned river valley estuary (Conomos et al. 1985). Variation in historic tidal regimes has been altered by numerous local water diversions, hydrologic management of federal and state water project operations in the Sacramento-San Joaquin Delta, extensive levee-building and channelization to support agriculture, waterfowl management, and private hunting clubs (Arthur et al. 1996, Goals Project 1999). Ecosystem restoration goals for the SFE impose additional changes to local hydrology with implementation of tidal wetland restoration projects.

Experimental reintroduction

Propagule collection. Seeds were collected from the two closest natural populations (1.2 and 3.7 kilometers from the restoration site) in an attempt to match source populations to climate and environmental conditions at the restoration site, recognizing the potential effects of local selection on donor populations and the need to maximize the evolutionary potential of the reintroduced population (Pavlik et al. 1993, Knapp and Rice 1994, Knapp and Dyer 1998). Because genetic diversity may also vary across microsites within a population (Brown and Briggs 1991), donor populations were spatially stratified for propagule collection across marsh microhabitats. Branches with mature seed capsules were pruned from donor plants to avoid sacrifice of maternal donors. Seeds were separated from capsules, air-dried, and then held in cold storage in the laboratory.

Restoration experimental design. To examine the density, demography, and fitness response of *Cordylanthus mollis* to restoration management techniques, a reintroduction experiment was established. While recruitment gap size may influence regeneration dynamics of the endangered plants, it was essential to limit donor propagule collection, and hence the number of experimental treatments, to minimize impacts to extant populations and comply with endangered species research permit conditions. Recruitment gap size measurements, presence or absence of litter in gaps, and below-canopy PAR measured with a Decagon Devices Sunfleck Ceptometer in extant *Cordylanthus* populations were evaluated for a species-relevant selection of disturbance treatments for the restoration experiment (B. Grewell, unpublished data). Disturbance creation and resulting below-canopy PAR measurements were then tested in trial plots the year before the experiment was established.

During February 2000, prior to emergence of *Cordylanthus* at natural population sites, eight restoration blocks divided into twelve 1-m^2 plots were randomly located along a transect within the intertidal zone supporting the appropriate host plant community. Restoration planting treatments were arranged in a randomized block design and included a factorial combination of canopy-gap disturbance in 2 levels (canopy-gap disturbance, no disturbance), and planting time in 6 levels (March, April, May, November, December, no sow controls). One meter buffers were established around the perimeter of each block. To establish disturbance treatments, twenty 10-cm gaps per 1-m^2 plot were created in a random mosaic pattern by clipping above-ground plant community biomass at ground level and removing clipped material. If litter was present, it was also removed to expose bare ground in the gap. Plots were visited weekly to biweekly through the active growing season and re-clipped as needed to maintain gaps through the first seedling emergence period in 2001.

Following Fink and Zedler (1989a&b, 1991), pre-sowing seed treatment and a fixed sowing density of 300 seeds/m^2 were implemented following restoration planting guidelines for endangered *Cordylanthus maritimus* ssp. *maritimus* in southern California wetlands. Lots of 300 seeds per experimental treatment were counted and placed on filter paper-lined petri dishes. Seed was brought to room temperature, subjected to a freshwater flush treatment, and transported to the field for planting. Seeds were sown by hand in designated planting treatment months. To prevent loss of seed by birds or tides, seeds were pressed gently into the soil surface but not completely covered with soil. Plots were visually inspected weekly for seedling emergence. Following *Cordylanthus* establishment (2001), reproductively mature plants augmented experimental seed banks through natural dispersal processes. No seed was experimentally added to the blocks after treatment initiation in the year 2000. Plant response variables measured in 2001 and 2002 included density of surviving reproductive adults, plant community species presence, percent cover of plant associates, canopy layers and maximum canopy height.

Planting month treatments were pooled for final analyses as Spring (Mar-Apr-May sowing) and Fall (Nov-Dec sowing), as there were no within season differences in density response. The response data were 4th-root transformed to meet normality and variance assumptions required for the linear model. The effects of disturbance treatments and timing of seed introduction on established *Cordylanthus* density response the first and second year following seed introduction to restoration plots were analyzed with repeated measures ANOVA using the General Linear Model (GLM) in Systat v. 9.0 (SPSS, Inc. 1999).

Because it was not logistically feasible to monitor time to emergence, seedbank emergence rates, and corresponding seedling environment response to disturbance management at the scale of the primary restoration experiment, I established an additional 24 reintroduction plots at RUSH in November 2001. The 0.5 X 0.5 meter plots were randomly stratified within the *Cordylanthus* zone, and were spatially separated from the large reintroduction blocks. Twelve randomly selected plots received five 10-cm canopy-gap disturbance treatments prior to planting, and the remaining twelve plots were designated controls. I placed a planting grid over each O.25m^2 plot and planted 3 soft bird's beak seeds in each 10-centimeter subdivision of the grid for a total seed bank density of 75 seeds per plot. When seedlings emerged in March 2002, the planting grid was placed over each plot and numbers of live seedlings were recorded weekly for twelve weeks to determine proportion of emergence from the seed bank and seedling survivorship.

To evaluate environmental factors potentially correlated with seedling survivorship and rare plant fitness, soil cores were collected weekly for 12 weeks from restoration control and disturbance treatment plots, and also from reference population plots during the seedling emergence stage. Soil cores were analyzed for gravimetric soil water content and soil salinity at maximum seedling emergence was quantified from saturation extracts following methods described in Chapter 1. Tidal hydrology was continuously monitored among populations with Remote Data Systems WL-20 capacitance sensor shallow water level recorders with wireless infrared data links as described in Grewell et. al (2003).

To evaluate plant community response to disturbance management treatments, each O.25m^2 plot was subdivided into 5 transects, and vegetation height, plant species composition, and canopy architecture were evaluated along each transect by point intercept with a pin frame consisting of ten 2 mm diameter brass pins spaced 10 cm apart in a 0.5 meter frame constructed to correspond with the sampling units. The number of canopy layers, canopy height, and percent cover were recorded at peak summer growth (see methods, Keer and Zedler 2002). Photosynthetically active radiation (PAR) was measured 5 centimeters above the soil surface under the natural plant canopy with a Decagon SF-80 sunfleck ceptometer.

Demographic monitoring

Because the restoration and protection of a threatened species ultimately depends on population-level dynamics, demographic monitoring was used to identify variation between reintroduced and reference populations, and to identify particular stages in the life cycle where management intervention may improve establishment and conservation success. To frame demographic analyses, I created a simple graphical model of the life cycle of *Cordylanthus mollis* based on extensive natural history observations within extant populations. Because age alone is usually a poor predictor of demography in plant populations (Gurevitch et al. 2002), I developed a stage-structured model to describe the life of the rare plant and structure life table calculations (Fig. 3.2). Five life stage classes are designated by circles and include: seed, seedling, flowering, set capsule set, and seed maturation. The values $P_{x,x+1}$ indicate rates at which plants move up a stage class, and the values $F_{x,1}$ within diamonds represent the fecundity of the population which links the individual to the population level. The model represents a metapopulation of two patches (populations) of soft bird's beak linked by seed flow. While between-patch dispersal potential of the species is recognized, demographic evaluations presented in this paper consider within patch population dynamics. From this model, I designed demographic studies to quantify survivorship, transitions between life stages, and fecundity of reproductively mature adults.

In spring 2001, at first seedling emergence in restoration plots, I tagged 30 individual emergent seedlings in control plots at the reintroduced population, and in randomly located permanent plots within the nearby HILL reference population. Because fitness may vary with emergence time, one month later an additional 30 emergent seedlings (~ 5 cm tall) were marked at both sites for a total of 120- tagged plants. Seedlings were marked with engraved aluminum plant tags modified with wire loops and corrosion-proof anchors so that tags could be anchored > 5 cm distance from the marked plant to prevent potential severing of hemiparasite roots or host-parasite root connections. This method also prevented tags from interfering with seedling growth, and from washing away during high tides, but ensured that experimental plants could be identified. Plant growth (height) and life stage were recorded for each marked plant every two weeks through their life cycle. Stage and date of mortality was recorded as marked plants died. Individuals were dissected and additional fitness measurements including branch, flower, and seed capsule counts, and pre-dispersal seed granivory rates were recorded. Granivory rates were quantified as the proportion of seed capsules with evidence (observation of moth larvae within capsules, frass, and/or boreholes in reproductive tissues) of pre-dispersal predation. At each population site, mature seeds were counted in a subsample of 25 capsules from different plants for a per plant mature seed production estimate.

Marked plant demographic studies were refined and expanded in the second year. Because local hydrologic alterations implemented after the start of this study were negatively affecting the HILL reference population, permit conditions were amended to allow expansion of reference monitoring to include two additional populations (BBAY and BSRA) in 2002. All monitored populations were visited biweekly through the winter dormancy period to check for seedling emergence. When seedlings appeared in early March 2002, 25 seedlings were marked in RUSH restoration control plots and in five 1-m^2 plots in each of 3 reference populations (HILL, BBAY, BSRA) over an emergence period of 5 weeks. In addition, one soft bird's beak seedling was tagged in each 0.5 X 0.5 m seedling emergence plot with 12 plants tagged in disturbance-gap treatments, and twelve in controls. Growth, life stage transition, mortality, fitness, and plant community species composition and structure were measured as described for 2001 except that monitoring frequency was increased to weekly measures. In 2002, seedling densities were recorded weekly for plots with marked plants.

Life table and failure time analysis. Field data on the numbers of tagged plants surviving each life cycle stage were used to construct stage-specific cohort life history tables for each population that include both a schedule of survival probabilities and fecundity for individuals within each monitored population. In this study, a cohort is population of annual plants that have germinated and emerged from seedbank and are monitored from emergence until death. The number of plants surviving to each stage, N_x, was standardized to initial cohort of 1000. Stage specific survival, l_x, the proportion of plants living to stage x, and stage specific mortality, d_x, were calculated from the number of individuals that survive or die before the beginning of each life cycle stage. Next the mortality rate or 'chance of death', q_x, was calculated ($q_x = d_x / l_x$). Finally, the stage-specific survival rate, p_x, the proportion of plants alive at stage x that survive and transition to stage $x + 1$ was calculated ($p_x = 1 - q_x$). Fecundity (m_x) represents the population mean number of mature seeds produced per plant. Logarithmic survivorship curves were plotted to examine differences among populations.

Failure time survival analysis methods were used to statistically test whether the life table response of the rare plants varied among reintroduced and reference populations and between restoration disturbance treatments. Time to event (stage transition) data were analyzed as nonparametric Kaplan-Meier survivor probability curves and Mantel log rank tests were used to determine differences among populations (predictor grouping variables) and to test the hypothesis that all survival curves were the same for more than two predictor variables (Kleinbaum 1996, Fox 2001). Kaplan Meier survival analyses were performed using SYSTAT v. 9.0 (SPSS 1999).

To determine if restoration disturbance management effects the distribution of *Cordylanthus* emergence and flowering times I subjected demographic censored data to accelerated failure time regression models (see Fox 2001). Because growth chamber germination trials suggest the species has little seed dormancy when light is not limited (B. Grewell, unpublished data), I assumed a log logistic shaped survival distribution for emergence time analysis, while a gamma distribution was assumed for time to anthesis given the annual plant life history. Given these distributions, the regression coefficients were determined numerically using the maximum likelihood approach and subjected to χ^2

significance tests using the LIFEREG procedure in SAS v.8 for Windows (SAS Institute 2002).

Variation in fitness. Fitness measures of surviving adult plants were analyzed with analysis of variance using the General Linear Model (GLM) procedure. Tagged plants from reference populations (HILL, BBAY, BSRA) were compared to monitored plants in control plots at the RUSH restoration site. To evaluate plant fitness response to disturbance management, data from tagged plants in disturbance treatment plots were also compared to plants in control plots. Response variables were examined for homogeneity of variances and normality and transformed to meet the assumptions required for linear models. Height, branching, longevity and fecundity data were log-transformed; flower and seed capsule count data were 4th-root power-transformed; and survivorship, proportional emergence, seedling relative growth rate and granivory rate proportional data were arcsin(square-root) transformed prior to analysis. Population means for all dependant variables were analyzed first with MANOVA, and standardized canonical coefficients were evaluated. When significance was detected with the multivariate test, I proceeded with "protected" univariate tests (Scheiner 2001). Statistical analyses were performed with SYSTAT v. 9.0 (SPSS 1999).

To investigate relationships among environmental variables and plant species data, I performed a constrained linear multivariate redundancy analysis (RDA) (Jongman et al. 1987, ter Braak 1987, Lepš and Šmilauer 2003). Post hoc Monte Carlo permutation (randomization) tests were used to test for the significance of ordination scores (ter Braak 1995). The RDA ordination was performed using CANOCO v. 4.5 (ter Braak and Šmilauer 2002).

Seedling survival and potential host plant neighbor relationships. *Cordylanthus* seedlings are not host specific, but an appropriate host association is necessary for survival under field conditions. Because significant seedling mortality was observed at field sites, an observational study was implemented to explore near-neighbor relationships between tagged live seedlings, dead seedlings, and potential hosts in demographic monitoring plots. To determine a conservative sample size most likely to include seedling hosts, root lengths of live and dead seedlings outside the monitoring plots were measured, as well as root or rhizome lengths of closely associated species. All seedling roots were less than 5 cm long, and most were less than 2 cm suggesting host plants must be in very close proximity for parasite attachment. Identity, origin (native or exotic), condition (live or dead), and stem densities of all plant species within a 5.5 cm diameter circular plot around each tagged *Cordylanthus* seedling were recorded. Seedlings were monitored every two weeks. Seedlings that died before transition to flowering stage were recorded as mortalities, while seedlings that lived to flower were recorded as survivors.

Pearson's correlation coefficients were calculated to examine the relationship between *Cordylanthus* seedlings and near-neighbor potential host plant species, and to examine the correlation between host plant origin and seedling survival. Chi-square tests were used to determine whether the proportion of seedlings that died or survived were different between the RUSH reintroduction and HILL reference site or between early and late emerging species. All statistics were performed with SYSTAT v. 9.0 (SPSS 1999).

RESULTS

Disturbance management for rare plant establishment

Freshwater soak pre-treatment of seeds prior to planting does not appear to enhance germination of *Cordylanthus mollis* following seed planting. No experimental soft bird's beak seedlings emerged in the spring or summer of 2000 following treatment establishment in spring 2000. Fall treatment establishment was completed in 2000, and plots were inspected biweekly for seedling emergence through the winter. After all experimental seedbanks experienced overwintering and vernalization in natural field conditions, emergent seedlings were first observed in both HILL reference and in all experimentally seeded RUSH restoration plots on April 5, 2001. Canopy-gap is a successful disturbance restoration management technique that enhances *Cordylanthus* establishment in appropriate host communities. The density of established *Cordylanthus* relative to experimental treatments increased with disturbance management, and spring planting resulted in higher densities of established plants the first year of emergence (Table 3.1, Fig. 3.3). The density of *Cordylanthus* increased exponentially in 2002, following natural augmentation of the seedbank by reintroduced plants (Fig. 3.3). *Cordylanthus* establishment was spatially variable, as revealed by the significant block effect detected by this experimental design ($p \leq 0.0001$, Table 3.1) suggesting microhabitat conditions affect restoration success. Both disturbance management and timing of seeding play a role in the successful establishment of the rare plant. The interactive effect of disturbance management and timing of seeding was significant as disturbance enhanced germination of spring-seeded plots (p = 0.016, Table 3.1). The positive effect of canopy-gap disturbance management during seeding carried over into the second year following experimental disturbance, and while the interaction between disturbance and timing of season was significant over time (p= 0.09, Table 3.1), season of seeding for rare plant reintroduction was not significant by the second year of rare plant emergence (p=0.276, Table 3.1).

Comparative demography: reference populations

Among population life table response. Cohort life tables for *Cordylanthus* in restoration control plots and reference populations are presented to provide context for restoration population dynamics. Life tables constructed for RUSH restoration and HILL reference populations in 2001 reflect biweekly census for each life cycle stage through the emergent lifespan of the annual plants (Tables 3.2 and 3.3). Cohort life tables are also presented for RUSH restoration and three reference populations (HILL, BBAY, BSRA) for 2002 (Tables 3.4 – 3.7). Survivorship curves for these data were plotted to examine differences among populations, and survivorship pattern was not the same at all sites (Fig. 3.4). At BBAY, BSRA, and the RUSH restoration populations, seedling mortality was low and mortality rates increased over time as most plants lived to complete their annual life cycle and produce mature seed (Tables 3.2, 3.4, 3.6, 3.7 and Fig. 3.4). A different pattern of survivorship was observed at the HILL population where the mortality rate was highest at the seedling stage, exponentially higher than the other monitored populations, and overall survivorship was low (Table 3.3, 3.5 and Fig. 3.4).

Failure time analysis results confirm the observed differences between life tables and the corresponding survivorship curves. Cumulative survivorship and its standard error as calculated by the nonparametric Kaplan-Meier method show that the survivorship between RUSH and HILL in 2001 was very different (log rank test $\chi^2 = 13.60$, $p = \leq 0.0001$, Table 3.8). Failure time analysis of life tables for expanded reference monitoring in 2002 provides further evidence that survivorship among populations is heterogeneous (log rank test $\chi^2 = 58.88$, $p = \leq 0.0001$, Table 3.9). These data suggest survivorship at the RUSH restoration site compares favorably to the BBAY and BSRA reference sites, but is different than the HILL population where seedling mortality was extremely high.

Among population variation in fitness. An evaluation of plant fitness in 2002 indicates *C. mollis* performance varies among populations (Fig. 3.5). Plant growth was higher at RUSH and BBAY than BSRA and HILL, but branching did not vary among populations. Flower and seed capsule production were highest in the RUSH restoration population, and pre-dispersal granivory was not detected over the first two years of restoration establishment. Granivory by a larval seed predator was elevated at HILL and BSRA depressing overall fecundity in these populations. Results of MANOVA confirm significant differences in fitness among *C.mollis* in restoration control plots and reference populations (Wilks' $\lambda = 0.162$, $p \leq 0.0001$, Table 3.10). Examination of the standardized canonical coefficients of the first canonical variates from the MANOVA (Table 3.10) suggest that significant differences were primarily due to a negative correlation between seed capsule production and growth compared to granivory levels and overall fecundity across populations. That is, the pattern of seeds produced per plant as affected by plant growth and pre-dispersal granivory varies among populations. The univariate ANOVA tests suggest highly significant differences among populations for all measured fitness parameters except number of branches (Table 3.10).

The multivariate ordination diagram from the RDA shows the distribution of significant plant species assemblages relative to environmental gradients, and suggests which environmental factors best explain the survivorship of *Cordylanthus mollis* (Fig. 3.6). The relationship between plant and environmental data was significant ($F = 3.89$, $p=0.058$, Monte Carlo test). The first RDA axis explains approximately 85% of the variability in species data. The relative importance of individual environmental parameters in the RDA ordination diagram is indicated by length of the bold arrows. The strongest environmental gradient detected was potential host community origin. The proportion of surviving rare plants was highest at the BBAY reference site where the potential host community environment included predominantly native species, along with the greatest tidal hydroperiods, and elevated soil salinity at maximum seedling emergence. Plant community canopy heights and canopy layers were also somewhat correlated with survivorship. The potential native host species most significant in this relationship were *Distichlis spicata* and *Salicornia virginica*. At the other end of the environmental gradient, low *Cordylanthus* survivorship at HILL, and to a lesser extent at BSRA, is best explained by the prevalence of an exotic potential host plant community, muted tidal hydroperiods, and a more open plant community with elevated levels of incident radiation penetrating through the canopy. The exotic species most significant in the relationship are exotic *Hainardia cylindrica*, *Polypogon monspeliensis*, and *Cotula coronopifolia* L. Plant species variables at the RUSH restoration population were not strongly explained by the environmental variables in second year following establishment.

Seedling survival and potential host plant neighbor relations. The *Cordylanthus mollis* seedling neighborhood includes a mix of native and invasive exotic plant species. Overall, native species were positively associated with *C. mollis* seedling survival (r=0.36, p=0.001) while there was a negative association between survivorship and winter annual exotic species (r= -0.35, p=0.002). The positive and negative associations between host community species and *C. mollis* seedlings are shown in Table 3.11. The exotic winter annual grass *Hainardia cylindrica* (Willd.) was most negatively associated with survival of *C. mollis* seedlings (r = -0.32), while native perennials *Distichlis spicata* and *Salicornia virginica* were most positively associated with seedling survival (r = 0.38 and 0.21, respectively). *Cuscuta salina*, a native annual parasitic species was also positively correlated with seedling survival (r = 0.22). The exotic winter annual grass *Polypogon monspeliensis* (L.) Desf. and the winter forb *Juncus bufonius* L. appeared to be negatively correlated with *C. mollis* seedling survival (r = -.176 and -.209), but detection levels in marked plant monitoring plots were not high enough to reveal a significant effect.

Chi-square tests were used to see if the proportion of seedlings that died or survived to maturity were different between the RUSH restoration and HILL reference populations. There was no significant difference in native stem density around seedlings at RUSH and HILL. At both sites, surviving target seedlings had significantly more native stems in the immediate vicinity than seedlings that perished before transitioning to reproductive life stages ($p = < 0.0001$). At HILL, the density of exotic host plants exceeded that of natives in the 23.5-cm^2 area surrounding dead *C. mollis seedlings*, but the difference was not significant. There were more native stems than exotic stems around surviving seedlings at this site ($p = 0.003$). At RUSH, the difference in exotic and native stem densities was significant for both seedling survivals and mortalities ($p = 0.000$ and 0.001, respectively). Seedling survival at the RUSH restoration site was significantly higher than that at HILL ($\chi^2 = 4.887$, critical value at $\alpha = 0.05 = 3.841$).

Life table response to disturbance management

Disturbance management improves survivorship of reintroduced *Cordylanthus mollis*. Cumulative survivorship and its standard error were calculated by the Kaplan-Meier method for tagged *C. mollis* plants in restoration disturbance treatments and controls at Rush Ranch in 2002 (Fig. 3.7). The failure time analysis shows that life table vital rates of plants in disturbance treatments are improved over plants grown without disturbance management intervention (log rank test: $\chi^2 = 6.814$, df=1, $p=0.009$; Table 3.12).

Accelerated failure time regression analysis indicates that disturbance management does not influence time of seedling emergence from experimental seedbanks (Table 3.13). The regression coefficients for the control population are zero (Table 3.13) because this is the reference level for the analysis. The analysis shows that the disturbance treatment does not contribute significantly to the model ($\chi^2 = 0.02$, df=1, p=0.887).

In contrast, *Cordylanthus mollis* reach flowering stage earlier with disturbance management. Accelerated failure time regression analysis shows that disturbance treatment contributes significantly to the time to anthesis model ($\chi^2 = 3.98$, df=1, p=0.046; Table 3.14). The covariate in this model, time to emergence, is significant. This is not unexpected, as time from planting to anthesis is the dependent variable, and late emergence probably tends to delay anthesis.

Cordylanthus mollis fitness was enhanced with restoration disturbance management (Fig. 3.8). Results of MANOVA confirm overall improvement in fitness indicators of *C.mollis* in restoration disturbance treatments compared to plants in undisturbed control plots (Wilks' $\lambda = 0.382$, $p = 0.030$, Table 3.15). Univariate F tests suggest seedbank emergence rate, seedling relative growth rate, emergent lifespan, mature plant height, seed capsule production, and mature seeds produced per plant are greater with disturbance manipulation.

Results of redundancy analysis (RDA) that includes samples from the disturbance treatment and control plots are presented in Fig. 3.9. Relative importance of individual environmental parameters in the RDA ordination is indicated by length of the bold arrows. A high proportion of invasive exotic species and elevated soil salinity were associated with increased seedling emergence and seedling relative growth rate. Species particularly associated with disturbance plots were exotic *Hainardia cylindrica*, *Polypogon monspeliensis*, and *Cotula coronopifolia*. Control plots were associated with a native potential host plant community (primarily *Distichlis spicata*, *Salicornia virginica* and *Atriplex triangularis*) where seedling emergence levels were depressed. The first RDA ordination axis explained 41% of the variability in species data. The relationship between the plant and environmental variables was significant (Monte Carlo test, p = 0.036).

Invasive plant response to disturbance management

Relative abundance of native and exotic vascular plant species in *Cordylanthus mollis* restoration disturbance treatment plots was compared to the plant community composition of control plots. Species richness was greater in disturbance plots (7.3 ± 0.62 SE) than controls (5.4 ± 0.48 SE). Native plants dominated plots subjected to both experimental treatments (Fig. 3.10). Control plots included 87% native plant species compared to 15% plants of exotic origin. Disturbance treatments experienced significant recruitment of invasive plants. Native plants contributed 57% of total cover in disturbance plots, while invasive exotic plants accounted for 28% of total plant cover. Winter annual plants accounted for 20% cover of the exotic community in disturbance plots. Disturbance treatments experienced seed recruitment of invasive *Lepidium latifolium* L. This robust perennial invader was not present in the rare plant restoration area at the beginning of the experiment. *Cordylanthus mollis* relative abundance was highest in disturbance treatments (Fig. 3.10), but benefits of disturbance management to the rare plant may eventually be offset by the effects of invasive species.

DISCUSSION

This experimental reintroduction of an endangered plant to its historic range was intended to provide scientific information to restoration managers for larger-scale endangered plant recovery efforts. The results suggest that it is possible to establish a population of *Cordylanthus mollis* in a restoration site. Disturbance-gap manipulation coupled with direct seeding into appropriate host community habitats shows promise as a reintroduction technique. Canopy-gap disturbance is a management surrogate for the competitive or parasitic suppression of dominant host plants, and it may also provide a surrogate for physical processes such as sediment deposition that also generate disturbance gaps. In a reintroduction attempt, it is important to manage for survivorship and accelerate the growth of the founder population. This strategy will minimize decreases in average individual viability associated with small population sizes, and may facilitate the development of a sustainable population over time. While canopy-gap disturbance creation is labor intensive, results of this study indicate the surviving density and fitness components of *Cordylanthus mollis* are improved with disturbance management intervention.

Reintroduction strategies. A fixed planting density was used in this reintroduction experiment, and the density of surviving parasites increased exponentially in the second season. Recruitment in most plant populations is thought to be negatively density-dependent (Antononvics and Levin 1980). In this experiment, survival to maturity of *Cordylanthus* did not appear to be influenced by seedling density. These observations are in agreement with the recruitment and survival response of the root hemiparasite *Rhinanthus alectorolophus* to density (Matthies 2002). It appears facilitation among cohorts of conspecific hemiparasites can increase recruitment of young plants, and this may be due to reciprocal parasitism among root parasites through intraspecific haustorial connections (Matthies 2002). The dynamics of these interactions and their potential effects on *Cordylanthus* life cycle response to restoration are intriguing, but not fully understood.

The significant block effect observed in the reintroduction experiment emphasizes the importance of microsite conditions. Measurements of above ground biomass across the study site indicate better rare plant establishment in areas with higher above ground biomass of potential host plants (Grewell et al. 2003). Potential host plant identity and biomass are important screening criteria for *Cordylanthus mollis* reintroduction sites. Potential host plant communities with unsuitable exotic hosts and communities with extremely low biomass production prior to parasitism may not successfully support the additional parasite load.

Survival and critical life stage assessment. Failure time survival analysis models commonly used in medical research have been under-used in ecology, and provide statistical power to evaluate data that was formerly limited to visual inspection of life tables and survival curves (Fox 2001, Zen and Peart 2003). To my knowledge, failure time survival analyses have not previously been applied to rare plant restoration questions, and these analyses can increase our understanding of management impacts on population dynamics. Failure time models confirm restoration disturbance management does not effect *Cordylanthus* time to emergence from seed banks, yet time to flowering is shortened by disturbance management and helps explain the enhanced fitness associated with disturbance management.

Failure time survival analysis results confirm an immediate need to focus on the seedling life stage in population restoration efforts. The high level of seedling mortality observed at the HILL reference population site is of conservation concern. Baseline autecological measurements recorded in the HILL *Cordylanthus* population prior to local hydrologic diversions for an adjacent wetland mitigation projects documented much higher per plant seed production levels (Ruygt 1994). These observations point to the critical need for continued demographic monitoring of rare plant populations, and adaptive management responses for conservation intervention on a short timescale relevant to the biology of the species.

Results suggest that the identity of nearest neighbor plant species is correlated with seedling survival. Invasive winter annual species are of particular concern due to asynchronous life history characteristics. The winter annuals of concern in this community germinate after early winter rains (November – December), and are in the later stages of their annual life cycle when *Cordylanthus mollis* seedlings emerge in late spring (typically March). The invasive annual *Hainardia* and *Polypogon* grasses are alive and parasitized by young *C. mollis* seedlings (B. Grewell, microscopic confirmation). The exotic grasses are only available as hosts during the early seedling stage of the rare plants, and they die before the hemiparasite can complete its life cycle. The presence of invasive winter annual plants should be a screening criterion for restoration sites, and invaded sites should be considered low priority for restoration until invasive plants are eradicated. These results suggest that control of invasive exotic plants in the community should be the first step in the restoration process if the goal is to create sustainable populations of *Cordylanthus mollis*. Control efforts may take several seasons if seedbank recruitment or in-migration of invasive plants continues to pose threats to native species. Since exotic species removal may have unforeseen negative consequences, and *Cordylanthus* communities support multiple conservation species of concern, it may be necessary to test removal impacts in a community context prior to large-scale control efforts (D'Antonio and Meyerson 2002).

Species-specific demographic response. Comparative studies of rare plants and their congeners can be insightful with regard to shared autecological characteristics, but extrapolation of demographic behavior of one species to a congener can be problematic (Fiedler 1987). A factor common to both endangered hemiparasites appears to be the prevalence of exotic species in the high intertidal zone (Noe and Zedler 2001) that can limit the demographic success and recovery of the endangered species.

Environmental conditions associated with *Cordylanthus mollis* seedling establishment and growth are quite different from those reported for the endangered *C. maritimus* ssp. *maritimus* community in southern California. The flood frequency in the upper intertidal marsh supporting *C. maritimus* is infrequent (15 times in 1997, see Noe and Zedler 2001). Tidal flood frequency in the *C. mollis* reintroduced population (RUSH) was 50 times during the March – November 2001 growing season, while a flood frequency of 27 was recorded at HILL where *C. mollis* survivorship was low (Grewell et al. 2003 and B. Grewell unpublished data). Germination (as indicated by seedling emergence) was associated with "freshwater gaps" following rainfall events in southern California (Noe and Zedler 2001), while the highest densities of *C. mollis* seedling emergence in the field were correlated with elevated salinity (Fig. 3.9).

In contrast to endangered *Cordylanthus maritimus* ssp. *maritimus* reintroduction in southern California salt marshes (Parson and Zedler 1997), reintroduced *C. mollis* plants immediately established critical biological interactions with pollinators prevalent in natural populations (*Anthidium* and *Bombus*, Grewell et al. 2003) and seed capsule set rates were high. Pre-dispersal seed predation has been reported as a factor effecting seed production in other root hemiparasites (Menges et al. 1986, Molau et al. 1989). Pre-dispersal seed predators have been detected in all known natural populations of *C. mollis*, but the level of predation in sites with little hydrologic disturbance is low. In this system, pre-dispersal seed predation was shown to dramatically decrease fecundity of *C. mollis* populations at muted tidal sites. The moth larvae burrow in the sediment for a portion of their life cycle, and it is possible that a reduced hydroperiod improves their survivorship to the detriment of *C. mollis.*

Population status assessment. While population growth rate (λ) and population matrix projection models are often used to assess population viability (Caswell 2001), data requirements and model assumptions preclude their use for prognosis of *Cordylanthus mollis* viability at this time. This study provides data on seedling emergence from soil seed banks in restoration treatments, but data on seed survival and seed bank dynamics are lacking. Additional research is also needed to understand the variation in density dependent processes (i.e. pre-dispersal seed predation) between and among populations. To date, pre-dispersal seed predators have not been observed in the reintroduced (RUSH) population. The population dynamics of the reintroduced population are likely to change if seed predation becomes a factor.

The annual life cycle of this species suggests the need for continued demographic monitoring over a range of environmental conditions, as inter-annual fluctuations in the relative abundance of annual plants have been correlated with environmental variation (Pake and Venable 1995). Picó et al 2003 stress that demographic analysis must take into account multiple populations over a range of habitat variation for several years to approach understanding population dynamics and causes of variation in vital rates. While individual fitness components such as those measured in this study can suggest population responses to restoration actions, ultimately the calculation of population growth rates will integrate cumulative contributions of underlying demographic processes for an estimate of total fitness effect (see Ehrlén 2003). Perturbation analysis that includes sensitivity and elasticity analyses to account for additive and proportional changes in demographic rates can ultimately help identify how variation in particular demographic parameters can cause large changes in λ (de Kroon et al. 2000), but elasticity analyses may ignore important information about the actual range of demographic parameter variability (Davis et al. 2004) and along with perturbation analysis can not provide an accurate assessment of how demographic rates will vary in the future (Caswell 2001).

Empirical studies of other species suggest an inverse relationship between demographic elasticity and temporal variation in vital rates (Lande 1988, Ehrlen and van Groenendael 1998, Picó et al 2003) suggesting small-scale population processes can affect vital rates (such as seedling growth and fecundity) and their variability. Demographic data and fitness component measurements yielded by this study should be considered the first chapter in understanding the life history of this rare plant. While perturbation analysis of long term data sets is not yet possible, environmental data coupled with the life table analyses and failure time model results presented here identify factors associated with poor population performance, and this information is relevant for prescribing conservation and restoration management tactics.

Hemiparasites and exotic plant invasions. Understanding the interactions between invaders and native plants is essential to the management and restoration of native-dominated habitats (Corbin and D'Antonio 2004). When the native resident plants of concern are hemiparasites, a unique perspective is required. Root hemiparasites are often dependent on disturbance gaps for recruitment in host communities (Vanderweir and Newman 1984, ter Borg 1985, Menges 1990, Marvier and Smith 1997, Petrů and Lepš 2002). In Chapter 2 of this thesis, experiments show that hemiparasites can increase habitat heterogeneity and cause species richness to rise. Hemiparasites represent a unique functional group, and their influence on community diversity is considered an ecosystem process (Press 1998). Once established, the physiological effect on host biomass reduction shifts hemiparasites into the role of ecosystem engineers, as their effect on gaps creation in the community enhance plant species richness in the community. It has been demonstrated that the annual root hemiparasite *Rhinanthus alectorolophus* can also shift to the role of ecosystem engineer upon death, because high densities of dead annual root parasites opens gaps in the vegetation that can subsequently be colonized by weeds (Joshi et al. 2000). This experimental reintroduction of a hemiparasite demonstrates that disturbance gaps linked to exotic species invasion may be essential to endangered hemiparasite establishment and persistence, while other experiments have demonstrated that root hemiparasites themselves can lower the resistance of low-diversity host communities to invasion (Joshi et al. 2000), Recognition of this dichotomy presents both challenges and potential solutions. Hemiparasites may be partners in the restoration of species rich communities, if regional control of invasive plants can be aggressively managed to reduce invasion risk.

Disturbance and invasion: challenges for restoration. The review by Hobbs and Huenneke (1992) on the dual role of disturbance in structuring plant communities in terms of maintenance of native plant species diversity versus facilitation of non-native plant invasions is directly relevant to the restoration challenges revealed by this research. *Cordylanthus mollis* no longer occurs under natural conditions, but persists in patchy refugia with anthropongenically altered disturbance regimes. When disturbance is reintroduced, endangered native and invasive plant recruitment are simultaneously enhanced. Endangered plants respond favorably to disturbance management with improved survival and fitness, but these effects ultimately may be overturned by invasion success. The potential displacement of reintroduced endangered species by invasive species indicates long-term monitoring of restoration efforts is imperative as early gains may not outweigh long-term losses. Conservation efforts must explicitly consider disturbance processes at multiple spatial and temporal scales. Restoration of landscape scale variability in natural disturbance regimes, including tidal flows, along with tidal wetland restoration to reconnect existing fragmented habitats may be vital to restoration efforts. Understanding the mechanisms underlying disturbance-stimulated invasion potential by invasive species should be a priority goal in the restoration process. At a more local scale, active conservation stewardship is needed on existing tidal wetland habitat reserves.

ACKNOWLEDGMENTS

I thank Eliška Rejmánková, Kevin Rice, and Ted Grosholz for comments that improved the manuscript. I also thank Peggy Lee Fiedler for insightful discussions regarding *Cordylanthus mollis*, rare plant demography, and wetland restoration. I thank Miles DaPrato, Rose Hyde, Steve Kidner, Wendy Trowbridge, and Diana Hickson for helpful assistance. Special thanks to Solano Land Trust, California Dept. of Fish and Game, and California Dept. of Parks and Recreation for research permits and site access; and to the CALFED Ecosystem Restoration Program (California Bay Delta Authority) for financial support.

LITERATURE CITED

Antonovics, J. and D.A. Levin. 1980. The ecological and genetical consequences of density-dependent regulation in plants. Ann. Review of Ecol. and Systematics 11:411-452.

Arthur, J.F., M.D. Ball, and S.Y. Baughman. 1996. Summary of federal and state water project environmental impacts in the San Francisco Bay-Delta estuary, California. p. 445-495 in: J.T. Hollibaugh (ed.). San Francisco Bay: The Ecosystem. Pacific Division American Association for the Advancement of Science. San Francisco, California, USA.

Bazzaz, F.A. 1983. Characteristics of populations in relation to disturbance in natural and man-modified ecosystems. Pp. 259-275 in: H.A. Mooney and M. Godron (eds.) Disturbance and Ecosystems: components of response. Springer-Verlag, New York, New York, USA.

Bazzaz, F.A. 1986. Life history of colonizing plants: some demographic, genetic, and physiological features. pp 96-110 in: H.A. Mooney and J.A. Drake (eds.) Ecology of biological invasions of North America and Hawaii. Springer Verlag, New York, New York, USA.

Boersma, P.D., P. Kareiva, W.F. Fagan, J.A. Clark, and J.M. Hoekstra. 2001. How good are endangered species recovery plans?" BioScience 51:643 649.

Brown, A.H.D. and J.D. Briggs. 1991. Sampling strategies for genetic variation in *ex situ* collections of endangered plant species. pp. 99-119 in: D.A. Falk and K.E. Holsinger. 1991. Genetics and Conservation of Rare Plants. Center for Plant Conservation. Oxford University Press. New York, New York, USA.

Caswell, H. 2001. Matrix Population Models: Construction, analysis and interpretation. 2nd. Ed. Sinauer Assoc. Sunderland, MA. USA.

Caswell, H., R. Lensing, and M.G. Neubert. 2003. Demography and dispersal: life table response experiments for invasion speed. Ecology 84:1968-1978.

Chuang, T. I., and L. R. Heckard. 1971. Observations of root-parasitism in *Cordylanthus* (Scrophulariaceae). American Journal of Botany 58: 218-228.

Chuang, T.I. and L.R. Heckard. 1972. Seed coat morphology in *Cordylanthus* (Scrophulariaceae) and its taxonomic significance. Am. J. Botany 59:258-265.

CNPS. 2001. Tibor, D. P. (Convening Editor). California Native Plant Society's inventory of rare and endangered plants of California. 6th Edition. CNPS, Sacramento, California.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. Science 199:1302-1310.

Conomos, T.J., R.E. Smith, and J.W. Garner. 1985. Environmental setting of the San Francisco Bay. Hydrobiologia 129:1-12.

Corbin, J.D. and C.M. D'Antonio. 2004. Competition between native perennial and exotic annual grasses: implications for an historical invasion. Ecology 85:1273-1283.

Davis, A.S., P.M. Dixon and M. Liebman. 2004. Using matrix models to determine cropping system effects on annual weed demography. Ecological Applications 14:655-668.

D'Antonio, C.M. and L.A. Meyerson. 2002. Exotic plant species as problems and solutions in ecological restoration: a synthesis. Restoration Ecology 10:703-713.

D'Antonio, C. M., D. C. Odion and C. M. Tyler. 1993. Invasion of maritime chaparral by the introduced succulent *Carpobrotus edulis*. Oecologia. 95:14-21.

de Kroon, H.J. van Groenendael and J. Ehrlen. 2000. Elasticities: a review of methods and model limitations. Ecology 81:607-618.

Denslow, J.S. 1980. Gap partitioning among tropical rainforest trees. Biotropica 12 (Suppl.):47-55.

Ehrlén, J. 2003. Fitness components versus total demographic effects: evaluating herbivore impacts on a perennial herb. Am. Naturalist 162:796-810.

Ehrlén, J. and J. van Groenendael. 1998. Direct perturbation analysis for better conservation. Conservation Biology 12:470-474.

Fiedler, P.L. 1987. Life history and population dynamics of rare and common mariposa lilies (*Calochortus* Pursh: Liliaceae). J. Ecology 75:977-995.

Fink, B. and J.B. Zedler 1989a. Endangered plant recovery: experimental approaches with *Cordylanthus maritimus* ssp. *maritimus.* In: H..G. Hughes and T.M. Bonnicksen, eds. Proceedings of the first annual meeting of the Society for Ecological Restoration and Management. Madison, Wisconsin. January 16-20, 1989.

Fink, B., and J. B. Zedler. 1989b. Maximizing growth of *Cordylanthus maritimus* ssp. *maritimus*, an endangered salt marsh plant. Progress Report for the California Department of Transportation (Interagency Agreement # 11B351.26). November 20, 1989.

Fink, B. and J.B. Zedler. 1991. Salt marsh bird's-beak seed broadcasting and habitat enhancement in San Diego County. Supplemental report to the California Dept. of Transportation, San Diego, California, USA.

Fox, G.A. 2001. Failure time analysis: studying times to events and rates at which events occur. pp. 235-266 In: Scheiner, S.M. and J. Gurevitch (eds.) Design and Analysis of Ecological Experiments, 2nd. Edition. Oxford University Press. New York, New York. USA.

Gerlach, Jr., J.D. and K.J. Rice. 2003. Testing life history correlates of invasiveness using congeneric plant species. Ecological Applications 13:167-179.

Goals Project. 1999. Baylands Ecosystem Habitat Goals. A report of habitat recommendations prepared by the San Francisco Bay Area Wetlands Ecosystem Goals Project. U.S. Environmental Protection Agency, San Francisco, California/S.F. Bay Regional Water Quality Control Board, Oakland, California, USA.

Grewell. B.J., M.A. DaPrato, P.R. Hyde, & E. Rejmankova. 2003. Experimental reintroduction of endangered soft bird's beak to restored habitat in Suisun Marsh. Final report submitted to CALFED Ecosystem Restoration Project 99-N05.

Grubb, P.J. 1977. The maintenance of species richness in plant communities. The importance of the regeneration niche. Biol. Review 52:107-145.

Gurevich, J., S.M Scheiner, and G.A. Fox. 2002. The Ecology of Plants. Sinauer Associates, Inc. Sunderland, Massachusetts, USA.

Hobbs, R. and L.F. Huenneke. 1992. Disturbance, diversity and invasion: implications for conservation. Conservation Biology 6:324-337.

Hobbs, R.J. and H.A. Mooney. 1995. Spatial and temporal variability in California annual grassland: results from a long-term study. J. Veg Sci 6:43-56.

Joshi, J., D. Matthies, and B. Schmid. 2000. Root hemiparasites and plant diversity in experimental grassland communities. J. Ecology 88:634-644.

Keer, G.H. and J.B. Zedler. 2002. Salt marsh canopy architecture differs with the number and composition of species. Ecol. App 12:456-473.

Kleinbaum, D.G. 1996. Survival analysis: a self-learning text. Springer-Verlag, New York, New York. USA.

Knapp, E.E. and A.R. Dyer. 1998. When do genetic considerations require special approaches to ecological restoration: p. 3450-363 in P.L Fiedler and P.M. Kareiva (eds.) Conservation biology for the coming decade. Chapman and Hall, New York, New York, USA.

Kanpp, E.E.and K.J. Rice. 1994. Starting from seed: genetic issues in using native grasses for restoration. Restoration and Mgmt. Notes 12:40-45.

Lambrinos, J. G. 2000. The impact of the invasive alien grass *Cortaderia jubata* (Lemoine) Stapf on an endangered Mediterranean-type shrubland in California. Diversity and Distributions. 6:217-231.

Lande, R. 1988. Demographic models of the northern spotted owl (*Strix orientalis caurina*). Oecologia 75:601-607.

Marvier M.A. and D.L. Smith. 1997. Conservation implications of host use for rare parasitic plants. Conservation Biology 11:839-848.

Matthies, D. Positive and negative interactions among individuals of a root hemiparasite. Plant biology 5:79-84.

McConnaughay, K.D.M. and F.A. Bazzaz. 1990. Interactions among colonizing annuals: is there an effect of gap size? Ecology 71:1941-1951.

Menges, E.S. 1990. Population viability analysis for an endangered plant. Conservation Biology 4:52-62.

Menges, E.S. 1991. The application of minimum viable population theory to plants. pp 45-62 In: D.A. Falk and K.E. Holsinger (eds.) Genetics and Conservation of Rare Plants. Oxford U. Press, Oxford, U.K.

Menges, E. S. and C.V.Hawkes. 1998. Interactive effects of fire and microhabitat on plants of Florida scrub. Ecological Applications 8:935-946.

Menges, E.S., D.M. Waller, and S.C. Gawler. 1986. Seed set and seed predation in *Pedicularis furbishiae*, a rare endemic of the St. John River, Maine. Amer. J. Bot. 73:1168-1177.

Molau, U., B. Eriksen, and J.R. Knudsen. 1989. Predispersal seed predation in *Bartsia alpina*. Oecologia 81:181-185.

Noe, G. B., and J. B. Zedler. 2001. Spatiotemporal variation of salt marsh seedling establishment in relation to the abiotic and biotic environment. Journal of Vegetation Science 12: 61-74.

Parsons, L. S., and J. B. Zedler. 1997. Factors affecting reestablishment of an endangered annual plant at a California salt marsh. Ecological Applications 7 (1): 253-267.

Pake, C.E. and D.L. Venable. 1995. Is coexistence of Sonoran desert annuals mediated by temporal variability in reproductive success? Ecology 76:246-261.

Pavlik, B.M., D.L. Nickrent, and A.M. Howald. 1993. The recovery of an endangered plant. Creating a new population of *Amsinckia grandiflora*. Conservation Biology 7:510-526.

Pavlovic, N.B. 1994. Disturbance-dependent persistence of rare plants. p.159-193 in: M.L. Bowles and C.J. Whelan (eds.) Restoration of Endangered Species. Cambridge University Press. Cambridge, UK.

Petraitis, P.S., R.E. Latham, and R.A. Niesenbaum. 1989. The maintenance of biological diversity by disturbance. The Qtrly. Review of Biol. 64:393-418.

Petrů, M. and J. Lepš. 2000. Regeneration dynamics in populations of two hemiparasitic species in wet grasslands. Pp. 329-333 in Proceedings IAVS Symposium. Opulus Press. Uppsala, Sweden.

Picó, F.X., P.F. Quintana-Ascencio, E.S. Menges, and F. López-Barrera. 2003. Recruitment rates exhibit high elasticity and high temporal variation in populations of a short-lived perennial. Oikos 103:69-74.

Pickett, S.T.A. and P.S. White. 1985. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, San Diego, California, USA.

Press, M.C. 1998. Dracula or Robin Hood? A functional role for root hemiparasites in nutrient poor ecosystems. Oikos 82:609-611.

Press, M.C.,J.D. Graves, and G.R. Stewart. 1988. Transpiration and carbon acquisition in root hemiparasitic angiosperms. J. Exp. Botany39:1009-1014.

Press, M.C., J.D. Scholes, and J.R. Watling. 1999. Parasitic plants: physiological and ecological interactions with their hosts. pp. 175-197 in: Press, M.C., Scholes, J.D. and Barker, M.G.(eds.) Physiological Plant Ecology. British Ecological Society. Blackwell Scientific, Oxford, U.K.

Ruygt, J. 1994. Ecological studies and demographic monitoring of soft bird's beak *Cordylanthus mollis* ssp. *mollis* a California listed rare plant species. Napa Botanical Survey Services report to Natural Heritage Division, California Department of Fish and Game.

Scheiner, S.M. 2001. MANOVA: multiple response variables and multispecies interactions. p.99-115 in: S.M. Scheiner and J. Gurevitch (eds.). Design and Analysis of Ecological Experiments. Oxford University Press, New York, New York, USA.

Schemske, D.W., B.C. Husband, M.H. Ruckelhaus, C. Goodwillie, I.M. Parker, and J.G Bishop. 1994. Evaluating approaches to the conservation of rare and endangered plants. Ecology 75:584-606.

SYSTAT. 1999. SYSTAT Version 9.0 for Windows. SPSS, Inc. Chicago, Illinois.

ter Borg, S.A. 1985. Population biology and habitat relations of some hemiparasitic Schophulariaceae. P. 463-487 in: J. White (ed.) The Population Structure of Vegetation. Handbook of Vegetation Science. V.3. Junk Publishers, Dordrecht.

ter Braak, C.J.F. and P. Šmilauer XXXX CANOCO 4.5. Software for canonical community ordination. Center for Biometry, Wageningen, The Netherlands.

Vanderwier, J.M and J.C. Newman. 1984. Observations of haustoria and host preferences in *Cordylanthus maritimus* ssp. *maritimus* in Mugu Lagoon. Madrono 31:185-186.

Zens, M.S. and D.R. Peart. 2003. Dealing with death data: individual hazards, mortality and bias. Trends Ecol. Evol. 18:366-373.

Table 3.1. Repeated measures ANOVA results of the effect of gap disturbance management (disturbance), timing of seeding (season) and their interaction on established density of reproductive *Cordylanthus mollis* one and two years following seed introduction to restoration plots.

Source of Variation	**SS**	**df**	**MS**	**F**	**P**
Between Subjects:					
Disturbance	10.73	1	10.73	14.00	$\leq$ 0.0001
Season	94.23	2	13.02	16.99	$\leq$ 0.0001
Disturbance*Season	6.66	2	3.33	4.35	0.016
Block	91.14	7	13.02	16.99	$\leq$ 0.0001
Error	63.61	83	0.77		
Within Subjects:					
Disturbance	7.01	1	7.01	27.13	$\leq$ 0.0001
Season	0.68	2	0.34	1.31	0.276
Disturbance*Season	1.28	2	0.64	2.48	0.090
Block	26.70	7	3.81	14.76	$\leq$ 0.0001
Error	21.44	83	0.26		

Table 3.2. Cohort life table for the reintroduced population of *Cordylanthus mollis* at Rush Ranch in 2001 (n=60 standardized to population size 1000) monitored from seedling emergence to senescence. Fecundity values are mature seed produced per plant adjusted by the pre-dispersal granivory rate.

RUSH RANCH 2001 Restoration	Number Surviving to Stage x	Survival	Mortality	Mortality Rate (d_x/l_x)	Survival Rate ($1 - q_x$)	Fecundity (seeds/plant)
Life Cycle Stage, x	N_x	l_x	d_x	q_x	p_x	m_x
SEEDLING	1000	1.000	0.375	0.375	0.625	0
FLOWER	625	0.625	0.104	0.166	0.834	0
SEED CAPS. SET	521	0.521	0.042	0.081	0.919	0
SEED MATURATION	479	0.479	0.479	1.000		1590

Table 3.3. Cohort life table for the reference population of *Cordylanthus mollis* at Hill Slough in 2001 (n=60 standardized to population size 1000) monitored from seedling emergence to senescence. Fecundity values are mature seed produced per plant adjusted by pre-dispersal granivory rates.

HILL SLOUGH 2001 Reference	Number Surviving to Stage x	Survival	Mortality	Mortality Rate (d_x/l_x)	Survival Rate ($1 - q_x$)	Fecundity (seeds/plant)
Life Cycle Stage, x	N_x	l_x	d_x	q_x	p_x	m_x
SEEDLING	1000	1.000	0.683	0.683	0.317	0
FLOWER	317	0.317	0.033	0.104	0.896	0
SEED CAPS. SET	283	0.283	0.100	0.353	0.647	0
SEED MATURATION	183	0.183	0.183	1.000		73

Table 3.4. Cohort life table for the reintroduced population of *Cordylanthus mollis* at Rush Ranch in 2002 (n=25 standardized to population size 1000) monitored from seedling emergence to senescence. Fecundity values are mature seed produced per plant adjusted by pre-dispersal granivory rates.

RUSH RANCH 2002 Restoration	Number Surviving to Stage x	Survival	Mortality	Mortality Rate (d_x/l_x)	Survival Rate ($1 - q_x$)	Fecundity (seeds/plant)
Life Cycle Stage, x	N_x	l_x	d_x	q_x	p_x	m_x
SEEDLING	1000	1.000	0.320	0.320	0.680	0
FLOWER	680	0.680	0.800	0.118	0.882	0
SEED CAPSULE SET	600	0.600	0.400	0.067	0.993	0
SEED MATURATION	560	0.560	0.560	1.000		2006

Table 3.5. Cohort life table for the reference population of *Cordylanthus mollis* at Hill Slough in 2002 (n=25 standardized to population size 1000) monitored from seedling emergence to senescence. Fecundity values are mature seed produced per plant adjusted by pre-dispersal granivory rates.

HILL SLOUGH 2002 Reference	Number Surviving to Stage x	Survival	Mortality	Mortality Rate (d_x/l_x)	Survival Rate ($1 - q_x$)	Fecundity (seeds/plant)
Life Cycle Stage, x	N_x	l_x	d_x	q_x	p_x	m_x
SEEDLING	1000	1.000	0.880	0.880	0.120	0
FLOWER	120	0.120	0.000	0.000	1.000	0
SEED CAPSULE SET	120	0.120	0.040	0.333	0.667	0
SEED MATURATION	80	0.080	0.080	1.000		111

Table 3.6. Cohort life table for the reference population of *Cordylanthus mollis* at Southampton Bay, Benicia (BBAY) in 2002 (n=25 standardized to population size 1000) monitored from seedling emergence to senescence. Fecundity values are mature seed produced per plant adjusted by pre-dispersal granivory rates.

BENICIA - BBAY 2002 Reference	Number Surviving to Stage x	Survival	Mortality	Mortality Rate (d_x/l_x)	Survival Rate ($1 - q_x$)	Fecundity (seeds/plant)
Life Cycle Stage, x	N_x	l_x	d_x	q_x	p_x	m_x
SEEDLING	1000	1.000	0.160	0.160	0.840	0
FLOWER	840	0.840	0.120	0.143	0.857	0
SEED CAPSULE SET	720	0.720	0.160	0.222	0.778	0
SEED MATURATION	560	0.560	0.560	1.000		405

Table 3.7. Cohort life table for the reference population of *Cordylanthus mollis* at Benicia State Recreation Area (BSRA) in 2002 (n=25 standardized to population size 1000) monitored from seedling emergence to senescence. Fecundity values are mature seed produced per plant adjusted by pre-dispersal granivory rates.

BENICIA - BSRA 2002 Reference	Number Surviving to Stage x	Survival	Mortality	Mortality Rate (d_x/l_x)	Survival Rate ($1 - q_x$)	Fecundity (seeds/plant)
Life Cycle Stage, x	N_x	l_x	d_x	q_x	p_x	m_x
SEEDLING	1000	1.000	0.160	0.160	0.840	0
FLOWER	840	0.840	0.120	0.143	0.857	0
SEED CAPSULE SET	720	0.720	0.120	0.167	0.833	0
SEED MATURATION	600	0.600	0.600	1.000		73

Table 3.8. Kaplan – Meier survival analysis of the reintroduced *Cordylanthus mollis* population at Rush Ranch compared to the Hill Slough reference population in 2001. Life table vital rates of the restoration and reference populations differ (log rank test $\chi^2 = 13.595$, df=1, p = <0.0001).

POPULATION Life Stage	Number at Risk	Number Failing	K-M Survival Probability l_x (SE)
RUSH			
2:Seedling	192	18	0.906 (0.021)
3:Flower	144	24	0.755 (0.033)
4:Seed Capsule Set	96	25	0.559 (0.042)
5:Seed Maturation	48	48	0.000
HILL			
2:Seedling	240	42	0.825 (0.025)
3:Flower	180	44	0.623 (0.032)
4:Seed Capsule Set	120	49	0.369 (0.034)
5:Seed Maturation	60	60	0.000

Table 3.9. Kaplan – Meier survival analysis for the reintroduced *Cordylanthus mollis* population at Rush Ranch compared to the HILL, BBAY, and BSRA reference populations in 2002. Life table vital rates of the restoration and reference populations differ (log rank test: $\chi^2 = 58.883$, df=3, p = <0.0001).

POPULATION Life Stage	Number at Risk	Number Failing	K-M Survival Probability l_x (SE)
RUSH			
2:Seedling	100	9	0.910 (0.029)
3:Flower	75	11	0.777 (0.044)
4:Seed Caps. Set	50	11	0.606 (0.057)
5:Seed Maturation	25	25	0.000
HILL			
2:Seedling	100	23	0.770 (0.042)
3:Flower	75	23	0.534 (0.050)
4:Seed Capsule Set	50	24	0.278 (0.046)
5:Seed Maturation	25	25	0.000
BBAY			
2:Seedling	100	4	0.960 (0.020)
3:Flower	75	6	0.883 (0.035)
4:Seed Caps. Set	50	11	0.689 (0.059)
5:Seed Maturation	25	25	0.000
BSRA			
2:Seedling	100	4	0.960 (0.020)
3:Flower	75	5	0.896 (0.033)
4:Seed Caps. Set	50	10	0.717 (0.057)
5:Seed Maturation	25	25	0.000

Table 3.10. Results of MANOVA and “protected” univariate F test results on the effect of population site on fitness indicators of *Cordylanthus mollis* hemiparasites that survive to reproductive maturity. Fitness indicators included are log-transformed maximum height, branches, flower production, seed capsules set, and M_x (seeds/plant); and arcsin(square-root) transformed pre-dispersal granivory rates. Dependent variable canonical coefficients are standardized by conditional (within groups) standard deviations, while between canonical structure (canonical loadings) coefficients are correlations between individual response variables and dependent canonical variates.

MANOVA	Wilks' Lambda	F	df (effect)	df (error)	PR>F
(GLM)	0.162	6.685	18	133	≤ 0.0001

Standardized Canonical Coefficients

	CAN1	CAN2	CAN3
Height	0.897	1.117	0.353
Branches	1.124	0.455	0.357
Flowers	-2.066	-1.092	0.637
Seed Caps	-0.119	0.151	-0.545
Granivory	0.468	-0.398	0.828
Mx	0.358	0.206	0.202

Between Canonical Structure (Loadings)

	CAN1	CAN2	CAN3
Height	-0.314	0.773	0.5
Branches	0.013	0.213	0.73
Flowers	-0.571	0.401	0.676
Seed Caps	-0.488	0.31	0.445
Granivory	0.332	-0.703	0.485
Mx	-0.351	0.73	-0.129

ANOVA

Source	SS	df	MS	F	PR>F
Height	2.64	3	0.88	12.684	≤ 0.0001
Branches	38.912	3	12.971	1.931	0.136
Flowers	28.037	3	9.346	14.363	≤ 0.0001
Seed Caps	31.179	3	10.393	9.871	≤ 0.0001
Granivory	4.196	3	1.399	11.515	≤ 0.0001
Mx	168.883	3	56.294	12.006	≤ 0.0001
Error	691.558	312	2.217		

Table 3.11. Correlations between near neighbor potential host plant species density (stem density/23.5 cm^2) and *Cordylanthus mollis* seedling survival . Data reflect fate of 60 tagged seedlings at the HILL reference and Rush restoration population in 2001 (n=32 survivors and n=28 mortalities). Coefficients in bold print are significant Bonferroni adjusted probabilities.

Cordylanthus mollis
LIVE SEEDLINGS

Near Neighbor/ Potential Host Plant Species	Near Neighbor Origin	Correlation Coefficient	P Value
Apium graveolens	Exotic	0.147	1.000
Atriplex triangularis	Native	0.114	1.000
Cordylanthus mollis	Native	0.082	1.000
Cotula coronopifolia	Exotic	0.105	1.000
Cressa truxillensis	Native	-0.080	1.000
Cuscuta salina	Native	0.223	0.104
Distichlis spicata	**Native**	**0.375**	**≤ 0.0001**
Frankenia salina	Native	-0.162	1.000
Hainardia cylindrica	Exotic	-0.156	0.637
Jaumea carnosa	Native	0.182	1.000
Limonium californicum	Native	-0.123	1.000
Salicornia virginica	Native	0.223	0.104
Triglochin concinna	Native	0.103	1.000
Triglochin maritima	Native	-0.086	1.000
All Native Species	**Native**	**0.361**	**0.001**
All Exotic Species	**Exotic**	**-0.307**	**0.014**
Winter Annual Exotics	**Exotic**	**-0.353**	**0.002**

Cordylanthus mollis
SENESCENT SEEDLINGS

Near Neighbor/ Potential Host Plant Species	Near Neighbor Origin	Correlation Coefficient	P Value
Cordylanthus mollis	Native	-0.106	1.000
Cuscuta salina	Native	-0.080	1.000
Distichlis spicata	Native	-0.093	1.000
Hainardia cylindrica	**Exotic**	**-0.324**	**≤ 0.0001**
Juncus bufonius	Native	-0.209	0.480
Polypogon monspeliensis	Exotic	-0.176	1.000
Salicornia virginica	Native	-0.074	1.000
Spergularia marina	Native	-0.080	1.000

Table 3.12. Kaplan – Meier survival analysis for tagged *Cordylanthus mollis* plants in restoration disturbance treatments and controls at Rush Ranch in 2002. Life table vital rates of plants in disturbance treatments compared to un-manipulated control plots differ (log rank test: $\chi^2 = 6.814$, df=1, p = 0.009).

RESTORATION TREATMENT Life Stage	Number at Risk	Number Failing	K-M Survival Probability l_x (SE)
DISTURBANCE			
2:Seedling	48	2	0.958 (0.029)
3:Flower	36	3	0.878 (0.051)
4:Seed Capsule Set	24	3	0.769 (0.074)
5:Seed Maturation	12	12	0.000
CONTROLS			
2:Seedling	48	6	0.875 (0.048)
3:Flower	36	7	0.705 (0.069)
4:Seed Capsule Set	24	8	0.470 (0.082)
5:Seed Maturation	12	12	0.000

Table 3.13. Analysis of accelerated failure time model for *Cordylanthus mollis* time to emergence in restoration disturbance treatments compared to undisturbed control plots, using 358 non-censored values, 50 right-censored values, and a log logistic distribution (log likelihood = -500.31).

Variable	**df**	**Estimate**	**SE**	χ^2	$P > \chi^2$
Intercept	1	2.087	0.058	1300.24	< 0.0001
Treatment	1			0.02	0.887
Disturbance	1	0.012	0.082	0.02	0.887
Control	0	0	0		
Scale parameter	1	0.480	0.021		

Table 3.14. Analysis of accelerated failure time model for *Cordylanthus mollis* anthesis time in restoration disturbance treatments compared to undisturbed control plots, using 286 noncensored values, 122 right-censored values, and a gamma distribution (log likelihood = 739.17).

Variable	**df**	**Estimate**	**SE**	χ^2	P > χ^2
Intercept	1	2.878	0.0022	1761215	< 0.0001
Emergence Time	1	0.042	0.0003	24194.80	< 0.0001
Treatment	1			3.98	0.0459
Disturbance	1	0.003	0.001	3.98	0.0459
Control	0	0	0		
Scale parameter	1	0.012	0.0006		
Shape parameter	0	1.000	0		

Table 3.15. Results of MANOVA and "protected" univariate F test results on the effect of restoration treatment (clip-gap disturbance vs. controls) on fitness indicators of *Cordylanthus mollis* hemiparasites. Fitness indicators included are log-transformed maximum height, flower production, seed capsules set, and M_x (seeds/plant); fourth root transformed number of branches, and arcsin(square-root) transformed proportional emergence from seedbank, and seedling relative growth rate (10 weeks following emergence).

MANOVA (GLM)	Wilks' Lambda	F	df (effect)	df (error)	PR>F
	0.382	3.04	8	15	0.030
ANOVA					
Source	SS	df	MS	F	PR>F
Emergence	0.092	1	0.092	4.44	0.047
Sdlg RGR	3.110	1	3.110	30.04	< 0.0001
Longevity	2.118	1	2.118	8.02	0.010
Height	9.767	1	9.767	6.26	0.020
Branches	10.341	1	10.341	3.56	0.072
Flowers	69.752	1	69.752	3.50	0.075
Seed Caps	78.876	1	78.876	3.50	0.054
Mx	137.632	1	137.632	4.14	0.054
Error	1695.062	176	9.631		

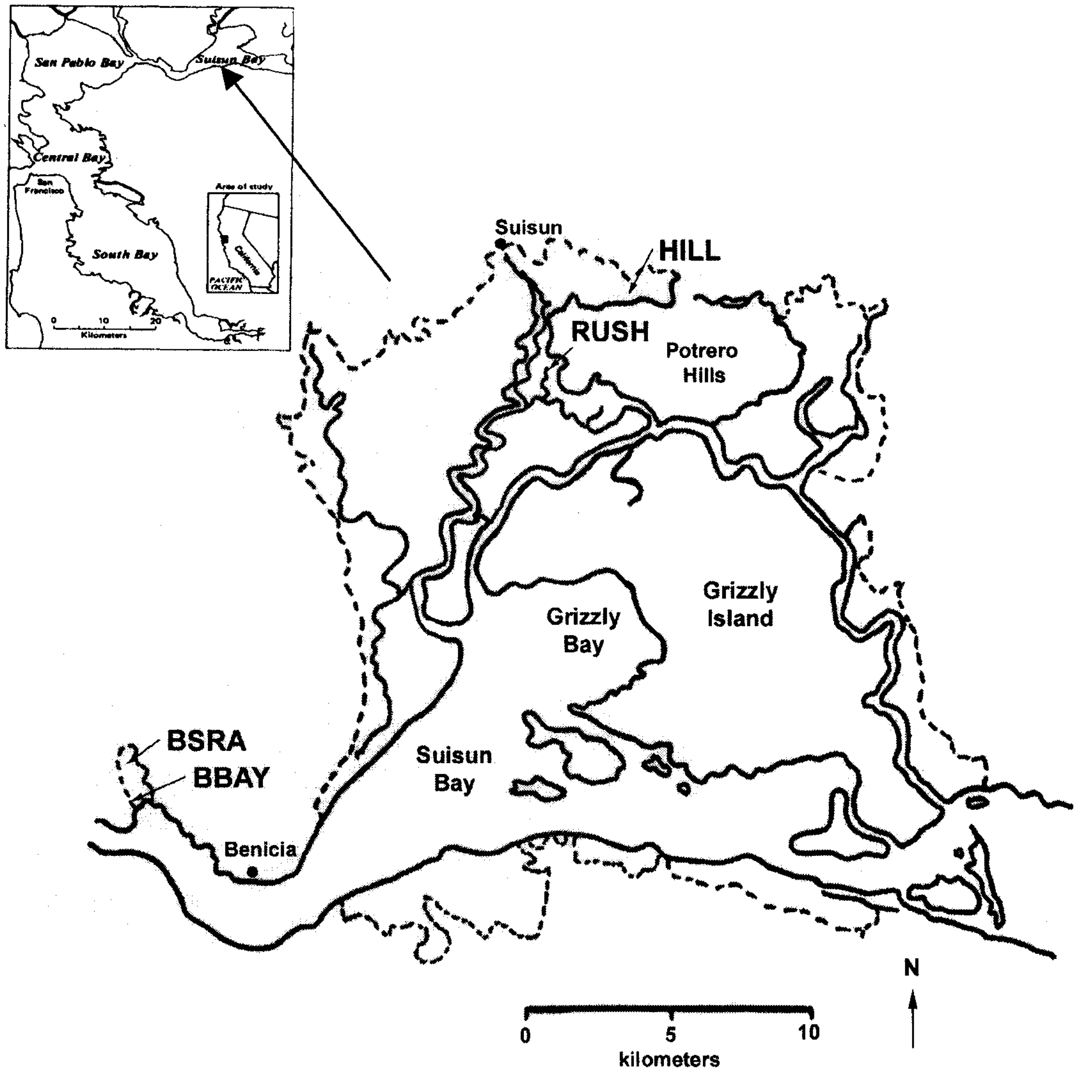


Figure 3.1. Map showing the *Cordylanthus mollis* reintroduction (RUSH) and reference population sites (BBAY, BSRA, and HILL) in the Suisun Marsh subregion of the San Francisco Estuary. Hatched lines indicate the Suisun Marsh wetland boundary. The inset maps of the San Francisco Estuary and the state of California show the location of the Suisun Marsh.

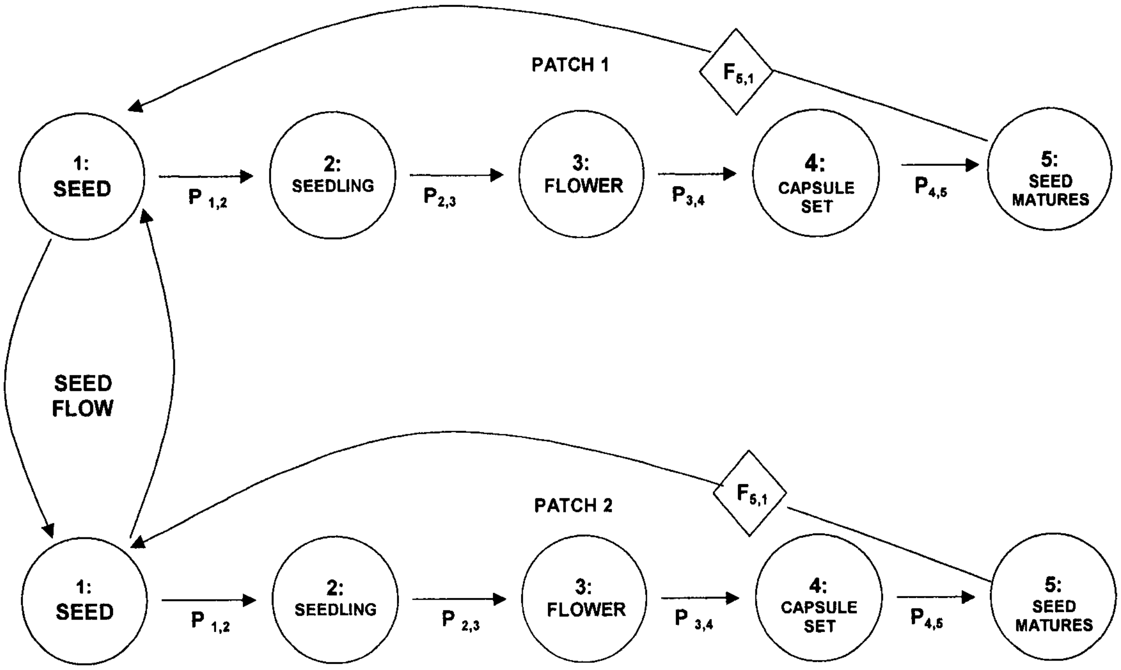


Figure 3.2. Life cycle model for two patches of *Cordylanthus mollis* potentially linked by seed flow. The populations each have five stage classes. The values $F_{x,1}$ = fecundities. The values $P_{x,x+1}$ = rates at which plants move up a stage class.

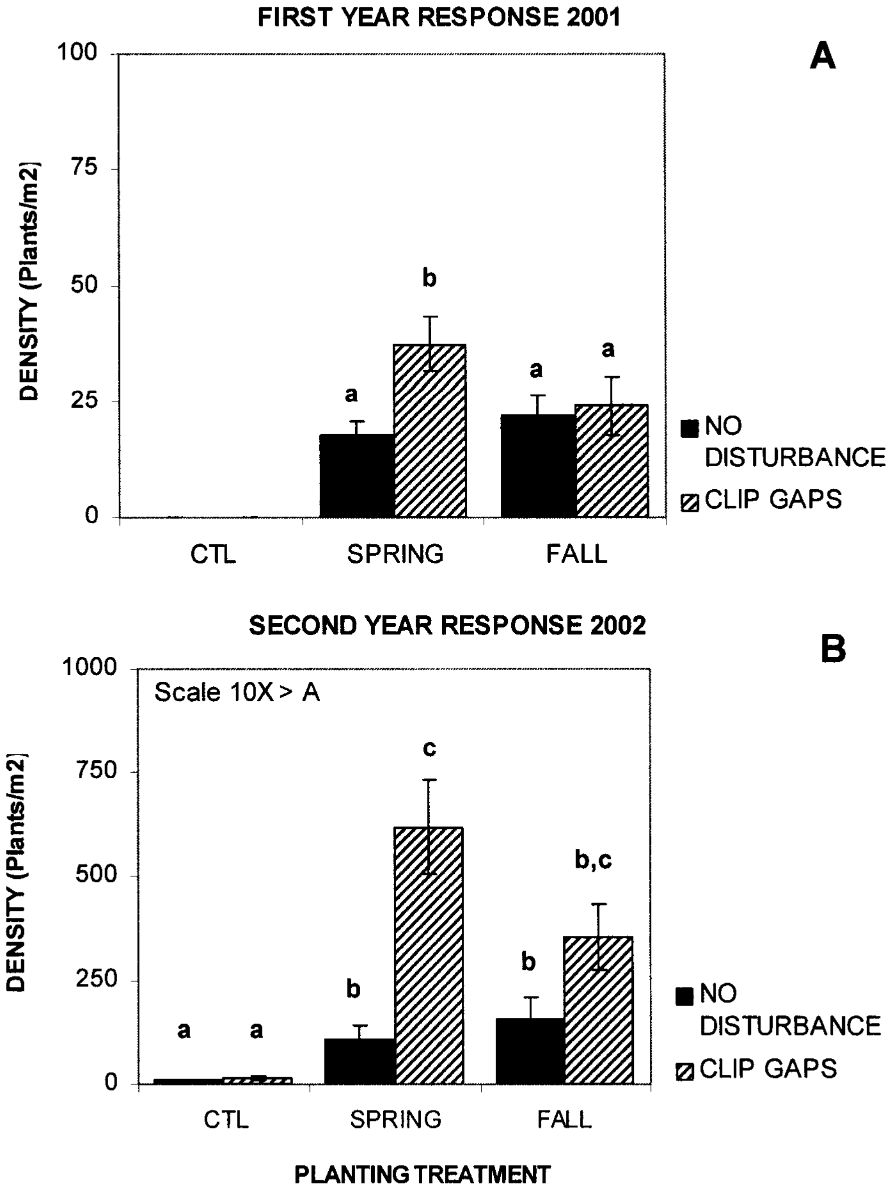


Figure 3.3. Density of *Cordylanthus mollis* within experimental treatments at peak summer bloom in the first (2001, A) and second (2002, B) growing seasons following treatment establishment in 2000. Note change in scale y-axis (B). Bars are treatment means ± 1 SE.

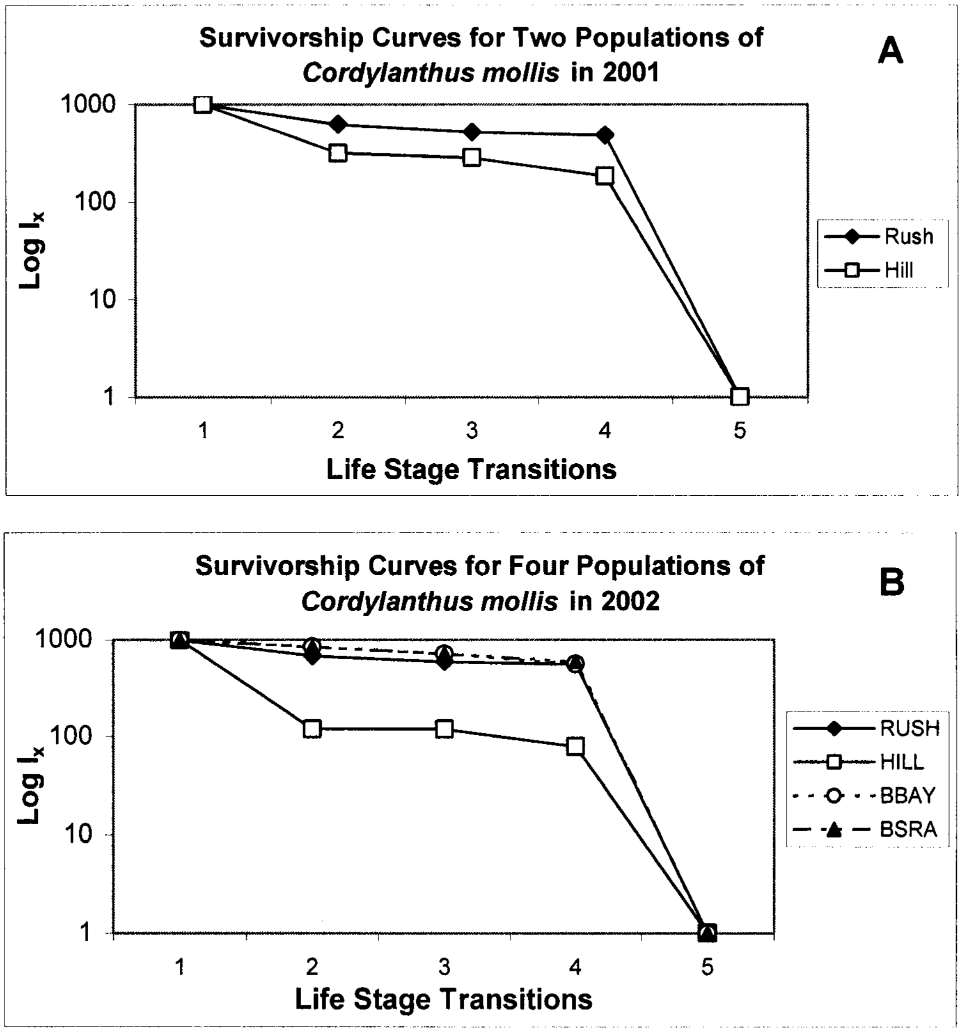


Figure 3.4. Standardized survivorship curves for emergent stages of (A) the reintroduced population of Cordylanthus mollis at Rush Ranch and the Hill Slough reference population in 2001 and (B) the reintroduced population at Rush Ranch and three reference populations at Hill Slough, Benicia – Southampton Bay, and Benicia State Recreation Area in 2002 based on data in Tables 3.1 – 3.6. Life stages are coded by number as follows: (1) seedling (2) flowering (3) seed capsule set (4) seed maturation and (5) mature plant senescence.

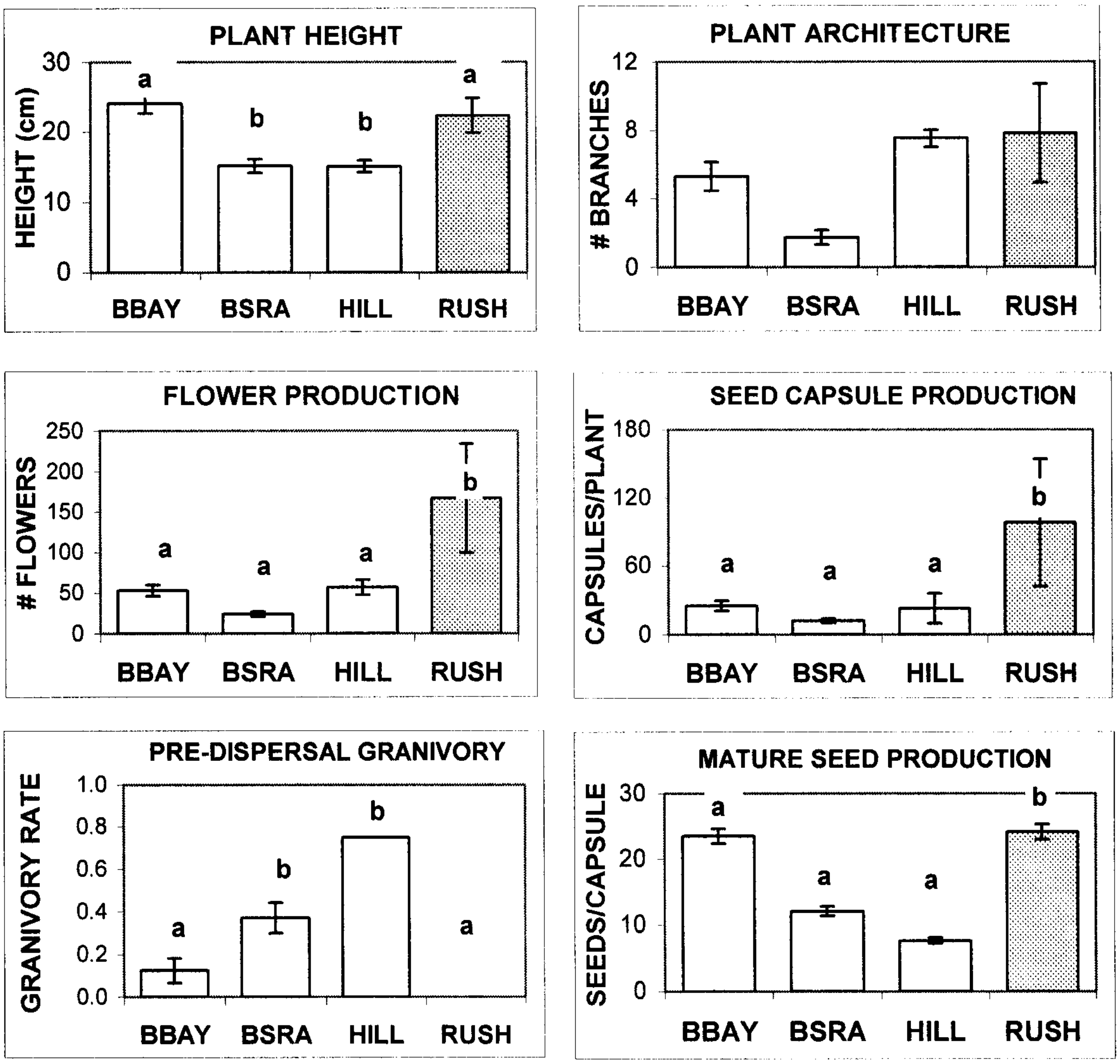


Figure 3.5. Fitness measures of Cordylanthus mollis plants that survive to reproductive maturity in 2002 at the Rush Ranch restoration and three reference population sites. Bars represent means ± 1 SE. Shaded bars represent the restoration population. Fitness metrics that are different among sites at $p = 0.05$ are marked by different lower case letters.

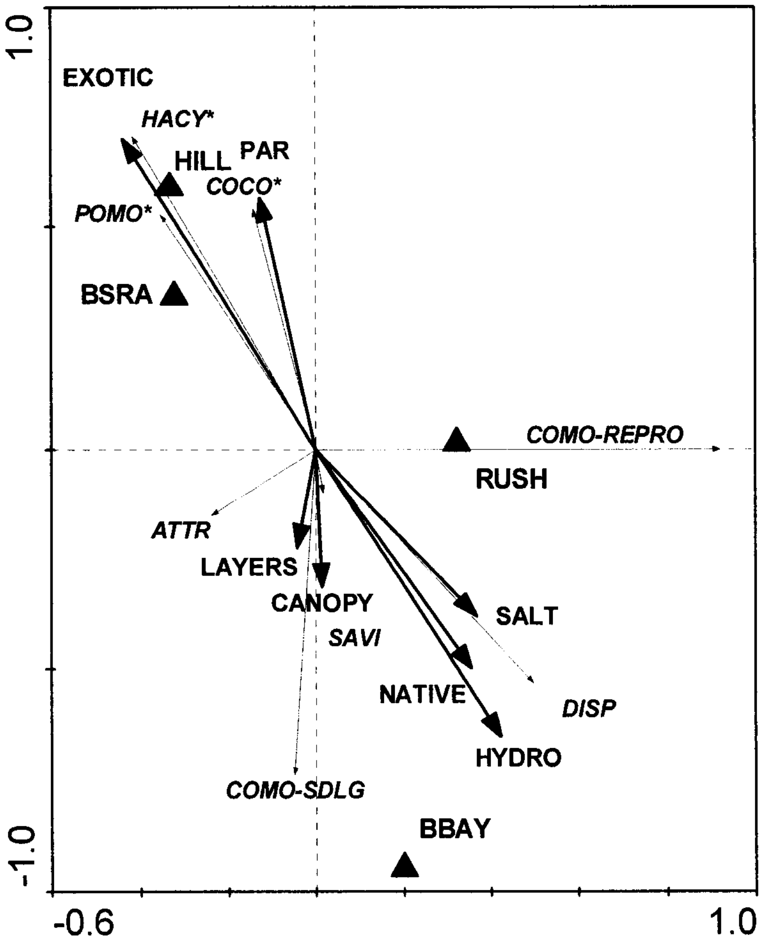


Figure 3.6. Redundancy analysis (RDA) ordination diagram of plant species and habitat conditions at endangered *Cordylanthus mollis* reference population compared to control plots at the restoration site. Populations (nominal variables) are indicated by diamond symbols (RUSH, BBAY, BSRA, and HILL). Bold arrows show the direction and relative importance (arrow length) of the environmental variables (NATIVE = proportional native host plant environment, EXOTIC = proportional exotic host plant environment, CANOPY = plant canopy height, LAYERS = plant canopy layers, PAR = below canopy photosynthetically active radiation, SALT = soil salinity at maximum rare plant seedling emergence, and HYDRO = tidal hydroperiod). Thin arrows represent plant species data including relative abundance of *COCO** = *Cotula coronopifolia*, *DISP* = *Distichlis spicata*, *HACY** = *Hainardia cylindrica*, *POMO** = *Polypogon monspeliensis*, and *SAVI* = *Salicornia virginica*). Asterisks indicate invasive winter annual species of exotic origin. Target endangered plant (*COMO* = *Cordylanthus mollis*) species data are included (*COMO-SDLG* = relative survival of COMO seedlings,while *COMO-REPRO* = relative reproductive success calculated from mature seed production of surviving individuals.

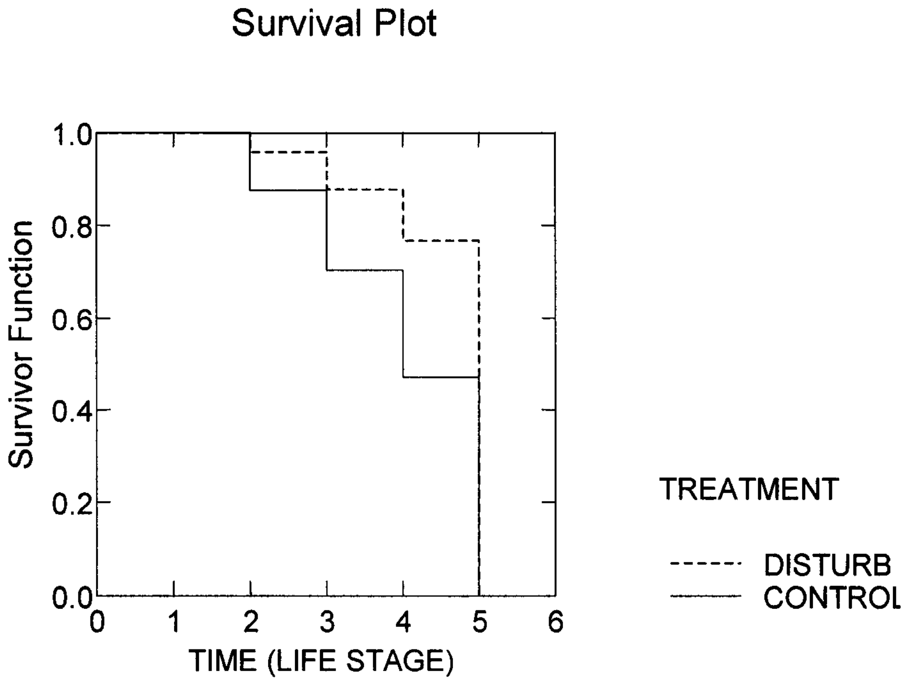


Figure 3.7. Kaplan Meier survival analysis for response of *Cordylanthus mollis* to restoration disturbance and control treatments at Rush Ranch. Time steps are failure time analysis of life stage transitions (1 = seed bank, 2 = emergent seedling, 3 = flowering, 4 = seed capsule set, and 5 = seed maturation stage).

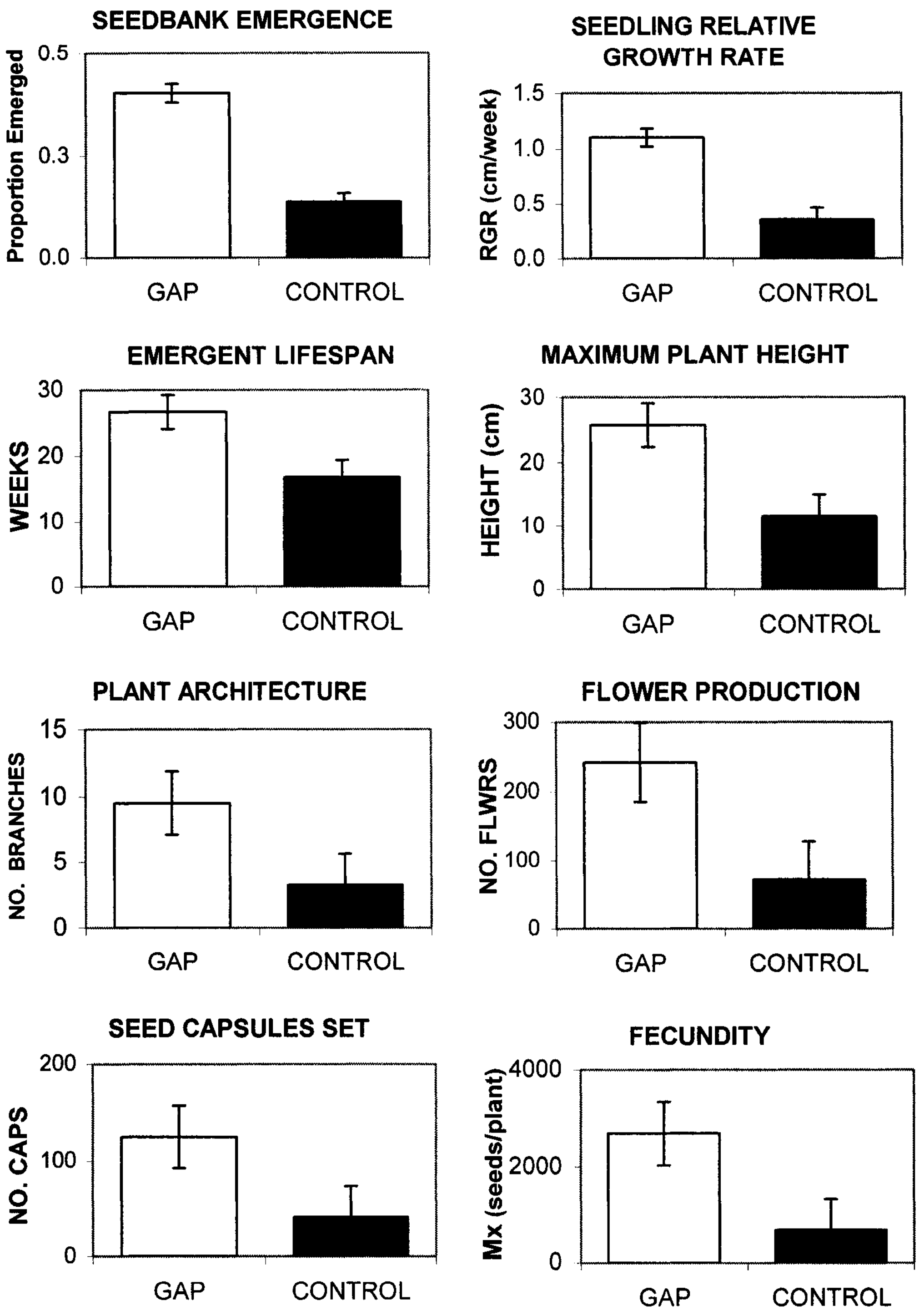


Figure 3.8. Fitness response of *Cordylanthus mollis* to canopy manipulation treatments in 2002. Bars represent means ± 1 SE.

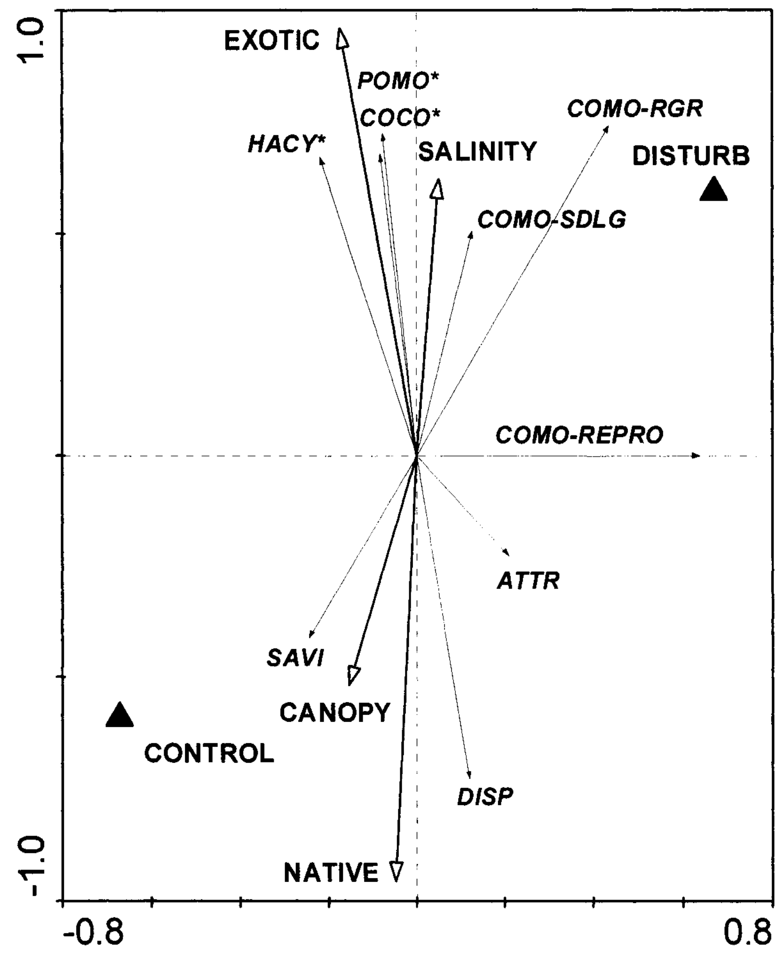
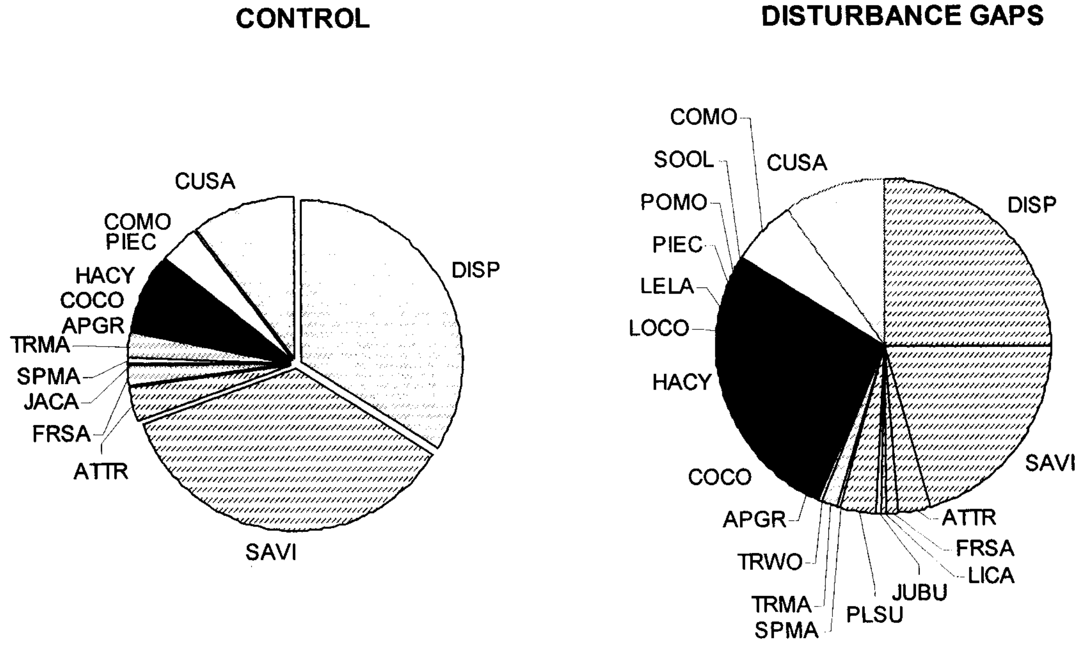


Figure 3.9. Redundancy analysis (RDA) ordination diagram for the *Cordylanthus mollis* (COMO) restoration site. Experimental treatments (nominal variables) are indicated by diamond symbols with DISTURB = clip-gap disturbance treatments and CONTROL = unmanipulated control plots. Bold arrows show the direction and relative importance (arrow length) of the environmental variables (NATIVE = proportional native host plant environment, EXOTIC = proportional exotic host plant environment, CANOPY = plant canopy structure, SALINITY = soil salinity at maximum COMO seedling emergence. Thin arrows represent plant species data including relative abundance of *COCO** = *Cotula coronopifolia*, *DISP* = *Distichlis spicata*, *HACY** = *Hainardia cylindrica*, *POMO** = *Polypogon monspeliensis*, and *SAVI* = *Salicornia virginica*). Asterisks indicate invasive winter annual species of exotic origin. Target endangered plant (*COMO* = *Cordylanthus mollis*) species data are included (*COMO-SDLG* = relative emergence of COMO seedlings from experimental seedbanks, *COMO-RGR* = 10 week relative growth rate of COMO seedlings, and *COMO-REPRO* = relative reproductive success calculated from mature seed production of surviving individuals).



CONTROL

DISTURBANCE GAPS

Figure 3.10. Percent cover of native and exotic vascular plant species in *Cordylanthus mollis* restoration treatment plots at Rush Ranch two years post-reintroduction (2002). Hatched proportions represent native species (ATTR= Atriplex triangularis; CUSA = *Cuscuta salina*; DISP=*Distichlis spicata*; FRSA= *Frankenia salina*; JUBU= *Juncus bufonius*; LICA=*Limonium californicum*; PLSU=*Plantago subnuda*; SAVI= *Salicornia virginica*; TRMA=*Triglochin maritima*; TRWO=*Trifolium wormskioldii*). Open proportions represent the endangered plant (COMO= *Cordylanthus mollis*) Charcoal filled proportions represent invading exotic species (APGR=*Apium graveolens*; COCO= *Cotula coronopifolia*; HACY= *Hainardia cylindrica*; LELA= *Lepidium latifolium*; LOCO= *Lotus corniculatus* L.; PIEC= *Picris echioides* and POMO= *Polypogon monspeliensis;* and SOOL= *Sonchus oleraceous* L.).