The biology and ecology of *Lepidium latifolium* L. in the San Francisco Estuary and their implications for eradication of this invasive weed

By

Renée O'linda Spenst
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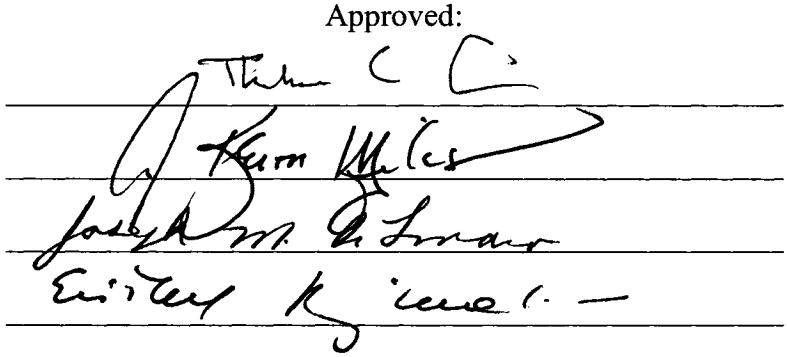

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Abstract

Lepidium latifolium (perennial pepperweed) is a widespread and invasive weed that is problematic throughout the western United States, and internationally. The aim of this research is improve understanding of *L. latifolium* biology and ecology and the influence of each on control efficacy in San Francisco Estuary tidal wetlands, with particular regard for variation along the salinity gradients in the estuary. To address these issues, I conducted three discrete but related analyses: 1) examined how seed germination and viability of perennial pepperweed change with increasing salinity in San Francisco Estuary tidal wetland sites. 2) determined if salinity, flooding, and native vegetation cover, influenced recruitment of *L. latifolium* from early developmental stages through inflorescence production. 3) assessed the relative importance of environmental constraints to *L. latifolium* distribution; then compared the role of pepperweed, relative to recognized environmental constraints, in determining other wetland species distributions; and assessed the effect of prior year *L. latifolium* cover on native and non-native species. 4) evaluated response to herbicide treatments in low and high density *L. latifolium* stands and examined post-treatment changes in native abundance at three tidally-influenced sites representing salinity gradients in the estuary. My research indicates that salinity influences every early life history stage, from viability and germination through inflorescence development and seed production. Adult plants respond to salinity at a regional scale, with declining abundance corresponding to increasing salinity. Within sites salinity continues to be a significant determinant of abundance, but plants are more closely tied to foliar nitrogen and flooding surrogates (mean soil particle size, and elevation). Patterns of herbicide efficacy resembled patterns of recruitment such that plants weakened by salinity, and more so by the combination of salinity and flooding

were most susceptible to treatments. Recommended control programs will evaluate site attributes as well as control probabilities in the development of a comprehensive management strategy.

Introduction

Lepidium latifolium, known by the common names of perennial pepperweed or tall white top, is a species that is gaining increasing recognition as a global invader. The herbaceous perennial is native to Asia and parts of southeastern Europe (Young *et al.*, 1997). The first known occurrence of *L. latifolium* was in a single field in Stanislaus County (Bellue, 1936). It was most likely introduced to California in shipments of sugar beet seeds in the 1930's (Robbins *et al.*, 1951). *Lepidium latifolium* is now found in all California counties except Del Norte, Humboldt, and Imperial (Young and Turner, 1995). It is thought to spread via small and copious seeds, or vegetative propagation (Trumbo, 1994), and establishes in a wide range of habitats, including alpine meadows (Howald, 2000), rangelands, alkali sinks, riparian corridors, and tidal wetlands (Renz, personal communication). Because of its invasive and near ubiquitous nature, the California Department of Food and Agriculture lists it as a class B noxious weed. The California Invasive Plant Council rates it as "high", a composite scoring of ecological impact, invasive potential, and distribution (Cal-IPC, 2006).

In tidal wetlands, *L. latifolium* frequently has a bimodal distribution, occurring next to channels and along the upland transition (personal observation). Once established, *L. latifolium* develops a dense root system and a nearly monocultural canopy, excluding native floral species (Trumbo, 1994). Additionally, *L. latifolium* alters the physical environment in a number of ways: salt ion pumping through the soil profile (Blank and Young, 1997), change in soil organic matter content, and increased shading (personal observation).

Lepidium latifolium is well established in San Francisco area marshes (May, 1995), and is most widespread in brackish and freshwater marshes (Grossinger *et al.*, 1998). May (1995) found that pepperweed tends to be found at upper tidal elevations, which may indicate flooding limitation since elevation can be a surrogate for flooding tolerance. Limited flooding tolerance has also been demonstrated in freshwater, seasonal wetlands (Chen and Qualls, 2002; Fredrickson *et al.*, 1999). Wetland researchers believe that pepperweed is positively correlated to disturbance, lower salinities, less frequent inundation, and sandier soils (Baye and Collins, pers. comm. *in* Grossinger *et al.*, 1998). In tidal wetlands, flooding, salinity, and nutrients are common sources of edaphic limitation in many plant species (Mitsch and Gosselink, 1993), but the shape of their relationship to pepperweed has not been thoroughly elucidated (Howald, 2000).

Life history and dispersal dynamics are poorly understood, particularly with respect to seed and seedbed ecology (Young, 1999). The role of seeds in *L. latifolium* dispersal has not been quantified (Howald, 2000), but is potentially important given a high magnitude of seeds produced (Young *et al.*, 1997) and rapid expansion rate (Zouhar, 2004). *Lepidium latifolium* is known to spread vegetatively (*e.g.* Renz, 2002), and forms a large and vigorous creeping root system that fragments easily, with fragments as small as 2.5 cm giving rise to new individuals (Wotring *et al.*, 1997). The combination of these traits makes *L. latifolium* control particularly challenging.

While resource managers rate *L. latifolium* as a high priority for control, management options are limited. Given the invasive nature of this species, a policy of non-intervention virtually guarantees that populations of *L. latifolium* will continue expanding. Herbicide use is limited to aquatic-approved herbicides. Of these, none has

achieved local eradication (*e.g.* Renz, 2002; Renz and DiTomaso, 1999; 2001; Young *et al.*, 1998), perpetuating a continual treatment scenario.

An integrated approach that capitalizes on weaknesses in *L. latifolium* life history characteristics, and integrates knowledge of site attributes governing invasability by *L. latifolium* in order to limit future invasion potential, is necessary in order to maximize control efficacy. The goal of this research is to elucidate the conditions in tidal wetlands under which *L. latifolium* is favored and to determine weaknesses in the life history and population biology of *L. latifolium* to help control its spread throughout Estuary marshes. The specific objectives are: 1) to examine variability in viability and germination of *L. latifolium* seeds, as determined by seed source and salinity; 2) to discern the effect of salinity, flooding, and vegetation on seedling recruitment; 3) to examine *L. latifolium* distribution patterns in San Francisco Estuary tidal wetlands, as compared to other wetland species; and 4) to examine ecological aspects of *L. latifolium* control in San Francisco Estuary tidal marshes.

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Chapter 1

Differential germination timing and success of perennial pepperweed (*Lepidium latifolium* L.) seeds determined by seed source and salinity

Prepared for submission

By

Spenst, R.O., S.P. Leininger, and T.C. Foin

Abstract

Perennial pepperweed (*Lepidium latifolium*) is an invasive plant that tolerates a wide range of salinities and hydrologic conditions. Populations are found growing throughout the salinity gradient in the San Francisco Estuary, California, from freshwater to saline tidal marshes. The importance of seed establishment to *L. latifolium* distribution is not well understood. The purpose of this research was to examine how seed germination and viability of *L. latifolium* change with increasing salinity in San Francisco Estuary tidal wetland sites. Seeds were collected from three sites encompassing the range of estuarine salinities. Viability was examined for each seed source over the following growing season. Seeds were buried in the field in low and high density *L. latifolium* patches and were periodically extracted. Viability was compared to seed stored under laboratory conditions. Viability was lowest at the most saline site. After 7 months, viability in the high density patch at the freshwater site had declined compared to low density and lab stored seed. Neither the brackish nor saline sites exhibited any decline in viability over the course of the growing season. Germination rates were tested in the lab using a factorial design crossing seed source and salinity level. For each of the three seed sources, germination rates declined with higher salinity. Seed collected from the most saline site had the lowest germination success, regardless of salinity treatment. The effect of salinity on viability, germination, and germination timing has important implications for *L. latifolium* establishment in tidal wetlands. Seed viability and germination rates under varying salinity treatments act as a predictive model for *L. latifolium* establishment in tidal wetlands.

Keywords: *Lepidium latifolium*, perennial pepperweed, germination, viability, tidal, wetlands, marsh, San Francisco Estuary, salinity

Introduction

Lepidium latifolium is a native to temperate parts of Europe, the Mediterranean basin, and southwestern Asia (Lye, 1989). It tolerates a broad range of environmental conditions, and establishes in a wide range of habitats including rangelands, alkali sinks, riparian corridors, and tidal wetlands (Renz, 2002). *Lepidium latifolium* is currently invading 20 states and is especially problematic throughout the western United States (USDA, 2006). In California it is listed as a "high" priority weed by the California Invasive Plant Council (Cal-IPC, 2006), and the California Department of Food and Agriculture lists it as a class B noxious weed due to its invasive and widespread nature. Population increases in tidal wetlands in the San Francisco estuary have made control and eradication efforts a priority for resource managers. Specific knowledge of *L. latifolium* biology is necessary to identify weaknesses that lead to effective control.

Improved understanding of *L. latifolium* dispersal and establishment constitutes one area of *L. latifolium* biology that could have important implications for the development of control strategies. Means of spread in tidal wetlands are poorly understood, and may vary along the salinity gradient within an estuarine system. In seasonal wetlands, seed set can be as high as 16 billion seeds per hectare per year (Young *et al.*, 1997). Seeds are also highly viable, and under favorable conditions have >90% germination (Miller *et al.*, 1986). Larson and Kiemnec (2005) studied the implications of *L. latifolium* germination for arid steppe wetlands, and found that increasing salinity

decreased germination from 28 % in freshwater to 4 % in 11.2 parts per thousand (ppt) (16 dSm^{-1}) in a 14 day trial.

Lepidium latifolium can spread by both seed and vegetative propagation (Trumbo, 1994). It has been posited that root propagation and fragmentation are the most common means of local dispersal, while establishment from seed occurs (Zouhar, 2004) and may be the most common means of long distance dispersal. However this hypothesis has not been tested adequately. While we have observed seedling recruitment at multiple sites in the estuary, Renz (2002) found that seedlings were uncommon in established pepperweed patches in seasonal wetlands. These seemingly disparate findings are not necessarily contradictory. *Lepidium latifolium* seedlings are so small that until they become well established and develop a large root system, they are easily overlooked in the field. Shading or other physical limitations in well established stands may discourage seedling recruitment (Spenst, unpublished data). Seedling recruitment may be temporally variable, with high recruitment during particularly favorable years and low recruitment in other years, as has been hypothesized for *Spartina alterniflora* X *foliosa* hybrids (Ayres, personal communication). *Lepidium latifolium* may also have allelopathic properties; a property that has been demonstrated in other mustard species (Holtz, 2001; Aminidehaghi *et al.*, 2006), which deters establishment in existing stands.

The purpose of this research was to determine the potential importance of seed dispersal to *L. latifolium* establishment in tidal wetlands. We quantified the effects of salinity on seed germination and viability throughout the growing season. We hypothesized that seed viability and germination would be inversely correlated with increasing salinity. Improved understanding of this relationship will help to determine

the potential for establishment from seed, and provide insight for the development of improved *L. latifolium* eradication and control within the San Francisco Estuary.

Materials and methods

Lepidium latifolium seed was collected at Cosumnes River Preserve (hereafter Cosumnes River), San Pablo Bay National Wildlife Refuge (San Pablo), and Don Edwards San Francisco Bay National Wildlife Refuge (Don Edwards) during the summer of 2004. Field site locations are shown in Figure 1. Seeds were kept segregated by origin, and over-wintered under ambient temperature conditions in an un-insulated storage facility in Davis, California. We conducted two separate experiments: a field-based viability study, and a laboratory-based germination study.

Field Exposure Effect on Viability

We used 50 *L. latifolium* seeds each in nylon mesh bags to assess seed viability at the three sites of differing salinities, *i.e.*, freshwater (Consumnes River), moderate salinity (San Pablo), and high salinity (Don Edwards). The nylon bags had 0.2 mm mesh which prevented seed loss while still permitting water and gas exchange. Bags were placed in low and high density patches of *L. latifolium* in order to examine density-dependent effects on seed viability. Within each patch, four bags were buried 2.5 cm below the surface in low ($\leq$40% cover) and high density ($\geq$70% cover) pepperweed patches, with 8 replicates at each density level, at each of the three sites in March 2005. Seed bags were retrieved at 1, 3, 5, and 7 months of exposure (April, June, August, and October, respectively). Salinity was measured with a refractometer at each plot during

each retrieval visit. Field viability was then compared to the viability of laboratory stored seeds to assess the effects of field conditions.

Following field retrieval, bags were rinsed with deionized water and the seeds counted. Twenty seeds were then selected at random from each bag and placed in a Petri dish lined with filter paper. The filter paper was moistened with deionized water. Twenty lab-stored control seeds were also placed in individual Petri dishes, with five replicates per seed source. The dishes were covered and placed in a temperature controlled greenhouse set to range from 15° to 27° C for 7 days and remoistened when necessary. After 7 days, all of the seeds that germinated were removed. The remaining seeds were scarified to encourage germination by carefully cutting longitudinally between the cotyledons and the radicle. The scarified seeds were then returned to the greenhouse for 3 more days to continue germinating.

Seeds that did not germinate in the greenhouse after scarification were then treated with tetrazolium red (2,3,5-triphenyl-2H-tetrazolium chloride) following the procedures described in the AOSA manual (Peters, 2000). These procedures consisted of soaking the scarified seed in 1% tetrazolium red mixture for 12-24 hours. The embryo was then carefully removed from the seed coat using a dissecting scope and probes. The tetrazolium dyes living tissue a bright red. The seed was considered viable as long as the radicle, hypocotyl, and at least half of the cotyledons were dyed red. The data from the germination, scarification, and tetrazolium phases of the study were combined to give a full picture of *L. latifolium* seed viability. Results were analyzed using ANOVA for repeated measures.

Seed Source or Salinity Effect on Germination - Laboratory

Four salinity treatments were established using Instant Ocean© brand salts and tap water, consisting of 0 ppt, 5 ppt, 15 ppt, and 25 ppt, with six replicates per treatment. Higher salinity concentrations (30 and 35 ppt) were excluded from the trial because germination did not occur at measurable rates in previous trials (unpublished data). Salinity was measured and maintained throughout the experiment. The trial continued until no seeds germinated for two consecutive measurement periods (*i.e.*, 62 days).

Seeds were placed on filter paper on a foam float in a water bath with the appropriate, randomly assigned salinity level. The experiment was conducted in a greenhouse where daily temperature fluctuated between 15° and 27° C. Seeds were considered germinated when the length of the radicle equaled or exceeded 1 mm. Seeds that did not germinate within the timeframe of the study were tested for viability using the tetrazolium red staining procedures described above.

Treatment results were compared using ANOVA. Germination timing and rates were analyzed using Multi-Response Permutation Procedures (MRPP), a nonparametric method for examining multivariate differences between groups (McCune and Grace, 2002). We used the $p \leq 0.05$ significance level.

Results

Field Exposure Effect on Viability

Average site salinities, measured between April and October, were 0.3 ppt (± 0.1 [1.96 SE]) with a seasonal range between 0 to 1 ppt at Cosumnes River; 24.5 ppt (± 1.2) with a seasonal range of 13 to 31 ppt at San Pablo; and 30.4 (± 1.2) with a seasonal range of 22 to 37 ppt at Don Edwards. Field exposures of 1 (April) and 7 (October) months

provided the greatest contrast in seed viability results (Figure 2). Field exposure in months 3 (June) and 5 (August) resulted in intermediate viabilities and did not differ statistically from the data presented (results not shown). Seeds from Don Edwards had the lowest viability, while seeds from San Pablo and Cosumnes River performed similarly across the month 1 measurements (Figure 2) (Tukey's mean separation test, $p < 0.05$). Month 7 measurements showed that seed viability in the high density pepperweed patches at Cosumnes River declined significantly relative to lab and low density treatments. This pattern did not occur at either of the more saline sites.

The effect of salinity on seed viability was best described by a second order polynomial equation (Figure 3). Viability was high for brackish (0.5-29 ppt) and freshwater sites (0-0.5 ppt), but declined for salinities exceeding approximately 23 ppt, with complete curtailment predicted for plants growing at salinities exceeding 45 ppt.

Seed Source and Salinity Effect on Germination

Increasing salinity also depressed germination rates. When seed source data was combined by treatment, it was possible to isolate the effect of salinity on germination. Increased salinity reduced the percentage of seeds that germinated, and increased the number of days to germination (Figure 4); these differences were significant (MRPP analysis). By day 31 of the trial, percent germination between freshwater and 5 ppt salinity did not differ significantly, converging between 70 % and 75 % germination. Seeds germinated most rapidly in the freshwater treatment, followed closely by the 5 ppt (Figure 4). Germination in the 15 ppt treatment slightly exceeded 15% over the course of the trial, while germination at 25 ppt was 1% (Figure 4).

By examining the seed germination rates under different salinity treatments, separated according to seed source, it was possible to examine how the source of the seed influences subsequent germination under various salinities (Figure 5). In the 0 ppt treatment, seeds from the freshwater seed source, Cosumnes River, had the highest percent germination of all the trials with 98 % germination. Germination of seeds from the brackish source, San Pablo, was 93 %, whereas seeds from the most saline source, Don Edwards, had only 29 % germination success. The fresh and brackish sources did not significantly differ, but both differed significantly from the saline source. Seeds collected from parent plants grown in the highest salinity conditions had below 50 % germination rates in all trials. While seed from Don Edwards consistently exhibited the lowest germination rates, they had the greatest germination success in the 5 ppt treatment, with 41 % germination. Germination of seeds from all three seed sources declined below 21 % at 15 ppt, and to below 2% at 25 ppt.

Of the seeds that did not germinate during the 62-day trial, a larger number of seeds from Cosumnes River (average 60% seeds at 15 ppt and 0% at 25 ppt) and San Pablo (average of 45% seeds at 15 ppt and 3% at 25 ppt) remained viable. Only a small number of seeds from Don Edwards that failed to germinate remained viable (average of 5% at 15 ppt and 2% at 25 ppt) (Tukey's test). Seeds that failed to germinate but were still viable occurred in both the 15 and 25 ppt treatments, but were most common in the 15 ppt treatment.

Discussion

Our research demonstrated that increasing salinity is negatively correlated to viability and germination rates. Seed source influences seed viability and germination

potential. *L. latifolium* seeds were highly viable and exhibited high germination rates, particularly if the seed source was located in either freshwater or brackish conditions, and those conditions prevailed at the time of germination. This research supports the findings of two earlier germination studies (Miller 1986, Larson and Kiemnec, 2005) and extends knowledge of *L. latifolium* recruitment to tidal wetlands. Field exposure had very little impact on seed viability. Although, there was a slight decrease in viability after 7 months in freshwater sites, field exposure did not curtail viability at the other sites. Even with the slight decrease in viability at the freshwater site, *L. latifolium* seed retained high viability for at least one growing season.

Salinity also had a strong influence on seed germination. At low salinity levels this manifested itself as a slight delay in germination even though seeds were viable. At higher salinity levels the delay was still apparent and germination was almost completely inhibited. This suggested that higher salinity sites may be much more resistant to seed establishment.

The effect of salinity on seed quality was also quite pronounced. This was most evident at the high salinity site. Morphological differences, in the form of a dimpled seed coat, were observed in the Don Edwards seeds, when compared to either of the other two seed sources. At Don Edwards, seeds had dramatically reduced viability and germination rates in comparison to seeds from the brackish and freshwater sources. This may be due to a reallocation of resources within the parent population due to salinity-induced stress or from salinity stress acting on the seed itself prior to seed coat hardening. The effect of seed source also seemed to influence resistance of seeds to high salinity environments. This was evidenced by the reduced rate of viability in seeds that failed to germinate.

Increased seed viability and germination in low salinity conditions suggested that recruitment from seeds was possible and perhaps even likely in freshwater and brackish habitats. The likelihood of recruitment from seed declined as salinity increased, with a germination threshold occurring at 25-30 ppt. In this upper salinity range, our results indicated that recruitment from seed would probably be quite rare.

Although our results suggest that seed viability and germination are low at elevated salinities, a common trend in wetland plant species (*e.g.* Rubio-Casal *et al.*, 2003; Ungar, 1978, 1982, 1996; Shumway and Bertness, 1992; Naidoo and Kift, 2005), a number of factors can influence early recruitment success (Espinar *et al*, 2005, Noe, 2002). Field conditions are often variable and changes in salinity may occur due to seasonal variations in rainfall or periodic freshwater flooding. Under favorable conditions, even seeds with lower viability rates may experience increased germination rates [known variously as "windows of germination" (Noe and Zedler, 2001) or "windows of opportunity" (Eriksson and Fröborg, 1996)]. Also, seed from adjacent lower salinity sites may have higher viability rates, which in turn may enable pepperweed to colonize a site where local seed may be unable to colonize.

Conclusive evidence of allelopathy in *L. latifolium* has not been demonstrated previously (Young *et al.*, 1997). However, reduced viability in high density *L. latifolium* patches at Cosumnes River is consistent with an allelopathic response. The pattern is similar to one demonstrated by Aminidehaghi *et al.* (2006) for two congeners. They found that *L. perfoliatum,* clasping pepperweed, had an inhibitory effect on *L. sativum*, garden cress, at high concentrations, but a facilitative effect at low concentrations. Viability limitation did not occur at either of the more saline sites. Further research is

needed to determine whether *L. latifolium* is allelopathic, and if so, why the allelopathic effects are ameliorated at higher salinities. Other potential explanations for include shading (Gibson *et al.*, 2002), and competition for resources (*e.g.* Minchinton *et al.*, 2006). Both are common contributors to recruitment limitation in plants.

In the context of previous research, *L. latifolium* is a prolific seed producer (Young *et al.,* 1997). While seedlings have not commonly been found in established stands (Renz, 2002), our research indicates that seeds from freshwater and brackish sources are highly viable and germinate readily. Since seeds are quite prolific, inflorescence control may be an important component of management strategies, particularly in freshwater, low-density, and un-invaded areas. In more saline conditions, spread of *L. latifolium* is probably primarily from vegetative spread and episodic events.

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Figures

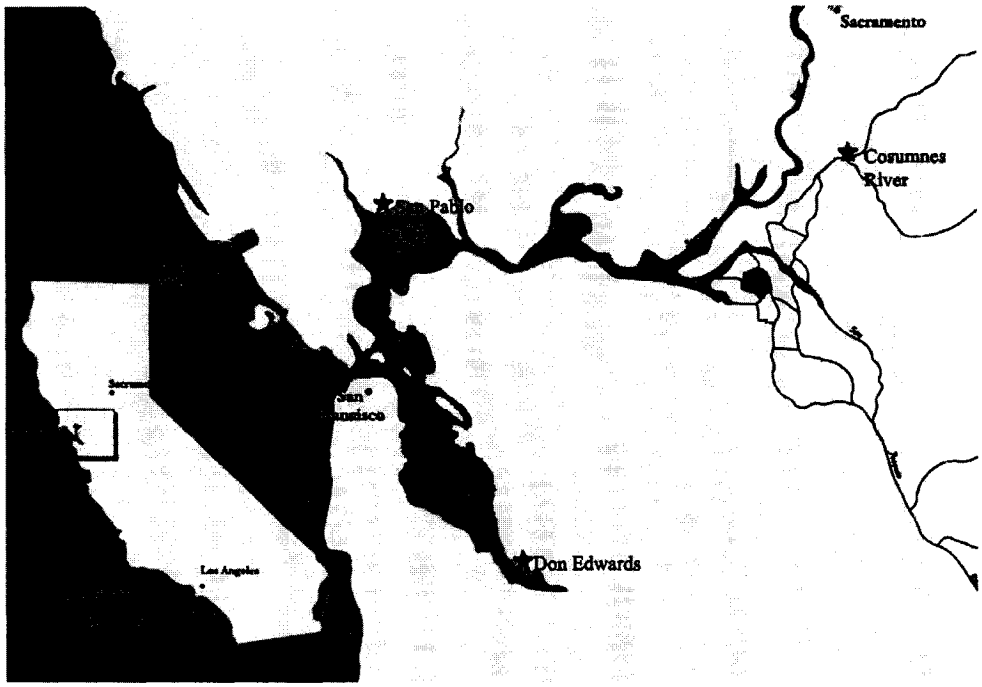

Figure 1.1 Study site locations, San Francisco Estuary, California, USA.

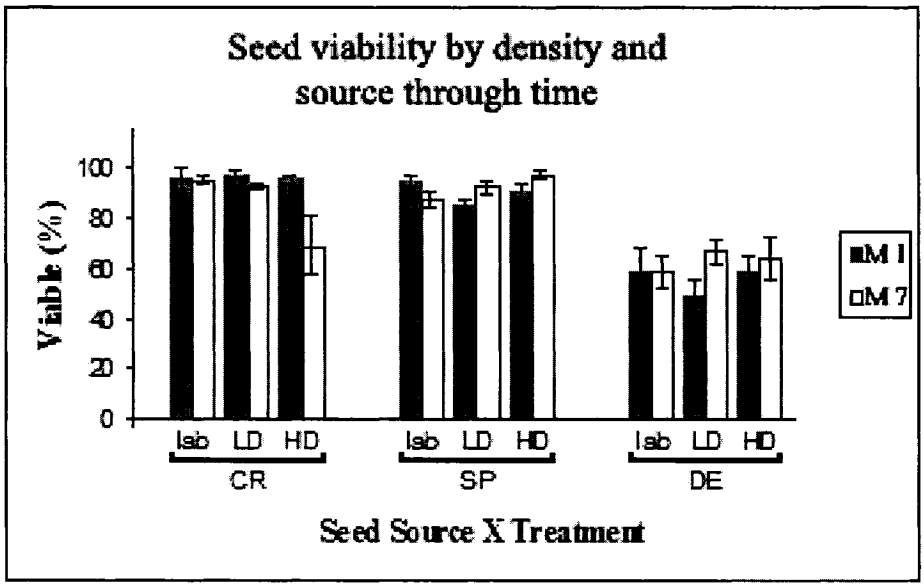

Figure 1.2. Changes in viability through 2005 growing season. Seed viability percentages for the first, April (M1), and final, October (M7), measurements are shown for each treatment: lab, low density field (LD), and high density field (HD); grouped by site, Cosumnes River (CR), San Pablo (SP), and Don Edwards (DE). Error bars show ± 1.96 SE

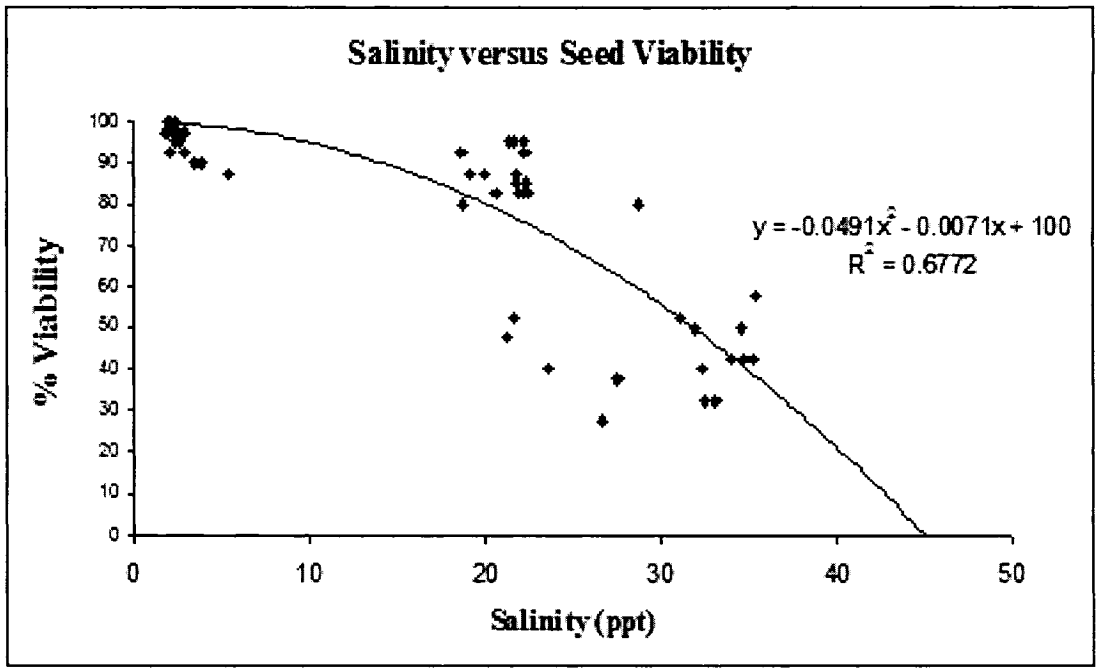

Figure 1.3. The effect of salinity on (%) seed viability. For the field seed viability study, salinity was measured at each plot in order to examine the relationship between salinity level and seed viability, and viability was averaged over time.

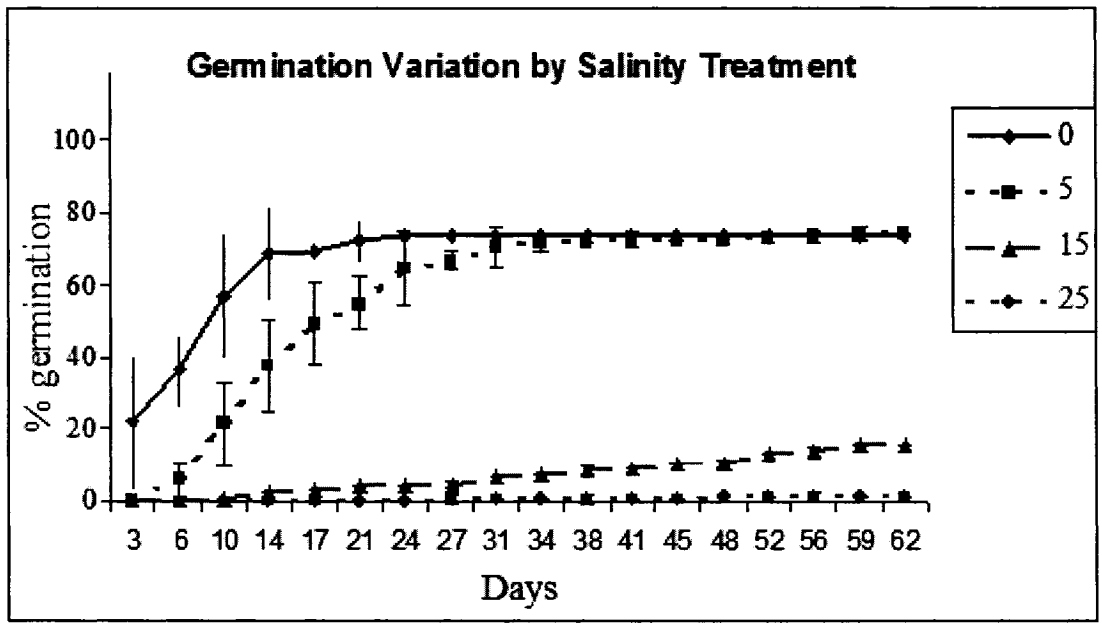

Figure 1.4. Germination variation by salinity treatment. In a greenhouse experiment, seeds from each site were placed on floats in water baths of either 0, 5, 15, or 25 ppt, and germination was monitored. This graph shows seeds (lumped by source) with sites pooled to illustrate the effect of salinity on germination.

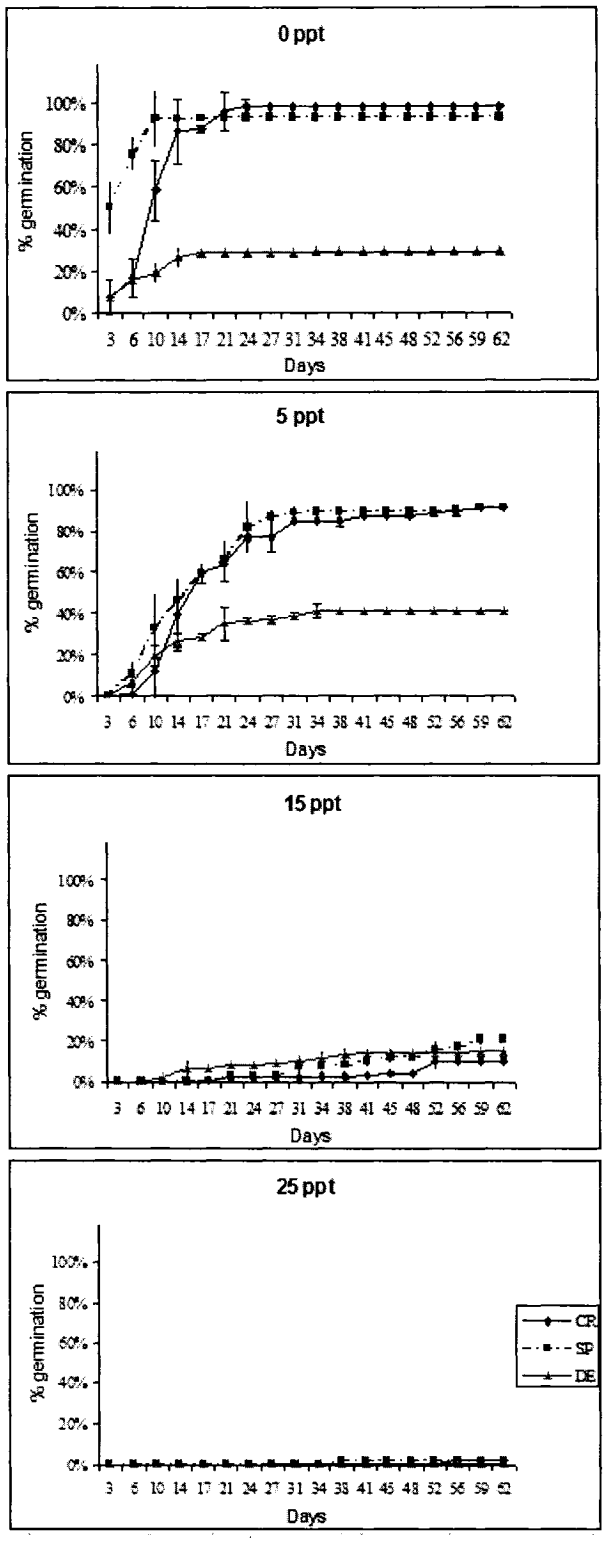

Figure 1.5. Germination (%) by seed source and salinity. Seed sources are Cosumnes River, San Pablo, and Don Edwards. Salinity levels are 0, 5, 15, and 25 ppt. Error bars are ± 1.96SE.

Chapter 2

Salinity, flooding, and vegetation produce seedling recruitment bottlenecks in *Lepidium latifolium* L.

Abstract

Lepidium latifolium (perennial pepperweed) is a highly invasive species that spreads rapidly and readily colonizes wetlands. The importance of seedling recruitment to its invasion success has not been well documented. Physical stresses are generally viewed as the predominant forces shaping species distributions in tidal wetlands. I determined if salinity, flooding, and native vegetation cover, influenced recruitment of *L. latifolium*. Specifically, I studied recruitment response to conditions common to tidal wetlands in the San Francisco Estuary. I compared recruitment response to salinity levels of 0, 10, 20, and 30 ppt, with daily or weekly flooding, on either bare ground or vegetation typical of that salinity, in a wetland mesocosm. I showed that *L. latifolium* recruitment was negatively correlated to increasing salinity at the defined developmental stages (*i.e.*, cotyledon, two-leaf, four-leaf, small rosette, large rosette, and stem), with one exception, while less frequent flooding, bare ground, and the interaction of those variables with salinity became important beyond the first two stages. Within the salinity-induced decreased recruitment response, bare ground and infrequent flooding provided the most suitable conditions for *L. latifolium* recruitment. Salinity was the dominant factor that governed recruitment success, but the roles of flooding frequency and bare ground emerged as development progressed. Low-salinity, less frequent flooding, and bare ground facilitated highly successful recruitment; under these combined conditions, eradication or control of *L. latifolium* would be difficult.

Keywords: *Lepidium latifolium*, perennial pepperweed, salinity, flooding, recruitment, tidal, wetlands, San Francisco Estuary

Introduction

Lepidium latifolium, commonly known as perennial pepperweed, is a Eurasian weed that is highly invasive in wetland and riparian areas throughout California (Howald, 2000). Bellue (1936) reported the first known occurrence within California in Stanislaus County and by 1941, populations were documented in San Joaquin, Solano, and Yolo counties (Robbins *et al.*, 1941). *Lepidium latifolium* shares vital attributes and a life history characteristic of prototypic exotic plants including the r-selected traits of small seeds, short generation time, and large annual seed crops (Baker, 1974; Rejmanek, 1996), coupled with a vigorous creeping root system (Robbins *et al.*, 1941). Seed set can be as high as 16 billion seeds per hectare per year (Young *et al.*, 1997). Seeds exhibit high viability and longevity (Robbins *et al.*, 1941; Miller *et al.*, 1986). *Lepidium latifolium* can spread by both seed and vegetative propagation (Trumbo, 1994). It establishes in a wide range of habitats, including rangelands, alkali sinks, riparian corridors, and tidal wetlands (Mark Renz, personal communication). The rapid establishment of *L. latifolium* across the western states, and the source of original introduction suggest that seed dispersal is probably the principal means of long distance expansion, despite reports that seedlings are rarely found in the field (Renz, 2002).

An extremely rapid rate of dispersal and colonization can be inferred by comparing Bellue's original citing of a single 3.7 m^2 stand (Bellue, 1936) to its statewide distribution following five decades of expansion (Mooney *et al.*, 1986). *Lepidium latifolium* routinely produces numerous seed, but the role of seed in colonization has not been quantified. Given the wide range of environmental conditions present in areas susceptible to *L. latifolium* invasion and variation in the distribution of mature

populations (Grossinger *et al.*, 1998), recruitment survivorship may vary correspondingly. In the San Francisco Estuary, *L. latifolium* exhibits a combination of salinity tolerance and broad competitive ability across a range of environmental conditions. Populations are common in fresh and brackish wetlands. In high salinity wetlands, *L. latifolium* may be limited to higher elevations (May, 1995), areas of freshwater influx, and sandier soils (Grossinger *et al.*, 1998).

Wetlands are generally viewed as more resistant to invasion by exotic speices than terrestrial systems, with salt marshes as the least hospitable because of the combined stresses of salinity and flooding (Mitsch and Gosselink, 1993). The prevailing view is that these edaphic stresses control vegetation abundance and distribution patterns in salt marshes (*e.g.* Bertness and Hacker, 1994; Pennings and Callaway, 1992). Within the range of tolerable physical conditions, plant species interactions shape diversity, distribution, and abundance (Bertness and Hacker, 1994, Pennings and Callaway, 1992). Of ecological interest is the relationship between established drivers (salinity and flooding) and mediators (vegetation presence or absence) of native species distribution in tidal wetlands, and their influence on *L. latifolium*. I asked how the primary edaphic factors, salinity and flooding, mediated by native vegetation, affected *L. latifolium* recruitment, and the implications of those interactions for the San Francisco Estuary. Specifically, I compared recruitment under various salinity, flooding, and vegetation regimes in an experimental mesocosm. I predicted that the competitive relationships, in the context of prevailing salinity and flooding conditions, would determine the rate of *L. latifolium* growth and its long-term establishment capability. I also predicted that salinity would emerge as the predominant factor influencing recruitment, followed by flooding

and vegetation. My intent was to illuminate weaknesses in *L. latifolium*'s biology that will assist in the development of a control strategy for tidal wetlands in the San Francisco Estuary.

Materials and Methods

I used a split-split plot experimental design, with salinity assigned to the main plots, and flooding and vegetation independently assigned to the split plots, with repeated measures of the split plots (Figure 1). There were two (salinity) replicates at the main plot level, and three replicates at the split plot level, for a total of 6 replicates per treatment. There were four levels of salinity (0, 10, 20, and 30 ppt) and two frequencies of flooding (daily and weekly). The experimental unit was a 5-gallon bucket, plumbed with the appropriate flooding and salinity regime, either planted with native vegetation (detailed below) or kept bare. From each main plot salinity retention basin, water was pumped into either a daily or weekly inflow system. Buckets were plumbed with a drainage pipe in the center that was flush with the soil surface, and pots were flooded to saturation in accordance with the assigned flooding frequency. An outflow pipe in each bucket returned water to each retention basin. Within the subplots, *L. latifolium* seeds were sown into bare soil, or into native vegetation. Native species were selected based on which species would be dominant at each assigned salinity level, despite varying growth forms amongst the species, so that each native-salinity pairing was representative of naturally co-occurring pairs. The pairings were as follows: *Scirpus acutus* in freshwater conditions; *Potentilla anserina* at 10 ppt; *Scirpus americanus* at 20 ppt; and *Salicornia virginica* at 30 ppt. *L. latifolium* seeds were sewn into the appropriate

treatment at a constant rate for all buckets (1 gram of seeds, approximately 900 seeds, per bucket). This rate was determined from average seed rain estimates sampled from area wetlands the season prior to commencement of the experiment.

The experiment was conducted outdoors in ambient temperature conditions in Davis, California. Native vegetation was planted into 5-gallon buckets in the spring of 2003 to allow native vegetation to become well established prior to *L. latifolium* seed additions. All had attained approximately 75% cover or better by the start of the experiment except the *S. virginica*, which had approximately 40% cover. The native species were of local stock. *Lepidium latifolium* seeds were collected at three sites in the San Francisco Estuary: Cosumnes River Preserve (average channel salinity 0.3 ppt with April-October range between 0 and 1 ppt); San Pablo Bay National Wildlife Refuge (24.5 ppt, range 13 to 31 ppt); and Don Edwards San Francisco Bay National Wildlife Refuge (30.4 ppt; range 22 to 37 ppt). Seeds were collected during the summer of 2003. Seeds from the three locations were pooled and stored until being added to the sampling units the following February 2004.

The measured response variables for *L. latifolium* recruitment were a series of developmental stages: cotyledon, two-leaf, four-leaf, small rosette, large rosette, and stem. Seed set was also enumerated for the plants that reached that stage. Data were collected a minimum of once every 2 months, based on visual observation of *L. latifolium* development to each stage. The experiment was run over an 18-month period after seed additions, and seedling recruitment was monitored over two full growing seasons. Life history data were collected, based on combined totals for all replicates within each of the

16 treatments, and survivorship and reproductive rates were calculated, based on conservative estimates of survivorship.

Treatment results were compared using ANOVA. I measured recruitment to each life stage, but the rosette and stem stages were the primary focus of analysis. Data were normalized using the square-root transformation and outliers were rescaled to the 5th and 95th confidence intervals to improve conformance with the normality assumption of ANOVA (Neil Willits, personal communication).

Results

Survivorship and life history data are presented (Table 1a-b), grouped by salinity treatments. Stems bearing seeds were produced in two treatments, both with weekly flooding and bare ground. The 0 ppt treatment 5400 seeds (approximately 900 seeds per replicate) produced 1854 cotyledons, from which 2 seed producing stems recruited (survivorship rate=0.001). Each stem produced 286 seeds (reproductive rate=0.31). At 10 ppt, beginning with the same number of seeds, 283 cotyledons recruited, and produced 8 stems, each bearing 750 seeds (reproductive rate=21.21).

Comparing treatment effects, salinity, and any interactions including salinity (except salinity*flooding*vegetation on early life stages) significantly influenced *L. latifolium* recruitment to every stage class (Table 2). While daily (frequent) flooding did not limit recruitment at the two earliest life stages (cotyledon and two-leaf), it did limit recruitment to the subsequent life stage. Vegetation presence affected recruitment to every life stage except the two-leaf stage. The interaction of flooding and vegetation became important for stages beyond cotyledon development. The interaction between

salinity, flooding, and vegetation became important for recruitment to the rosette and stem stages.

Increased salinity was negatively correlated with recruitment at every life stage, except stem development in the 10 ppt treatment ($p \leq 0.05$, Tukey's mean separation test). The strong negative relationship between recruitment to the three latest life stages (small rosettes, large rosettes, and stems) and increasing salinity (Figure 2) supported my hypothesis that salinity was a dominant factor limiting early recruitment. Within the scope of the experiment, recruitment was greatest in the 10 ppt treatment. The freshwater treatment was the only other treatment where stems recruited, and recruitment was irregular (scale of Figure 2 masks recruitment of 2 stems at 0 ppt).

Rosette and stem recruitment are shown relative to salinity and flooding treatment factors, and were selected as representative of early recruitment bottlenecks in *L. latifolium* (Figure 3). Considering the large rosette stage, a more liberal estimate of recruitment potential than stems, as an indicator for suitable habitat conditions, it becomes apparent that the combination of bare ground and infrequent flooding allows some recruitment under salinities as high as 20 ppt (Figure 3). Also, frequent flooding is far less limiting to recruitment under low salinity conditions. Vegetation delayed and reduced recruitment at nearly every stage (Tukey's test, data not shown). The vegetated buckets with the 10 ppt salinity and weekly flooding were the only vegetated treatment in which large rosettes were able to recruit. Stem production did not occur in any vegetated buckets.

Discussion

I determined that *L. latifolium* recruitment, at least at certain phases of development, varied along salinity and flooding gradients. Salinity inhibited *L. latifolium* recruitment throughout early development. The interaction between salinity and flooding frequency was not constraining at low salinities, but became progressively more limiting to recruitment as salinity and flooding frequency increased. Recruitment limitation due to edaphic conditions is common among salt marsh species because early recruitment stages may be the most sensitive to harsh conditions (Shumway and Bertness, 1992; Beare and Zedler, 1987). My findings support the view of vegetation as an important determinant of species abundance and distribution. I found that native vegetation was able to delay, and in some cases preclude, *L. latifolium* recruitment, independently of edaphic factors, in agreement with previous findings (*e.g.* Pennings and Callaway, 1992; Hellquist and Black, 2004; Crain *et al.*, 2004).

Given the strong recruitment response to salinity, one unexpected finding was increased stem production in the 10 ppt salinity over the freshwater treatment, in contrast to the trends exhibited by small and large rosette recruits. There are a few potential explanations for this pattern. One explanation for the anomalous increase in stem recruitment in the 10 ppt treatment, over recruitment in freshwater, may be that strong intraspecific competition in the freshwater treatment (*alla* Koyama and Kira, 1956; Anten and Hirose, 1998) was ameliorated in brackish conditions (personal observation), resulting in competitive release. The life history data support strong intra-specific competition in the freshwater treatment. The data illustrate a much stronger recruitment bottleneck at the cotyledon stage under the 10 ppt treatment, in contrast the freshwater

treatment which showed a bottleneck of increasing strength as development progressed. Over the long term, stem development trends might resemble small and large rosette recruitment had time and other constraints permitted extension of the experiment. This explanation is also supported by natural distribution patterns, which suggest that *L. latifolium* performs optimally in freshwater conditions. It is highly unlikely that pepperweed required some salinity in order to achieve optimal performance.

A second potential explanation is hormesis. Salinity inhibits pepperweed recruitment at high concentrations, but may stimulate biochemical or physiological function at low concentrations, such that an enhanced response in growth or productivity is realized over normal or optimal conditions. Hormesis has been established in animal and plant taxa, most commonly in relation to radiation (*e.g.* Stevens *et al.*, 1999) and herbicides (*e.g.* Schabenberger *et al.*, 1999) for plants, and may be the outcome of allelopathic responses (*e.g.* An, 2005). Stebbing (1981) demonstrated increased growth in response to suboptimal salinity in *Campanularia flexuosa* (a hydroid). Noel *et al.* (2006) demonstrated hormesis, toxicity, density dependence and an Allee effect simultaneously influencing population growth rate of a soil arthropod, *Folsomia candida*, suggesting that either mechanism need not be working in exclusion. One or more of these factors may be contributing to the increased stem production at 10 ppt, a result that remains unexplained.

Pepperweed recruitment patterns, coupled with field observations (personal observation) suggest that pepperweed distribution integrates the outcome of priority effects and competition, within the range of physically tolerable conditions. Competition has commonly been invoked to explain the role of vegetation in determining species

abundance and distribution (*e.g.* Pennings and Callaway, 1992; Hellquist and Black, 2004; Crain *et al.*, 2004), and alternative views include inhibition (Connell and Slatyer, 1977), also known as priority effects, where the first colonizer is able to dominate the site, but cannot competitively displace an earlier arrival. Consistent with the priority effects model, *Lepidium latifolium* was able to recruit into bare patches, but could not consistently displace native vegetation. However, once the species establishes, it is able to spread and outcompete natives (personal observation). The priority effects scenario is common among accounts of disturbance-mediated facilitation of invasive species. For instance, wrack disturbance facilitated *Phragmites australis* spread in a New England marsh (Minchinton, 2002). The *Spartina* spp.-invaded mudflats of San Francisco Bay are also an area of natural disturbance and little competition.

In relation to San Francisco Estuary tidal marsh distributions, the mesocosm recruitment pattern exhibited by *L. latifolium* was qualitatively similar to observed patterns, but field distribution patterns suggested that the effect of salinity might diminish as seedlings achieved a size threshold, a pattern demonstrated by Beare and Zedler (1987). If *L. latifolium*'s current distribution in the estuary reflects the results of seed recruitment, at least for the initial colonization, then it stands to reason that as salinity increases, recruitment probability may become increasingly dependent on episodic low-salinity events and seasonal amelioration, and on vegetative propagation. Recruitment in other salt marsh species has been tied to these factors (Zedler, 1983; Zedler *et al.*, 1986; Beare and Zedler, 1987).

A key implication of this research is that control of *L. latifolium* will be most effective when specifically tailored to individual site conditions. *Lepidium latifolium*

responded differently to subtle combinations of factors, which means control decisions must be dynamically matched to the situation at hand. Seeds likely play a much greater role in population establishment and expansion in freshwater and brackish wetlands, where plants are expectedly healthier, more robust, and have greater reproductive success.

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Tables

Table 2.1a. Life history table. Part I. 0 and 10 ppt. X=stage; a_x=number surviving to stage X; l_x=proportion of original cohort surviving to stage X; d_x=proportion of original cohort dying during interval; q_x=mortality rate per stage; k_x=killing power, equals $\log_{10}a_x - \log_{10}a_{x+1}$; F_x=total offspring produced; m_x=mean offspring/individual at each stage.

	X	a_x	l_x	$d_x = l_x - l_{x+1}$	$q_x = d_x/l_x$	$\text{Log}_{10}a_x$	$\text{Log}_{10}l_x$	$k_x = \log10ax - \log10ax+1$	F_x	m_x	l_xm_x
0 ppt Daily BG	coty	1969	1.00	0.33	0.33	3.29	0.00	0.17			
	2 leaf	1323	0.67	0.38	0.56	3.12	-0.17	0.36			
	4 leaf	580	0.29	0.20	0.69	2.76	-0.53	0.51			
	sm rosette	179	0.09	0.06	0.61	2.25	-1.04	0.41			
	lg rosette	69	0.04	0.04	1.00	1.84	-1.46				
	stem	0	0.00								
0 ppt Daily Veg	coty	1094	1.00	0.17	0.17	3.04	0.00	0.08			
	2 leaf	903	0.83	0.68	0.82	2.96	-0.08	0.74			
	4 leaf	163	0.15	0.14	0.94	2.21	-0.83	1.26			
	sm rosette	9	0.01	0.01	1.00	0.95	-2.08				
	lg rosette	0	0.00								
	stem	0	0.00								
0 ppt Weekly BG	coty	1854	1.00	0.34	0.34	3.27	0.00	0.18			
	2 leaf	1227	0.66	0.34	0.51	3.09	-0.18	0.31			
	4 leaf	599	0.32	0.26	0.82	2.78	-0.49	0.74			
	sm rosette	109	0.06	0.02	0.41	2.04	-1.23	0.23			
	lg rosette	64	0.03	0.03	0.97	1.81	-1.46	1.51			
	stem	2	0.00			0.30	-2.97		572	286.00	0.31
0 ppt Weekly Veg	coty	657	1.00	0.35	0.35	2.82	0.00	0.19			
	2 leaf	429	0.65	0.45	0.69	2.63	-0.19	0.51			
	4 leaf	134	0.20	0.20	0.98	2.13	-0.69	1.65			
	sm rosette	3	0.00	0.00	1.00	0.48	-2.34				
	lg rosette	0	0.00								
	stem	0	0.00								
10 ppt Daily BG	coty	267.00	1.00	0.83	0.83	2.43	0.00	0.77			
	2 leaf	45.00	0.17	0.15	0.91	1.65	-0.77	1.05			
	4 leaf	4.00	0.01	0.00	0.00	0.60	-1.82	0.00			
	sm rosette	4.00	0.01	0.00	0.00	0.60	-1.82	0.00			
	lg rosette	4.00	0.01	0.01	1.00	0.60	-1.82				
	stem	0.00	0.00								
10 ppt Daily Veg	coty	556.00	1.00	0.51	0.51	2.75	0.00	0.31			
	2 leaf	274.00	0.49	0.37	0.75	2.44	-0.31	0.61			
	4 leaf	68.00	0.12	0.10	0.78	1.83	-0.91	0.66			
	sm rosette	15.00	0.03	0.03	1.00	1.18	-1.57				
	lg rosette	0.00	0.00								
	stem	0.00	0.00								
10 ppt Weekly BG	coty	283.00	1.00	0.62	0.62	2.45	0.00	0.42			
	2 leaf	108.00	0.38	0.19	0.51	2.03	-0.42	0.31			
	4 leaf	53.00	0.19	0.06	0.32	1.72	-0.73	0.17			
	sm rosette	36.00	0.13	0.02	0.19	1.56	-0.90	0.09			
	lg rosette	29.00	0.10	0.07	0.72	1.46	-0.99	0.56			
	stem	8.00	0.03			0.90	-1.55		6003	750.38	21.21
10 ppt Weekly Veg	coty	283.00	1.00	0.35	0.35	2.45	0.00	0.18			
	2 leaf	185.00	0.65	0.31	0.48	2.27	-0.18	0.28			
	4 leaf	97.00	0.34	0.21	0.61	1.99	-0.47	0.41			
	sm rosette	38.00	0.13	0.10	0.71	1.58	-0.87	0.54			
	lg rosette	11.00	0.04	0.04	1.00	1.04	-1.41				
	stem	0.00	0.00								

Table 2.1a. Life history table. Part II. 20 and 30 ppt.

	X	a_x	l_x	$d_x = l_x - l_{x+1}$	$q_x = d_x/l_x$	$Log_{10}a_x$	$Log_{10}l_x$	$k_x = log10a_x - log10a_{x+1}$	F_x	m_x	l_xm_x
	coty	108	1	0.888889	0.888889	2.033424	0	0.95424251			
20 ppt	2 leaf	12	0.11111	0.092593	0.833333	1.079181	-0.95424	0.77815125			
Daily	4 leaf	2	0.01852	0	0	0.30103	-1.73239	0			
BG	sm rosette	2	0.01852	0.018519	1	0.30103	-1.73239				
.	lg rosette	0	0								
.	stem	0	0								
	coty	232	1	0.586207	0.586207	2.365488	0	0.38321675			
20 ppt	2 leaf	96	0.41379	0.293103	0.708333	1.982271	-0.38322	0.5351132			
Daily	4 leaf	28	0.12069	0.107759	0.892857	1.447158	-0.91833	0.97003678			
Veg	sm rosette	3	0.01293	0.012931	1	0.477121	-1.88837				
.	lg rosette	0	0								
.	stem	0	0								
	coty	43	1	0.162791	0.162791	1.633468	0	0.07716595			
20 ppt	2 leaf	36	0.83721	0.023256	0.027778	1.556303	-0.07717	0.01223446			
Weekly	4 leaf	35	0.81395	0.139535	0.171429	1.544068	-0.0894	0.08167005			
BG	sm rosette	29	0.67442	0.465116	0.689655	1.462398	-0.17107	0.50815549			
.	lg rosette	9	0.2093	0.209302	1	0.954243	-0.67923				
.	stem	0	0								
	coty	133	1	0.541353	0.541353	2.123852	0	0.33852181			
20 ppt	2 leaf	61	0.45865	0.300752	0.655738	1.78533	-0.33852	0.46311054			
Weekly	4 leaf	21	0.15789	0.142857	0.904762	1.322219	-0.80163	1.0211893			
Veg	sm rosette	2	0.01504	0.015038	1	0.30103	-1.82282				
.	lg rosette	0	0								
.	stem	0	0								
	coty	7.00	1.00	0.43	0.43	0.85	0.00	0.24			
30 ppt	2 leaf	4.00	0.57	0.14	0.25	0.60	-0.24	0.12			
Daily	4 leaf	3.00	0.43	0.00	0.00	0.48	-0.37	0.00			
BG	sm rosette	3.00	0.43	0.43	1.00	0.48	-0.37				
.	lg rosette	0.00	0.00								
.	stem	0.00	0.00								
	coty	149.00	1.00	0.60	0.60	2.17	0.00	0.40			
30 ppt	2 leaf	60.00	0.40	0.32	0.78	1.78	-0.40	0.66			
Daily	4 leaf	13.00	0.09	0.09	1.00	1.11	-1.06				
Veg	sm rosette	0.00	0.00								
.	lg rosette	0.00	0.00								
.	stem	0.00	0.00								
	coty	4.00	1.00	0.25	0.25	0.60	0.00	0.12			
30 ppt	2 leaf	3.00	0.75	0.50	0.67	0.48	-0.12	0.48			
Weekly	4 leaf	1.00	0.25	0.00	0.00	0.00	-0.60	0.00			
BG	sm rosette	1.00	0.25	0.25	1.00	0.00	-0.60				
.	lg rosette	0.00	0.00								
.	stem	0.00	0.00								
	coty	17.00	1.00	0.76	0.76	1.23	0.00	0.63			
30 ppt	2 leaf	4.00	0.24	0.24	1.00	0.60	-0.63				
Weekly	4 leaf	0.00	0.00								
Veg	sm rosette	0.00	0.00								
.	lg rosette	0.00	0.00								
.	stem	0.00	0.00								

Figures

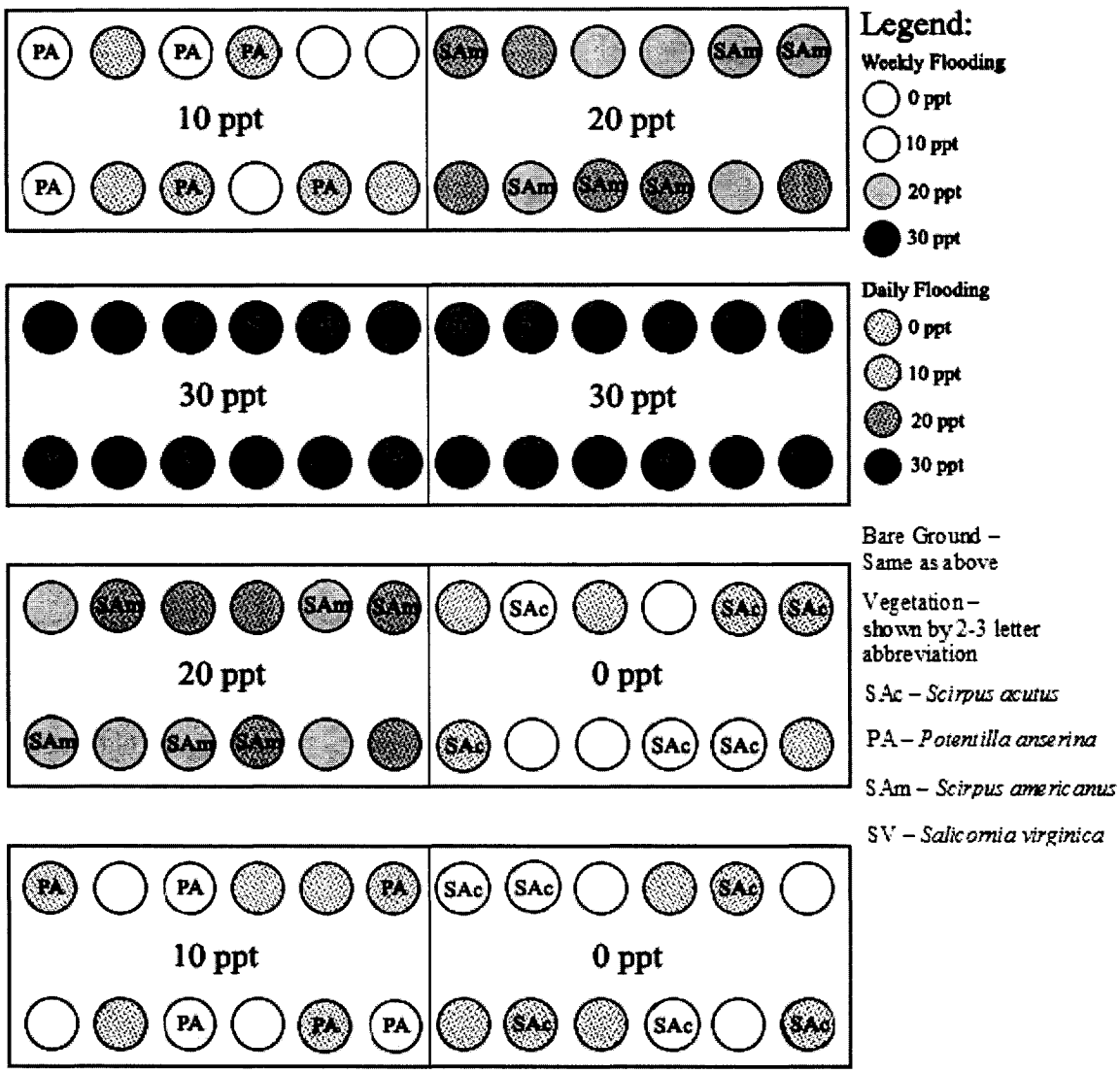

Figure 2.1. Recruitment mesocosm split-split plot experimental design. Salinity was randomly assigned to the main plots and flooding frequency and presence or absence of vegetation to the split plots. There were four salinity levels, 0, 10, 20, and 30 ppt. Within each salinity level, pots were flooded daily or weekly. Vegetated pots were assigned salinity-appropriate pairings: *Scirpus acutus* – 0 ppt; *Potentilla anserina* – 10 ppt; *Scirpus americanus* – 20 ppt; and *Salicornia virginica* – 30 ppt. The "split"-split plot refers to repeated measures of recruitment through time. The dependent variables were the following recruitment states: cotyledon, two-leaf, four-leaf, small rosette, and stem.

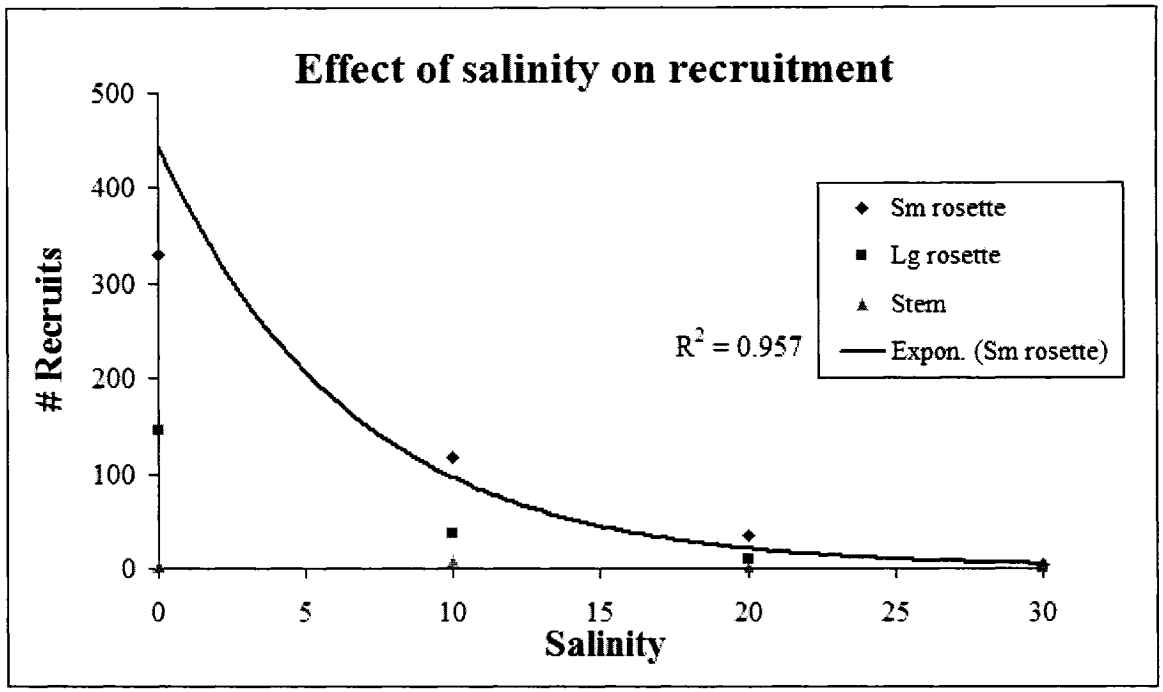

Figure 2.2. The effect of salinity on recruitment to each of three stages, small rosettes, large rosettes, and stems. Patterns of recruitment to both small and large rosette stages show a strong negative correlation between numbers of recruits and increasing salinity. Stem recruitment occurred at 0 and 10 ppt, with 2 stems recruiting at 0 ppt, and 8 stems recruiting at 10 ppt.

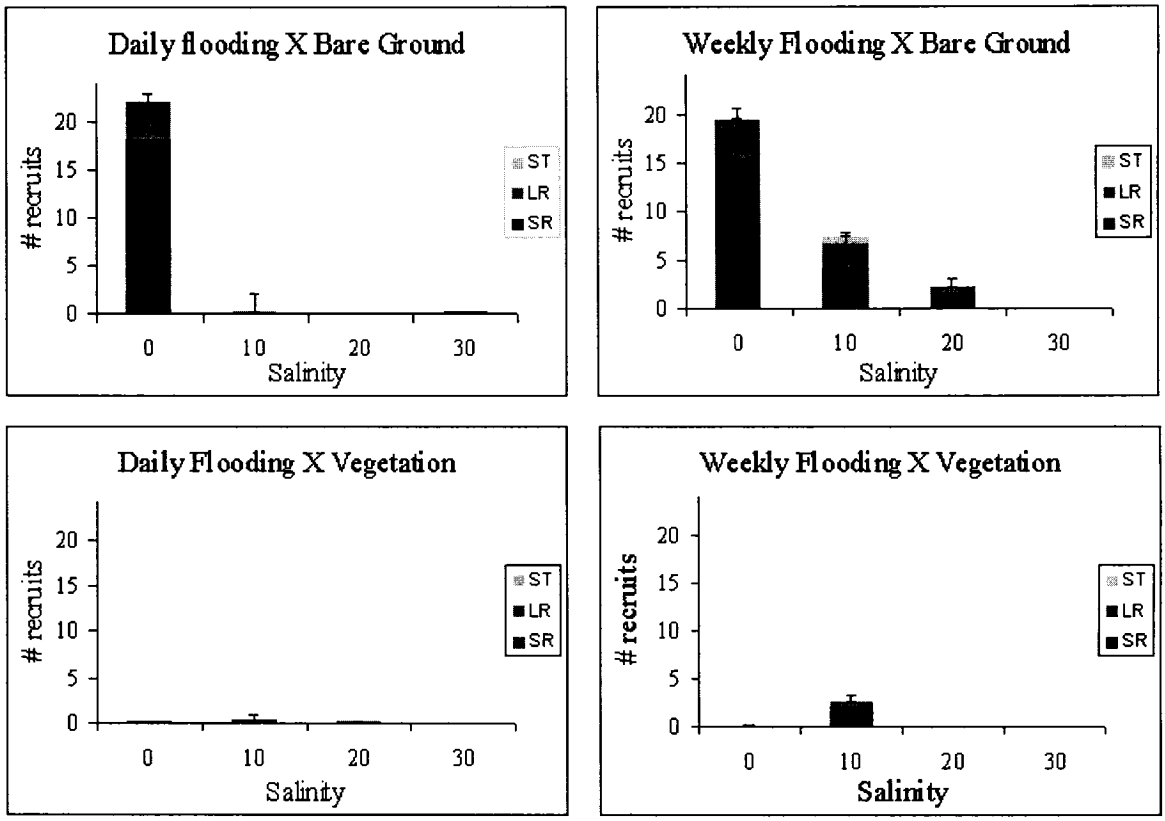

Figure 2.3. A two way comparison of the effects of flooding frequency and salinity on recruitment to small rosettes (SR), large rosettes (LR), and stems (ST). Graphs compare recruitment to later life stages across 4 levels of salinity (0, 10, 20, 30 ppt), and 2 levels of flooding (daily, weekly). Error barsh show ± 1.96 SE.

Chapter 3

Patterns of *Lepidium latifolium* L. distribution in San Francisco Estuary tidal wetlands and consequences for species composition

Abstract

The goal of this research was to improve understanding of pepperweed distributions in San Francisco Estuary tidal marshes, and to examine the effects of pepperweed abundance, relative to environmental variables, on other plant species distributions. Salinity limits species composition and distribution in wetlands, but knowledge of its effect on pepperweed is limited. To assess pepperweed response to salinity and other potentially important environmental variables; and to examine the influence of pepperweed invasion on extant plant communities, I conducted three discrete but related analyses: 1) examined the role of pepperweed, relative to recognized environmental constraints, in determining species distribution (hereafter termed 'wetland species'); 2) assessed the relative importance of environmental constraints for pepperweed distribution; 3) examined the influence of pepperweed cover in the prior or current year on richness and abundance of native and non-native species. I found that prior year pepperweed cover and soil particle size were strong determinants of other wetland species cover across three sites of different salinity gradients. Elevation was important at the freshwater and saline sites, but not at the brackish site. The importance of nitrogen, salinity, and the interaction of soil particle size and salinity increased as salinity increased. Pepperweed distribution was largely correlated to the same environmental variables within the three study sites, with one exception: the importance of elevation increased corresponding to increasing salinity. When examining trends across all three sites, pepperweed abundance was most closely associated with foliar nitrogen and soil salinity. Prior year pepperweed cover was negatively correlated with native species cover and richness in the next year, but that effect did not apply to nonnative abundance or richness, implying that the native wetland plant communities

were highly invasible. Pepperweed and environmental constraints had equally strong limiting effects on the distribution of other wetland species. My research demonstrated that pepperweed was not strongly limited by environmental constraints at the freshwater end of the tidal spectrum, but was increasingly confined to a particular range of environmental conditions as salinity increased. Consequently, the importance of flooding limitation, and other variables that influence flooding depth and duration, such as soil particle size and elevation, increased. At all sites, pepperweed played an important role in displacing other native wetland species in tidal marshes, and may facilitate future colonization by other nonnative species.

Keywords: Perennial pepperweed; *Lepidium latifolium*; salinity; elevation; nitrogen; soil particle size; San Francisco Estuary; wetlands; marshes;

Introduction

Perennial pepperweed (*Lepidium latifolium* L.; hereafter pepperweed) is a highly invasive plant that is able to successfully colonize a wide range of habitat types of varying salinities (May, 1995), including riparian corridors, rangelands, alkali sinks, wet meadows, and hay pastures (Howald, 2000). Over the past decade and a half, populations throughout California have expanded, both in patch size and range (Howald, 2000). Pepperweed combines salinity tolerance and broad competitive ability across a range of environmental conditions, in contrast to the suite of traits exhibited by many invasive wetland plants (*e.g. Spartina alterniflora, Phragmites australis, Salsola soda*) that

generally display either salinity tolerance or strong competitive ability, but not both. (Bertness, 1991; Hellings and Gallagher, 1992; Grossinger *et al.*, 1998, respectively).

Pepperweed competitive ability may be tied to high soil nitrogen levels (Blank *et al.*, 1997). In general, high nutrient levels are common in invaded sites compared to uninvaded sites. Soil nitrogen has been implicated in colonization dynamics of *Lepidium latifolium* (Blank, 2002; Renz and Blank, 2004), as well as other well-known invasive wetland species including *Typha glauca* (Woo and Zedler, 2002); and *Phragmites australis* (Rickey and Anderson, 2004). Invasive species may be more greatly advantaged by high nitrogen availability than native species (*e.g.* Rickey and Anderson, 2004). High foliar nutrient levels found in invasive species promote high relative growth rates (Vitousek 1990) compared to those of native species (Harrington *et al.* 1989, Pattison *et al.* 1998, Baruch and Goldstein 1999). High relative growth rates, coupled with early spring emergence and overwintering of basal rosettes may give pepperweed a competitive advantage over other plant species (Blank, 2002).

Other edaphic limitations have been researched more extensively in freshwater and seasonal wetlands than in tidal wetlands. Chen *et al.* (2002) found that pepperweed was adapted to flooding, but displayed reduced biomass, decreased root/shoot ratios, and increased adventitious rooting as compared to unflooded controls, demonstrating sufficient plasticity to enable the species to grow, but not to thrive, under flooded conditions. Prolonged flooding, exceeding 2 years has been shown to eradicate pepperweed (Fredrickson *et al.*, 1999). Renz (2002) found that increased inundation period halted or reversed expansion in three seasonal wetland sites compared to

abundance in previous years. He found that soil moisture, soil salinity, and species composition were not strong predictors of pepperweed distribution.

In tidal wetlands, flooding, salinity, and nutrients are common sources of edaphic limitation in many plant species (Mitsch and Gosselink, 1993), but the shape of their relationship to pepperweed has not been thoroughly elucidated (Howald, 2000). May (1995) found that pepperweed tends to be found at upper tidal elevations, which may indicate flooding limitation since elevation can be a surrogate for flooding tolerance. In a seasonal freshwater wetland, Verdi and colleagues (personal communication) failed to find a correlation between pepperweed distribution and elevation at the Cosumnes River Preserve, California, suggesting that elevation may be less constraining in freshwater than saline sites. Wetland researchers have opined that pepperweed is more productive in disturbed habitats of lower salinities, less frequent inundation, sandier soils (Baye and Collins, pers. Comm. *in* Grossinger *et al.*, 1998), and high soil nitrogen levels (Blank *et al.*, 1997). With respect to salinity limitation, pepperweed population dynamics may exhibit a pattern common to other wetland species where early stages of recruitment are highly salinity sensitive, but once plants achieve a size threshold, they are able to persist under elevated salinities (Beare and Zedler, 1987). In order to specifically address the question of salinity effects, I selected tidally influenced sites that span salinity gradients in the San Francisco Estuary.

If pepperweed distribution is largely dependant on environmental constraints, then the nature of edaphic limitation is important for determining the full invasion potential of pepperweed in tidal wetlands, and would be useful for predicting areas that are at high risk for future invasion. For previously invaded areas, it is possible to

examine the effect of invasion on the extant plant community. In addition to the detrimental effect of the invasion itself, in some cases invasive plants can generate a negative feedback loop, facilitating subsequent invasions by other nonnative species (Grosholtz *et al.*, 2003).

I examined pepperweed and native wetland species distributions within the San Francisco Estuary in order to evaluate the range and predictability of pepperweed invasion, and the impact of invasion on the extant plant community, including its potential for creation of a negative feedback loop favoring colonization by other nonnative plants. The purpose of my research was to improve understanding of pepperweed distributions in tidal marshes, and to examine the effects of pepperweed abundance, relative to certain environmental variables, on other species distributions. Within that framework, three distinct objectives emerged. First, I compared prior year pepperweed distribution, along with current year environmental and species data to examine the influence of pepperweed and other environmental variables on current species distribution. Then I assessed the relative importance of site attributes based on the strength of their correlation to pepperweed cover and stem number. Lastly, I examined if the abundance of pepperweed from year one, or pepperweed growing during year two influenced the number or percent cover of native species. My goal was to improve understanding of the role of environmental variables and other wetland species in influencing pepperweed distribution in order to identify vulnerabilities in its biology that could facilitate control.

Materials and Methods

Data were collected at multiple sites, selected to represent the range of salinities in the estuary. Sites ranged from full strength seawater (Don Edwards National Wildlife Refuge [hereafter Don Edwards]), to brackish (San Pablo Bay National Wildlife Refuge, [San Pablo]) to fresh water (Cosumnes River Preserve, [Cosumnes River]) (Figure 1). The average temporal channel and soil salinity ranges measured in March, April, July, and October were 20-36 ppt channel, 28-35 ppt soil at Don Edwards, 5-27 ppt channel, 15-28 ppt soil, at San Pablo, and 0-1 ppt channel, and 2-3 ppt soil, at Cosumnes River. The sampling units consisted of 2.0 m^2 quadrats, located in low density ($\leq$30% cover), or high density ($\geq$70% cover) pepperweed patches, all containing multiple pepperweed stems, and in adjacent uninvaded patches. There were 8 replicates of each invasion level at each site. In year one, pepperweed cover and stem number were measured. In year two, environmental variables, species cover, and pepperweed stem number were measured over the course of the growing season in February, April, July, and October.

Species composition, percent cover, pepperweed stem number, channel salinity, soil salinity, elevation, soil particle size, and disturbance, and foliar nitrogen were recorded for each sample at the prescribed month. All species were classified to genus and species, and absolute percent cover (potentially in excess of 100% if multiple canopies were present) was recorded for each species in each plot at each sampling period. Salinity was measured using a refractometer on soil samples that were hydrated to saturation, then centrifuged at 3000 rpm's for 10 minutes each in a superspeed centrifuge (DuPont Sorvall RC-5B). Elevations were measured using an autolevel and a tripod, and sighting from the nearest benchmark. Soil particle size was measured using

laser diffraction methodology (*In* Eshel *et al.*, 2005) to obtain a particle size distribution for exemplar soil samples, using a Beckman Coulter LS-230. Disturbance was based on visual estimates of locally obvious disturbance, including animal paths through the plots, and pieces of debris such as driftwood, garbage, or wrack. Don Edwards, in particular, had abundant deposits of large debris including tires, bowling balls, construction timbers, and old railroad ties. Foliar nitrogen was selected as a measure of the amount of nitrogen that was available for uptake by pepperweed. Briefly, I collected all live leaf tissue from an exemplar plant within each plot. Leaf tissue was dried at 60˚C to constant weight, then ball-milled for 3 days, or longer, or until tissue was uniformly and finely ground. Randomly selected samples, each weighing five micrograms, were analyzed at the Stable Isotope Facility, University of California, Davis, using a Europa Scientific Hydra 20/20 continuous flow isotope ratio mass spectrometer and Europa ANCA-SL elemental analyzer to convert N to N_2 gas. Results were given as mg N/gram of leaf sample.

Statistical Analyses

Correlation

First, percent cover of pepperweed from the sampling in year one was used as a predictor variable, along with the environmental variables, to examine the strength of prediction for other wetland plant species in the following year, using Canonical Correspondence Analysis (CCA). Results were compared across and within each site in order to examine patterns of influence for each variable.

Regression of pepperweed and environmental variables

Next, pepperweed stem number and percent cover from year two were combined into a representative variable (*i.e.*, 'stemcover') using Principal Components Analysis (PCA). Stem cover was regressed against the following predictor variables: time (month), soil salinity, channel salinity, soil particle size, elevation, disturbance, and foliar nitrogen for each of the sampling periods. Results were analyzed using stepwise regression. I conducted multiple analyses in order to compare within and across sites. I grouped data from across all sites to examine the relative importance of each variable at the larger scale; then separated data by site, in order to examine local patterns. Uninvaded plots were not included in this analysis.

Once each of the above analyses were completed, comparing the results of the CCA with the results of the within site stepwise regression allowed me to compare the environmental variables with the strongest correlation to other wetland species, excluding pepperweed, to those with the strongest correlation to pepperweed. Seasonality and second order interactions were not included in both models, so could not be compared.

Influence of pepperweed on natives

I then compared if pepperweed cover in the year prior to measuring species cover influenced either the number or abundance of native species or non-native species. In order to examine this question, I used multivariate analysis (MANOVA), where native cover and number of native species were dependent variables, and month, and percent cover pepperweed in 2003 and 2004 were effects measures. I repeated the analysis substituting non-native cover and number for the dependent variables, and then again

using a composite variable that combined cover and number for natives and non-natives, respectively.

Results

Correlation Analysis

Comparing the relative importance of year one and two pepperweed cover to environmental variables, I found that pepperweed percent cover, when measured at the height of the growing season in year one (LLJ03), was a strong determinant of other species cover in year two (Figures 2a-2c), as was concurrently measured pepperweed cover (LL04)(Figures 2a-2c). Of the environmental variables, soil particle size (SPS) was a consistently important determinant of species cover across sites. Elevation (Elev) was important at CR (Figure 2a) and DE (Figure 2c). The importance the variables salinity (Ssal), soil particle size*soil salinity, and foliar nitrogen (N), as determinants of species distribution, increased as salinity increased, from low importance (Figure 2a) to high importance (Figure 2c). All reported results were significant at the $p \leq 0.05$ level, unless otherwise stated (Table 1).

Regression of pepperweed and environmental variables

Foliar nitrogen, time, and soil salinity (listed in order of addition to regression model) influenced pepperweed distribution across all sites (Figure 3) (Table 2). However, the importance of these variables shifted when each site was examined separately. At Cosumnes River, nitrogen, soil particle size, and seasonality were most strongly correlated to 'stemcover'. At San Pablo, nitrogen, soil particle size, elevation, and soil salinity were most strongly correlated to stemcover. At Don Edwards, the same

variables from San Pablo, along with seasonality were significant, but the order of addition to the stepwise model differed as follows: nitrogen, repeated measures, soil particle size, elevation, and soil salinity ($p=0.136$, significant at $p=0.15$ in the stepwise regression model. All other p values ≤ 0.01). While foliar nitrogen was strongly correlated to 'stemcover' within and across sites, its importance decreased at Don Edwards, relative to the other variables.

Reviewing the results of the CCA and the stepwise regression, the environmental variables influencing the distribution of other species and the distribution of pepperweed were similar at each site, with the exception of the role of elevation. At Cosumnes River, elevation was correlated with the distribution of other species, but not with pepperweed distribution. At San Pablo, the opposite trend was true: elevation was important to pepperweed distribution, but not to the distribution of the other species.

Influence of pepperweed on natives

Both native species richness and abundance were negatively correlated to 2003 pepperweed abundance across low and high density plots and within low density plots (Figure 4a) (data for April and July are shown since most species are actively growing at that time). Native cover was also significantly correlated to the current (2004) pepperweed cover (data not shown). Within high density plots no relationship was apparent between prior year pepperweed cover and subsequent non-native species cover (Figure 4b). Non-native species cover and number were not correlated to either 2003 or 2004 pepperweed abundances.

Discussion

One goal of this research was to quantify the range and predictability of pepperweed invasion in tidal wetlands by improved understanding of factors limiting its distribution. This investigation provided evidence of the roles of salinity, elevation (a measure for flooding frequency and duration), soil particle size, disturbance, and foliar nitrogen in determining pepperweed stem number and cover. Foliar nitrogen abundance was highly correlated to 'stemcover' across and within sites, but to a lesser degree at Don Edwards than within the other two sites or across all sites. In general, pepperweed stemcover was positively correlated with foliar nitrogen content. A potential explanation for the weakening of this relationship at Don Edwards is that the relative strength of correlation to nitrogen declined because the importance of other variables increased with increasing salinity.

Pepperweed has been shown to facilitate soil nitrogen availability in invaded seasonal wetland areas by enabling the production of nitrogen-cleaving enzymes (Blank, 2002). The strong correlation between 'stemcover' and foliar nitrogen across and within sites supported the linkage between nitrogen uptake and pepperweed productivity (*i.e.* stem number and % cover). High foliar nitrogen content encourages high relative growth rates (Reich *et al.*, 1995). Increased relative growth rates, coupled with early spring emergence and overwintering of basal rosettes form a suite of traits that give pepperweed a competitive advantage over other wetland plant species.

I determined that the strength of the relationship between pepperweed and elevation increased as salinity increased. On the whole, other wetland plant species did

not exhibit the same pattern. The influence of both elevation and soil particle size on pepperweed was potentially representative of increasing flooding limitation as salinity increased. Both variables strongly influence soil water retention (Pachepsky *et al.*, 2001; Guber *et al.*, 2003). Stemcover was positively correlated to increasing soil particle size and increasing elevation at the most saline site, while at the freshwater site stemcover exhibited a negative correlation to soil particle size, and there was not a relationship to elevation. The increased soil particle size in more saline sites provides correlational support for pepperweed preference of sandier soils (*in* Grossinger *et al.*, 1998).

This research also may help clarify the range of disparate conclusions regarding the importance of elevation, ranging from unimportant at a Cosumnes River Preserve seasonal wetland site (Verdi and colleagues, unpublished data) to the most strongly correlated variable at Don Edwards. My findings support the theory that increased edaphic stress caused by increased salinity restricts pepperweed distribution to a smaller range of elevation and soil conditions, both of which influence flooding depth and duration (*in* Grossinger *et al.*, 1998).

One of the most surprising findings was that although salinity emerged from this analysis as a variable that was correlated to pepperweed 'stemcover', its relative influence was lesser than many of the other variables measured. The importance of salinity may be its mediating effect on pepperweed in the context of other variables such as elevation and soil particle size. Grossinger *et al.* (1998) hypothesized that pepperweed is sensitive to flooding and to salinity, and increased levels of salinity decrease the range of flooding that pepperweed can handle. This research supports their hypothesis. Based on their predictions, I would expect salinity to cause a visually apparent decrease in

pepperweed abundance, limiting the patches to a restricted range of flooding conditions within the marsh, while conditions between patches would be expected to be quite similar; this prediction was consistent with field observations. Patches at Don Edwards were most restricted to higher elevations and adjacent to channels, but were largely coincident with disturbance (personal observation).

The strength of correlation between 'stemcover' and time, both within and across sites (except at San Pablo), reflected seasonality in pepperweed growth. I attributed the limited response to seasonal changes at San Pablo to comparatively less seasonal variability in the growth form of pepperweed (personal observation).

Although vegetation may strongly suppress pepperweed recruitment into a site initially (unpublished data), I found that once it became established, it had a strong influence on the composition of other species. In contrast to vegetation-induced recruitment limitation, the presence of other species did not appear sufficient to limit pepperweed once it became established. Pepperweed apparently was limited primarily by environmental constraints, and the interaction between particular environmental variables, more so than by competition from other species. This is consistent with the findings of Pennings and Callaway (1992) implicating environmental constraints at primary determinants of wetland species distribution.

While other species were unable to limit pepperweed once it established, pepperweed could have a fairly strong impact on the extant plant community within an invaded site. The strength of correlation of prior years pepperweed cover to the distribution of other species the following year was comparable or greater than the measured environmental variables. This suggests that pepperweed was able to increase at

the expense of other species. Furthermore, the potential existed for a negative feedback loop where nonnative species were unaffected by prior year pepperweed cover, but native species were negatively impacted. My findings indicated that pepperweed could have a direct, negative effect on native species through replacement, and in the worst-case scenario, natives would be disfavored.

A goal of this research was to improve understanding of the role of environmental variables and other wetland species in influencing pepperweed distribution. My findings indicated that pepperweed distribution was more closely linked to environmental conditions than to the presence or absence of other species once it established in a site. For the extant plant community, the potential for this species to displace natives over the long term, and to negatively influence both native species richness and abundance reinforce the need for effective management strategies.

Acknowledgements

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Tables

Table 3.1. Forward selection results from CCA: summary of p-values. Abbreviations are as follows: SPS (soil particle size); LLJ03 (*L. latifolium* cover in July 2003); LL04 (*L. latifolium* distribution measured repeatedly through 2004); Elev (elevation); N (nitrogen).

	Cosumnes River	San Pablo	Don Edwards
SPS	0.002	0.004	0.002
LLJ03	0.002	0.004	*
LL04	*	*	0.002
Elev	0.002	0.254	0.002
SPS*Elev	0.044	0.114	0.044
N	0.404	0.272	0.056
SPS*Ssal	0.740	0.014	0.046
Ssal	0.538	0.062	0.022

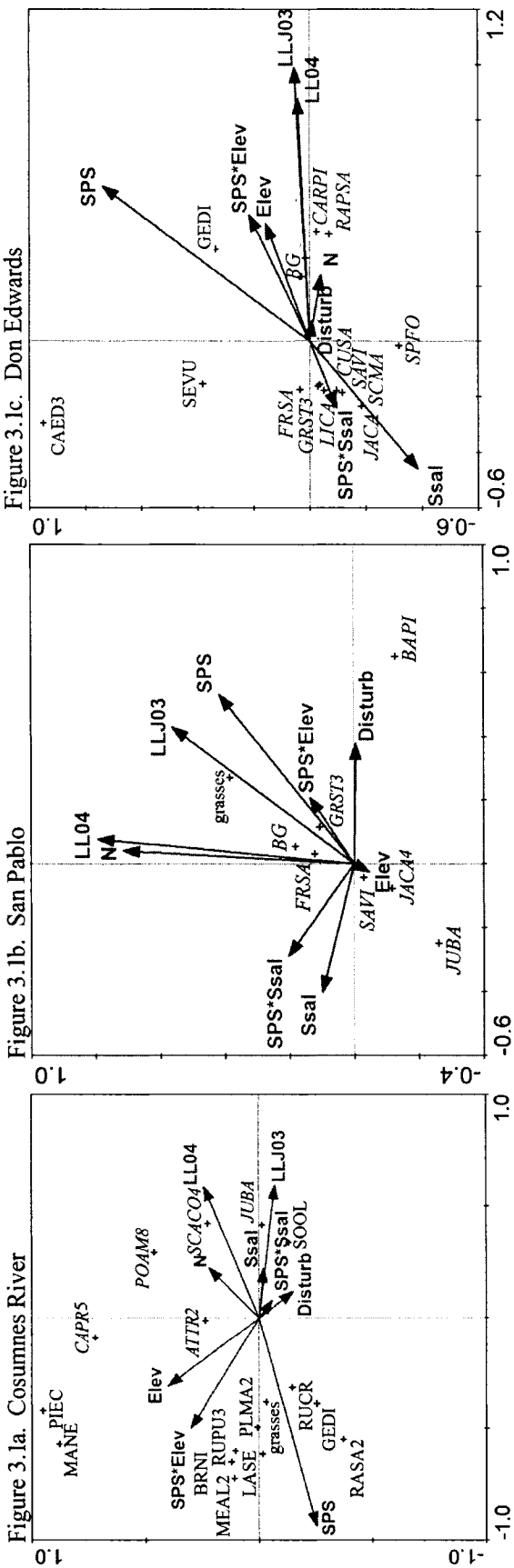
*variable not selected during forward selection of variables

Table 3.2. Influence of environmental factors on pepperweed: order of addition to the stepwise regression.

	All Sites	Cosumnes River	San Pablo	Don Edwards
Nitrogen	1	1	1	3
Repeated Measures	2	3	---	4
Soil Salinity	3	---	4	5
Soil Particle Size	---	2	2	2
Elevation	---	---	3	1

Figures

Refer to Figure 1.1 for a study site location map.



Figures 3.1a-c. Canonical Correspondence Analysis (CCA) biplots of species and environmental variables at three study sites in the San Francisco Estuary, California. Species position in the biplot, relative to the length and direction of the environmental variables (arrows), indicates the strength of that variable's effect on species distribution. Arrows represent the following variables: Soil Particle Site (SPS); elevation (Elev); *L. latifolium* measured in July 2003 (LLJ03); *L. latifolium* measured at repeated intervals throughout 2004 (LL04); foliar nitrogen (N); soil salinity (Ssal); and apparent disturbance (Disturb). Terms joined by a '*' represent interactions of the two variables. Species are represented by a 4-5 digit alpha-numeric sequence which corresponds to the abbreviations used by the Plants database (United States Department of Agriculture, 2006). Native species are italicized. Non-native grasses were individually identified, but were lumped for ease of interpretation.

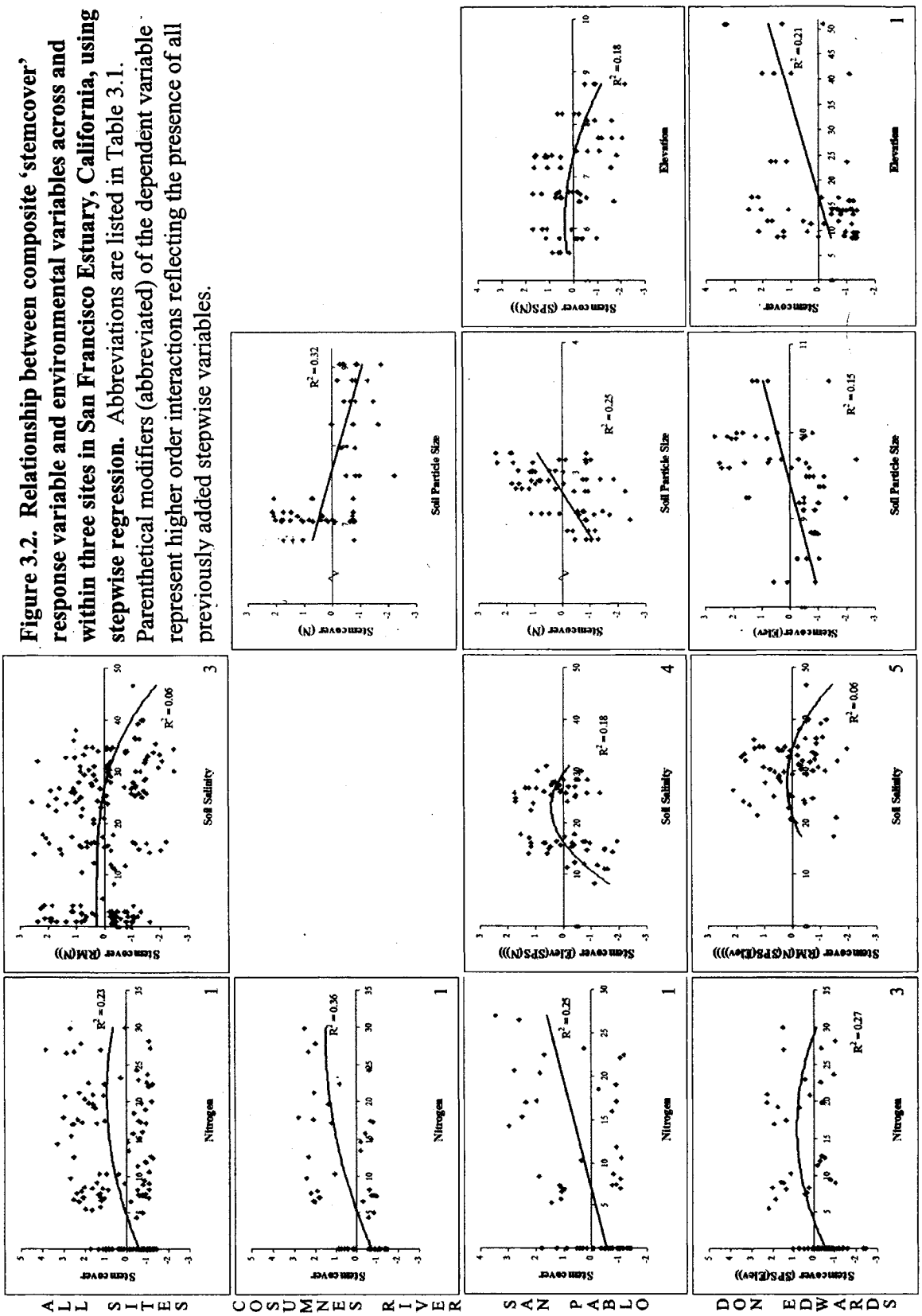


Figure 3.2. Relationship between composite 'stemcover' response variable and environmental variables across and within three sites in San Francisco Estuary, California, using stepwise regression. Abbreviations are listed in Table 3.1. Parenthetical modifiers (abbreviated) of the dependent variable represent higher order interactions reflecting the presence of all previously added stepwise variables.

Figure 3.3.a.

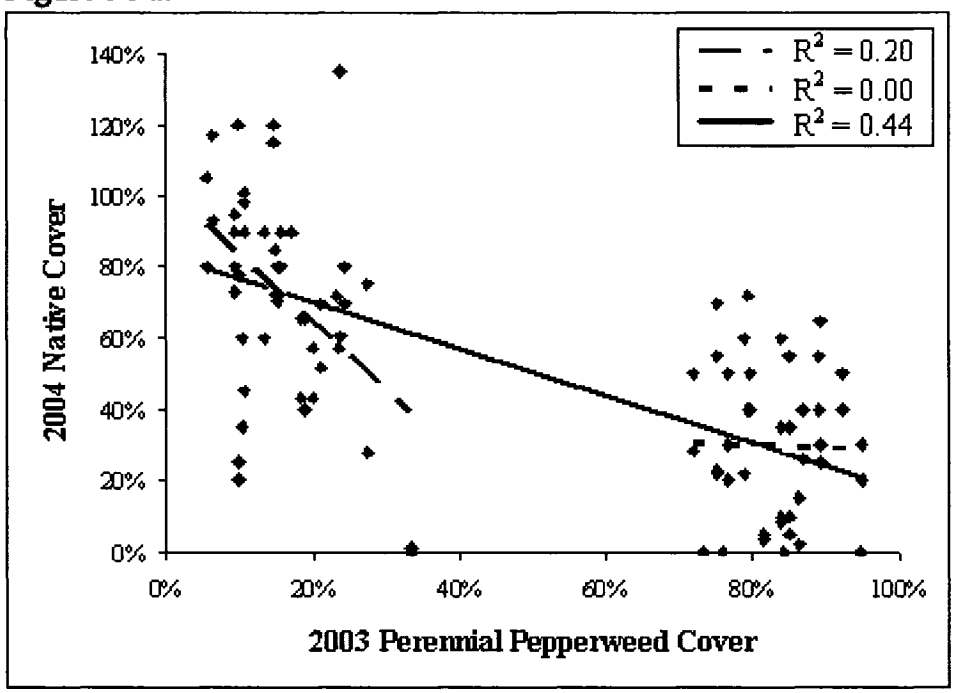
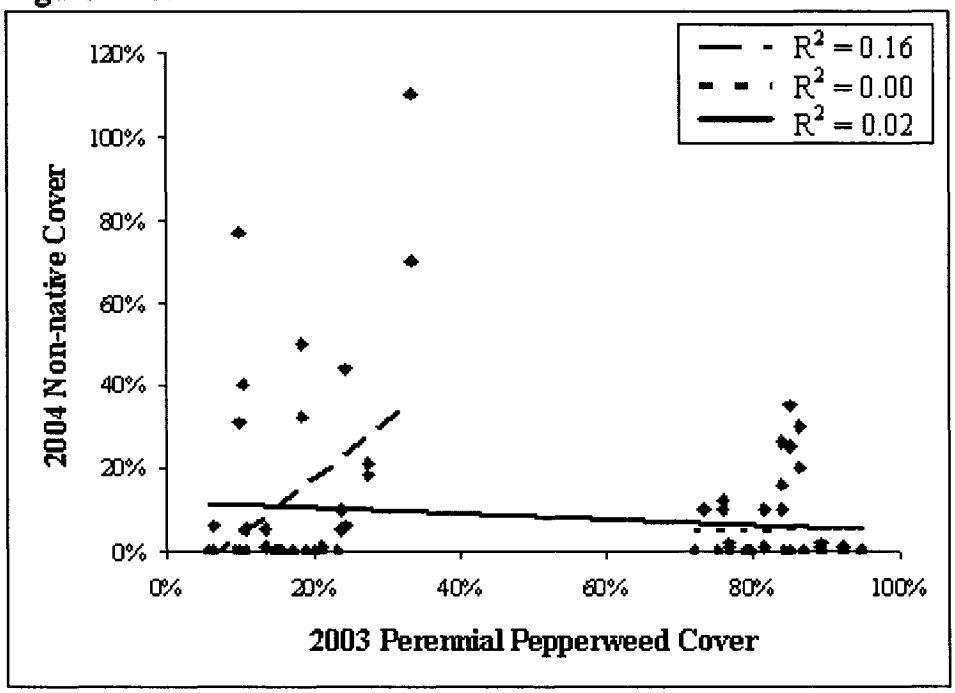


Figure 3.3.b.



Figures 3.3a-b. The relationship between 2003 pepperweed cover (%) and 2004 native and non-native species cover (%). There are three regression lines shown on each graph, regressing native or non-native species cover against all prior year pepperweed cover; against low density pepperweed cover; and against high density pepperweed cover. R^2 values are shown in the upper right corner of each graph.

Chapter 4

Ecological factors in the control of perennial pepperweed (*Lepidium latifolium* L.) in tidal marshes in the San Francisco Estuary

Abstract

Glyphosate has been routinely used to control *Lepidium latifolium* L. (perennial pepperweed) in the San Francisco Estuary, but it is uncertain how effective *L. latifolium* control treatments have been in tidal marshes. Since other studies have indicated that salinity is a dominant factor governing vegetation response, I hypothesized that increasing salinity would improve both *L. latifolium* control and native-dominated vegetation recovery. To test this theory, I examined response to two annual herbicide treatments, the influence of stand density, and post-treatment changes in native abundance at three tidally-influenced sites representing salinity gradients in the estuary. Across sites, mean percent cover was reduced from 85% to 23% in high density treated stands, and from 17% to 5% in low density treated stands. Least control was obtained at the freshwater site and treatment efficacy generally improved with increased salinity. Vegetation recovery was not uniform, or wholly predictable, along the salinity gradient alone. The combination of elevated salinities with a second edaphic stress, flooding, resulted in both improved treatment efficacy and greater native species recovery, as evidenced at the brackish site. Coincidently, the combination of edaphic stresses limited the species pool adapted to recolonize the treated plots. Experimental plots at the fresh and saline extremes were more likely to be colonized by non-natives. At these sites, increased bare ground for prolonged periods following treatment increased the probability of future invasion. My findings indicated that the efficacy of the spray program was dependent on salinity, flooding, and the species pool present at the site.

Keywords: *Lepidium latifolium*; perennial pepperweed; glyphosate; San Francisco Estuary; salinity gradient; salt marsh; wetlands; tidal; native; invasive

Introduction

Lepidium latifolium L., commonly known as perennial pepperweed, is a highly invasive plant that colonizes wetland and riparian areas. The first known introduction into California occurred in the 1930's (Bellue, 1936). In 1996 pepperweed appeared on the California Exotic Plant Pest Council's watch list as a species of great ecological concern (Cal-EPPC (now Cal-IPC), 1996), and has since been elevated to high, a composite scoring of ecological impact, invasive potential, and distribution (Cal-IPC, 2006). The California Department of Food and Agriculture lists it as a Class B noxious weed, due to its invasive and near ubiquitous nature. Although large, well-established populations seem to be associated with human related disturbances (Mooney *et al.*, 1986), I witnessed pepperweed colonization after natural disturbances of relatively pristine habitats at natural or protected marshes in north San Francisco Bay.

Historically, *L. latifolium* has been viewed as problematic in brackish and freshwater systems in the San Francisco Estuary, while uncommon in the more saline reaches of the estuary (Rejmanek, personal communication; Grossinger *et al.* 1998). Observations of populations at the U.S. Fish and Wildlife Service (USFWS) Don Edwards San Francisco Bay National Wildlife Refuge provide evidence to salinity tolerance of seawater concentrations, but distribution there is more restricted than in fresher sites.

Like *L. latifolium,* many halophytic plants grow best under freshwater and low salinity conditions, in the absence of competitors (Gray and Scott, 1977; Szwarcbaum and Waisel, 1973) and exhibit reduced growth under elevated salinities (Munns *et al.*, 1983). In wetlands, salinity is an important edaphic factor governing vegetation distribution (Mitsch and Gosselink, 1993), and can be a source of stress even to salinity-adapted species (Munns *et. al.*, 1983). The prevailing view of salt marsh ecology is that edaphic factors are the drivers of vegetation abundance and distribution patterns, in the context of which interspecific associations shape vegetation response (Bertness and Hacker, 1994). Because of the harsh conditions, there are few salt marsh-adapted species, with the number of adapted species increasing as salinity decreases (Mitsch and Gosselink, 1993).

Although resource managers ranked *L. latifolium* as one of the most important species for control throughout the estuary in an informal survey conducted in 2002, a successful protocol has not been established for *L. latifolium* control in tidal wetlands. An effective, successful strategy must include both elimination of the target species and revegetation by desirable native species (Young *et al.*, 1995), both of which may be at least partially dependent on salinity gradients. Since *L. latifolium* plants growing in sub optimal salinity conditions may already be experiencing stress, relative to freshwater populations, I suspected that the saline populations would be more susceptible to herbicide treatments, in which case, herbicide efficacy would improve with increasing salinity. The native plant community's post-treatment rebound potential may also vary across a salinity gradient, with slower revegetation in the high salinity sites in response to the stressful conditions, but with greater likelihood for native recolonization resulting

from the fewer number of species adapted to high salinities. Therefore, the selected approach may need to account for changes in both treatment efficacy and vegetation response as edaphic stresses increase.

Control efforts in seasonal and freshwater wetlands have been documented (*e.g.* Renz, 2002; Young *et al.*, 1998). At these sites, successful elimination of *L. latifolium* has been problematic. Consequently, the revegetation phases are not consistently attained. Previously documented experimental efforts to control *L. latifolium* have included mowing, tilling, disking, manual removal, flooding, and herbicide treatments alone and in combination with mowing or disking. Mowing, tilling, or disking alone have proven to be ineffective (Renz, 2002, Young *et al.* 1998). Manual removal is difficult due to the characteristics of underground stems that can grow as deep as 3 meters (Blank and Young, 2002), easily fragment, and can regenerate from fragments as short as 2.5 cm (Wotring *et al.*, 1997). Hogle (unpublished data) found that hand pulling of isolated, individual stems commonly precluded stem regrowth one year later, but that hand pulling efficacy rapidly diminished for stands with more than 6 stems. Hand pulling has been conducted at numerous sites throughout the estuary, but shares the same drawbacks as mowing. It is time and labor intensive, causes disturbance, and would require long-term and continuing efforts to deplete carbohydrate stores, particularly in well-established patches. Prolonged flooding limits *L. latifolium*, depending on the duration of flooding. Chen *et al.* (2002; 2005) found that prolonged flooding exceeding 50 days during the growing season reduced growth, but the species still survived and reproduced. Fredrickson *et al.* (1999) found that continuous flooding for 2 growing seasons was successful in eradicating *L. latifolium*. The relationship between flooding

and *L. latifolium* may be further blurred in tidal systems as tidal action infuses channel banks with oxygen and other nutrients, which can ameliorate the effects of flooding (Odum, 1980).

To date, herbicide treatment is regarded as one of the most effective control or eradication techniques available for managing *L. latifolium* invasions. Although herbicides do not offer an ideal solution in eradicating *L. latifolium*, they are one of the only effective options for treating well-established, mature stands. The chemicals chlorsulfuron, glyphosate, tryclopyr, imazapyr, and 2,4-D amine have all been tested for *L. latifolium* control efficacy (Renz, 2002; Young *et al.*, 1998; Trumbo, 1994). Of these, only glyphosate, imazypr, and 2,4-D can be used in tidal wetlands in California. Imazypr was only recently approved for use in California and has not been thoroughly tested for efficacy in California tidal wetlands, although it is widely used for invasive *Spartina* spp. control (Leson & Associates, 2005). Glyphosate has been widely used to control pepperweed in estuarine systems since the mid 1990's (Grossinger *et al.*, 1998), however, most results have not been documented, and it is unclear how results obtained in freshwater and seasonal systems translate to tidal systems where salinity and flooding are potentially more important. In seasonal freshwater wetlands, the results of treatments using glyphosate (Renz and DiTomaso, 2006) and 2,4-D (Young *et al.*, 1998) indicate that a single herbicide treatment will not control pepperweed growth, particularly in high density patches.

The goal of this study was to evaluate the effects of glyphosate applications on pepperweed abundance, and on resultant plant species recovery. Specifically, I: 1) examined changes in the control efficacy of multi-year applications of Aquamaster™

(aquatic formulation of glyphosate; EPA Reg No. 524-343, Monsanto Corp., St. Louis, MO) across a salinity gradient in the San Francisco Estuary; and 2) subsequently evaluated the effects of herbicide induced *L. latifolium* reduction on local plant community composition. I predicted that treatment efficacy would co-vary with increasing salinity. Results of this research were intended to provide guidance to the development of a comprehensive strategy for herbicide use across a range of tidal wetland environments.

Methods

Sites were selected to represent the range of salinities found within the San Francisco Estuary. I selected one freshwater but tidally influenced site located at the Cosumnes River Preserve (hereafter Cosumnes River) (N38°16', W121°26'); one brackish site, along Tolay Creek in the San Pablo Bay National Wildlife Refuge (San Pablo) (N38°07', W122°26'); and one saline-hypersaline site in the Don Edwards San Francisco Bay National Wildlife Refuge (Don Edwards) (N37°30', W122°06'). Channel salinities, measured four times through the growing season were 0-1 ppt at Cosumnes River, 5-27 ppt at San Pablo, and 28-36 ppt at Don Edwards. At each site, I located plots that met pre-selected *L. latifolium* percent cover criteria (*i.e.*, high density or ≥70% *L. latifolium* cover versus low density or ≤30% cover), then randomly assigned treatment or control within appropriate density plots with 8 replicates per treatment per site. The experiment was a randomized complete block design, pairing treated and untreated plots across high or low density *L. latifolium* cover. Plots had to contain multiple flowering stems at the time of plot establishment to be included in either cover class. In the selected plots, initial low density plot cover ranged between 4% and 30% cover. High

density plot cover ranged between 73% and 99%. Pre-treatment measures of species composition and cover revealed that treatment and control plots were statistically similar according to density within each site. Midway through the experiment, hydrology at the San Pablo site was altered by a culvert replacement and enlargement project. After the change, it became apparent that flooding could be an important covariate, so plots were scored binomially as frequently or infrequently flooded, based on the presence of standing water in the plot during field visits.

Plots were treated in May 2003 and again in May 2004. Each replicate consisted of a 2 m^2 quadrat, with the respective treatment applied to the entire quadrat, then sampled from the inner 1 m^2 quadrat to buffer edge effects from reinvasion. Species percent cover measurements were taken prior to each treatment, and in June and October of 2003 and 2004, and in May and October of 2005. Results were analyzed with ANOVA for repeated measures ($p \leq 0.05$).

Using a backpack sprayer, herbicide was applied between flowering and seed production stages, optimizing herbicide translocation (Renz and DiTomaso, 2004). Aquamaster© was applied at a rate of 1.5%, along with R-11© surfactant at a rate of 0.75%, and Prospreader© spreader-sticker at a rate of <0.04% (.05 oz/gallon), until leaves were coated, as directed by the label. In order to evaluate the effects of herbicide treatment on local plant composition, I compared the ratio of natives, non-natives, and bare ground in treated and control plots before and after treatment. Cover estimates were taken for all the species present in the sampling plots at each measurement. These data were pooled into broader classifications of native and non-native. Cover measurements

were taken prior to treatment and one full growing season after completion of the second (and final) treatment (29 months after the initial treatment).

Results

Herbicide treatments significantly reduced cover in both low and high density plots at all sites ($p \leq 0.05$). Mean percent cover in high density treated plots was reduced from 89% to 32% at Cosumnes River (Figure 1a), from 82% to 10% at San Pablo (Figure 1b), and 86% to 27% at Don Edwards (Figure 1c) between initial measurements taken in May, 2003 to May 2005. Mean percent cover in low density treated plots was reduced from 14% to 8% at Cosumnes River, from 18% to 4% at San Pablo, and from 13% to 5% at Don Edwards. *Lepidium latifolium* percent cover was comparable between treatment and control plots prior to herbicide application. Changes in *L. latifolium* cover between low and high density plots, and herbicide and control treatments are shown in Figure 1.

Examining trends across sites, increasing salinity improved herbicide efficacy. San Pablo had the greatest reduction in cover in low and high density treated plots, an effect I attribute to the combination of elevated salinities and higher flooding depth and duration, followed by Don Edwards, with the least change at Cosumnes River, the freshwater site. By month 29, both low and high density treated populations at Cosumnes River appeared to be rebounding. Neither of the other two sites mirrored that trajectory. *Lepidium latifolium* percent cover declined in the high density control plots at all three sites over the course of the study, as well as in the low density plots at San Pablo. Don Edwards was the only site that exhibited an increase in percent cover in the low density control plots over the course of the experiment.

Site position along the salinity gradient influenced species composition at the larger scale, but species composition prior to and following treatment was not predictable based on treatment alone. Site, *L. latifolium* density, and the interactions of these variables with treatment and with month were correlated with native species (%) cover (Table 1). Likewise, pretreatment site and density differences in native species composition were also important determinants of post treatment species composition (ANOVA; $p < 0.05$)(Figures 2a-2c). Table 2 lists dominant species, grouped by native/nonnative status (corresponding to Figures 2a-2c and Figure 3).

Herbicide treatment affected native cover, though the pattern of effect wasn't consistent across sites. San Pablo was primarily dominated by native species and *L. latifolium* (Figure 2b). Once *L. latifolium* was removed, native *Salicornia* sp., *Jaumea* sp., and *Grindelia* sp. recolonized the plots. Herbicide treatments did not increase native cover abundance at either of the other two sites.

Herbicide treatment also resulted in increased bare ground at all sites, particularly in the high density plots (Figures 2a-2c). Percentage of bare ground also increased with increasing salinity in both treated and control plots. This pattern was most apparent at the saline site, Don Edwards.

Species composition in pre-treatment, herbicide, and control plots is shown, grouped according to 'Native, Non-native, or *L. latifolium* (a subclass of Non-native) by site (Figure 3). Comparing control and herbicide plots, herbicide treatments decreased the relativized absolute cover of native species at the Cosumnes River and Don Edwards sites, but increased native cover at the San Pablo site. Absolute covers were visually estimated in the field, and could exceed 100%. Relativized absolute cover represents

rescaling absolute species cover, not including bare ground, to 100% within each plot in order to compare the relative abundance of dominant species in the plots. At Cosumnes River, the spray treatment resulted in a decrease in native species cover, and an increase in non-native cover, particularly *Picris echiodes*, *Sonchus oleraceus*, and introduced grasses. After absolute *L. latifolium* cover was relativized for both treated and untreated plots, its contribution to both plot types was similar. At Don Edwards, the reduction in *L. latifolium* abundance in the treated plots corresponded with an increase in *Salsola soda, Bromus* spp. (grouped with non-native grasses), and *Raphanus sativa.* At San Pablo, *L. latifolium* was replaced predominantly by native species.

Discussion

Treatment at each of the three sites produced quite different outcomes. Of the three sites, San Pablo represented the preferred management scenario. Herbicide treatments were most efficacious, and treated plots had the greatest amounts of native cover by the end of the monitoring period. At this site, increased flooding from the culvert replacement, coupled with the edaphic stress presented by elevated salinities, probably mediated *L. latifolium* growth and abundance, and further limited colonization to species adapted to both conditions. The prognosis for the site is favorable, and indicates that if *L. latifolium* is removed, recovery will be comparably straightforward and largely self-enacting.

For the other two sites (Consumnes River and Don Edwards) heavy disturbance, large non-native propagule pools, and relatively poor *L. latifolium* control indicated that a very different management scheme would be required. At both of these sites, treated

invaded plots either remained bare ground or were readily re-invaded by *L. latifolium* or other non-natives. Consumnes River had the highest number of non-native species, and the strongest *L. latifolium* rebound following cessation of treatments. Herbicide efficacy was slightly better at Don Edwards than at Consumnes River, supporting my predictions of species response along a salinity gradient, and indicating the importance of consideration of edaphic stresses to effective control. At Don Edwards, bare patches were common and naturally occurring, a condition that was exacerbated by herbicide treatments, which resulted in the creation of additional bare ground without advantaging native species.

In either case, it is important to ascertain whether control can be obtained, and if so, assess the impact of control of the target weed species on the plant community. This might involve a site assessment of nearest problem weeds, the likelihood of those weeds colonizing the newly opened habitat, and the steps necessary to prevent this outcome. One option might be intensive restoration plantings to minimize bare space. Another option might be targeted multi-species removal. At both sites, a no-action alternative should also be evaluated, particularly since the long term population trajectory of *L. latifolium* is not clear at this point. Cover in high density control plots declined across all sites, and the decline remains unexplained. One possibility is local resource depletion, similar to that observed at Honey Lake National Wildlife Refuge (California), where populations have exhibited a rebound this season following a downward trend (Blank, personal communication). If the no-action alternative is selected, *L. latifolium* populations should be monitored in order to estimate population trajectories, and management options should be consistently re-evaluated.

At Cosumnes River more so than the two other sites, I expect the full potential of *L. latifolium* recovery to be expressed because *L. latifolium* is well-suited to site conditions. At San Pablo, the combined stresses of moderate salinities with increased flooding depth and duration limited *L. latifolium*, improved treatment efficacy, and restricted the propagule pool to largely native species. This combination results in a best-case management scenario where *L. latifolium* removal areas will be largely naturally recolonized by native vegetation and little additional post-treatment restoration will be necessary. At Don Edwards, high-salinity conditions may weaken *L. latifolium*, but the non-natives and creation of bare ground are of concern, particularly since native recolonization was also slowed. Particularly at Cosumnes River, but also at Don Edwards, there were many non-native species that could easily pre-empt the areas opened by herbicide treatment.

My results were largely consistent with those of Renz (2002). However, the rate of control achieved in my low density tidal plots was lower than the rate of control that Renz (2002) attained in seasonal wetlands in California. At all of my tidal study sites, mean *L. latifolium* cover between treated and untreated low density plots was quite similar at the experiment's endpoint, even though treatment means differed statistically. The reason for this pattern is unclear. This might be due to differences in ground cover of resident vegetation at my sites, which may have resulted in increased incidental interception of the herbicide by other species, limiting contact with basal rosettes of *L. latifolium* in the low-density treatments. Herbicide interference was more likely in Renz's (2002) high-density treatments than in his low-density treatments (DiTomaso, personal communication).

In evaluating herbicide potential for efficacy in tidal wetlands in the San Francisco Estuary, this study indicated that the label prescribed rate for application of glyphosate, without mowing, was effective at reducing *L. latifolium* abundance in high density plots (≥70% cover) to average low density abundances when treated for two consecutive years. This level of control would necessitate continued treatment of the infested areas—a dubious prospect for most resource managers. Different herbicides may be considered, but herbicides approved for aquatic use are limited. Results of 2,4-D treatments are not any more promising (Renz and DiTomaso, 1999; 2001; Young *et al.*, 1998). The herbicide Habitat™ (a.i. imazapyr) may be a good alternative for *L. latifolium* control, but efficacy in California's tidal wetlands has not been well evaluated. Efficacy studies using Habitat, and a Habitat-glyphosate combination to control *Spartina* species are underway (*e.g.*, San Francisco Estuary Invasive *Spartina* Project, California State Coastal Conservancy) and preliminary results are promising (Leson & Associates, 2005). The glyphosate-imazapyr combination also has been proposed for use at the San Pablo Bay National Wildlife Refuge (Hogle *et al.*, unpublished document) and treatments are expected to commence by 2007 or sooner.

This research can be viewed in the broader context of how knowledge of the biology and ecology of a given species can be incorporated into the development of more effective management strategies. In this case, treatment efficacy generally increased with increasing salinity, but was most effective at the site that was also frequently flooded. These patterns may hold true for species with similar biology or ecology, particularly for species that have broad distributions along salinity gradients. Additional research is needed to determine which of the more specific findings of this study translate to other

invasive wetland species. Specific findings of this study may be of particular interest to other Mediterranean regions where pepperweed is problematic, including Australia (Kloot, 1973) and Spain (Romero and Amigo, 1992).

In summary, this study illustrated the need for effective control of pepperweed in tidal wetlands. While glyphosate offered some degree of control, it also raised the possibility of perpetual and destructive treatments. Salinity and secondarily, flooding, provided the backdrop within which various species interactions emerged. Native plant community recovery following herbicide treatment was largely dependent on achieving control of the target species, and on the propagule pool present at the site. This particular finding would most likely transcend herbicide selection, and has important implications for the management of restoration sites.

Acknowledgements

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Tables

Table 4.1. Modeled (ANOVA) effects of site, herbicide treatment, density, month, and their interactions on relative native species cover.

	Native cover (%)
site	<0.0001
treatment	0.4952
density	<0.0001
site*treatment	0.0176
site*density	<0.0001
density*treatment	0.344
site*density*treatment	0.1604
month	0.0031
month*site	0.0001
month*treatment	0.4376
month*density	<0.0001
month*site*treatment	<0.0001
month*site*density	0.9609
month*density*treatment	0.0015
month*site*density*treatment	0.1367

Table 4.2. Dominant native and non-native species at each site.

Native species	Site	Non-native species	Site
Atriplex triangularis	CR, SP, DE	*Bromus* spp.	CR, DE
Baccharis pilularis	SP	*Hordium marinum*	CR
Carex praegracilis	CR	*Lepidium latifolium*	CR, SP, DE
Cyperus eragrostis	CR	*Lolium multiflorum*	CR
Distichlis spicata	CR	*Malva neglecta*	CR
Epilobium spp.	CR	*Picris echiodes*	CR
Frankenia salina	SP, DE	*Plantago* spp.	CR
Grindelia stricta	SP	*Polypogon monspeliensis*	CR
Jaumea carnosa	SP, DE	*Raphanus sativa*	DE
Juncus balticus	CR	*Salsola soda*	DE
Salicornia virginica	SP, DE	*Sonchus oleraceus*	CR

*included in the grasses category

Figures

Figure 4.1a. Effects of herbicide treatment at Cosumnes River

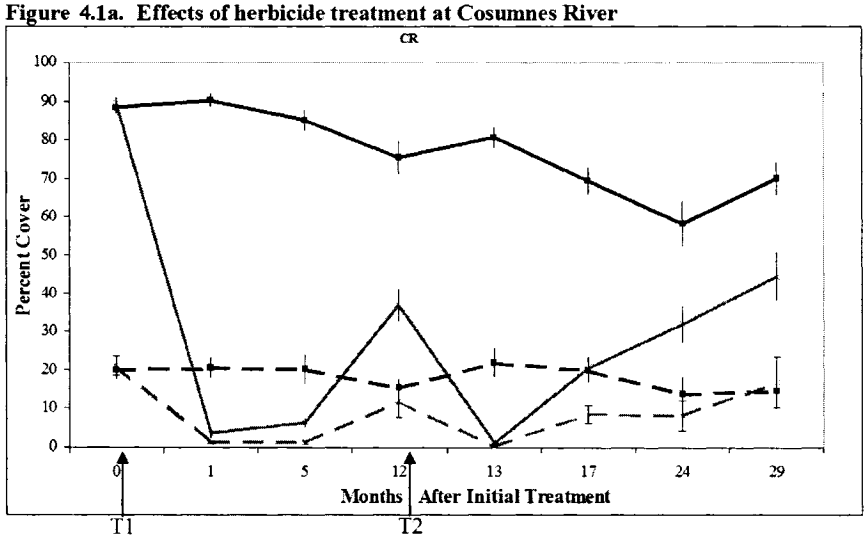


Figure 4.1b. Effects of herbicide treatment at San Pablo

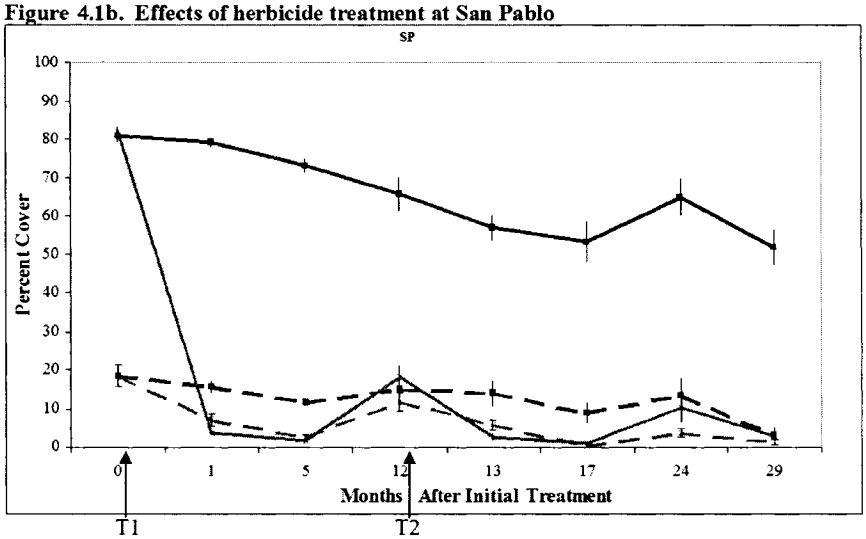
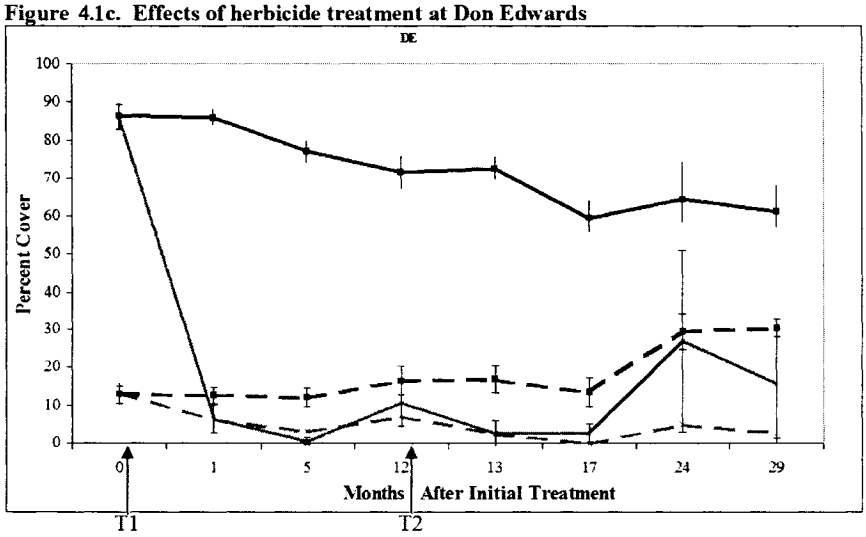


Figure 4.1c. Effects of herbicide treatment at Don Edwards



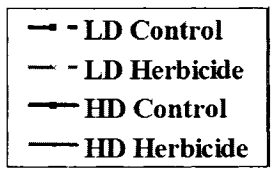


Figure 4.1a-c. Effects of herbicide treatment on percent cover of *Lepidium latifolium* at three San Francisco Estuary sites. Cover was measured just prior to 1st treatment (T1) through 2nd treatment (T2) to month 29. Treatments are low (LD) and high density (HD), control and herbicide, as shown in the legend below. Error bars represent ± 1.96 SE.

Figure 4.2a. Species composition (%) at Cosumnes River

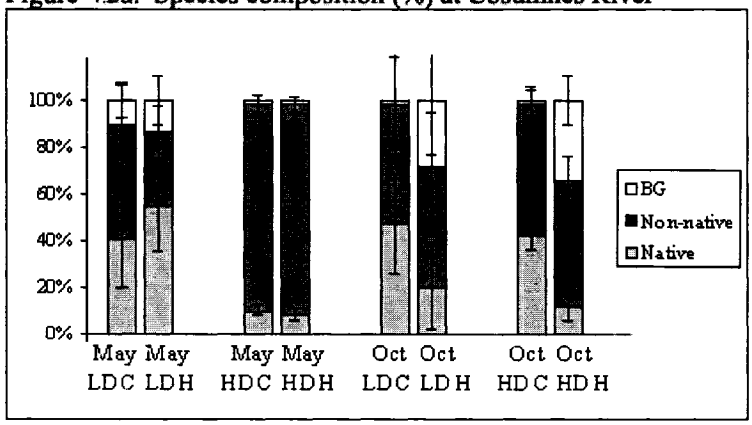


Figure 4.2b. Species composition (%) at San Pablo

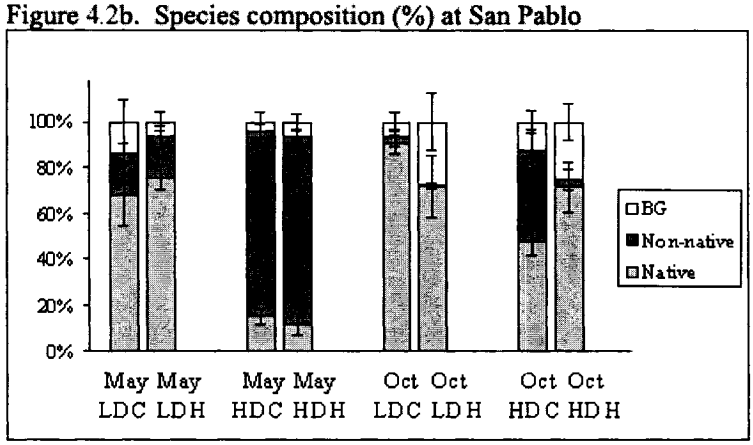


Figure 4.2c. Species composition (%) at Don Edwards

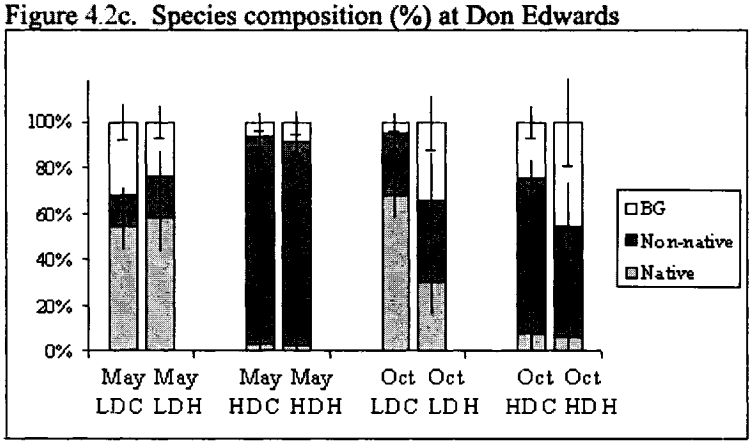


Figure 4.2a-c. Percent species composition at three San Francisco Estuary sites. Changes in plant community composition of % native, non-native, and bare ground in low density control (LD C), low density herbicide (LD H), high density control (HD C), and high density herbicide (HD H), as measured prior to the first herbicide treatment in May 2003 (pre-treatment), and the final measurement in October 2005 (29 months after initial treatment) at three sites in the estuary, Cosumnes River (CR), San Pablo (SP), and Don Edwards (DE). Non-native category includes *L. latifolium.* Error bars represent ± 1.96 SE.

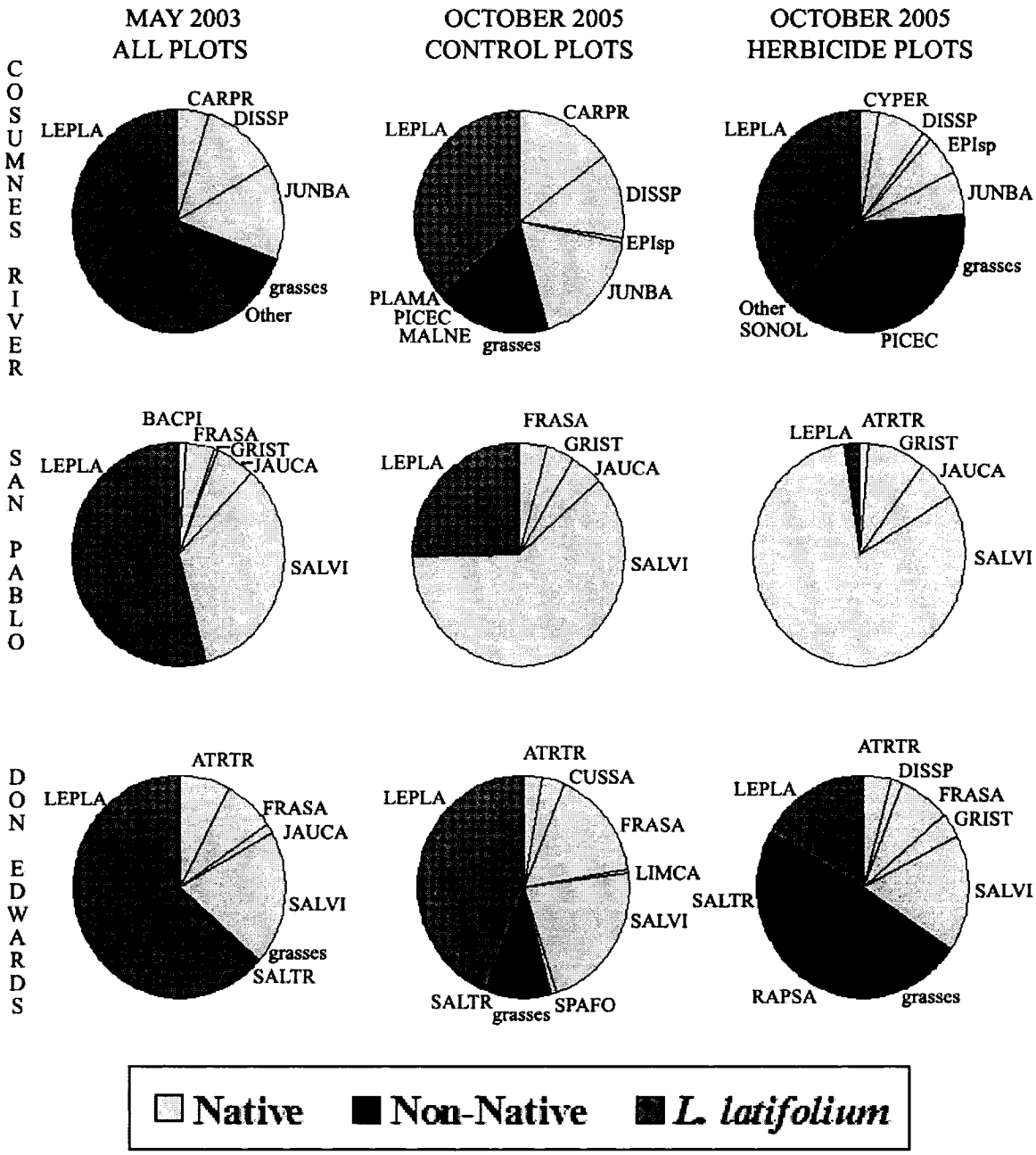


Figure 4.3. Absolute species abundance by site, comparing pre-treatment conditions in May 2003 to post-treatment conditions in October 2005, divided by control and herbicide plots. Absolute species cover data were relativized secondarily. Natives, non-natives, and *L. latifolium* (a separate category of non-native) are individually color coded in accordance with the legend. Species are abbreviated using a five letter sequence, the first three letters of the genus name and the first two letters of the species name, and correspond to the list in Table 4.2. Species coded as other at Cosumnes River had less than 1% cover. Some species were present at less than 1% overall cover (by treatment) and are not shown.

Conclusion

Salinity moderates *L. latifolium* abundance and distribution throughout its life cycle. Elevated salinity inhibited *L. latifolium* recruitment throughout early development. Under freshwater and brackish conditions, seeds were highly viable, exhibited high germinated rates. At higher salinity levels germination was delayed and nearly completely inhibited, suggesting that higher salinity sites may be much more resistant to seed establishment. During recruitment, the interaction between salinity and flooding frequency was not constraining at low salinities, but became progressively more limiting to recruitment as salinity and flooding frequency increased. Native vegetation was able to delay, and in some cases preclude, *L. latifolium* recruitment, independently of edaphic factors. My findings suggest that in freshwater and brackish conditions, where plants are expectedly healthier, more robust, and have greater reproductive success, seeds likely play a much greater role in population establishment and expansion, while in saline conditions, spread of *L. latifolium* may be primarily from vegetative propagules and episodic events allowing occasional recruitment from seed.

Although vegetation may strongly suppress pepperweed recruitment into a site initially, I found that once pepperweed became established, it had a strong influence on the composition of other species. In contrast to vegetation-induced recruitment limitation, the presence of other species did not appear sufficient to limit pepperweed once it became established. Pepperweed was limited primarily by environmental constraints, and the interaction between particular environmental variables, more so than by competition from other species. For the extant plant community, *L. latifolium* has a

strong potential to displace natives over the long term, and to negatively influence both native species richness and abundance.

Treatment efficacy generally improved with increasing salinity, but was most effective at the site that was also frequently flooded. At that site, the combination of flooding and moderate salinity, coupled with the largely native species pool resulted in a best case management scenario where *L. latifolium* removal areas were largely naturally recolonized by native vegetation, limiting the need for additional post-treatment restoration. Sites with heavy disturbance, less flooding depth or duration, and large non-native propagule pools presented the greatest challenge because of the strong probability for persistent bare ground or reinvasion in treated plots. This was particularly true at the freshwater site, where I expect the full potential of *L. latifolium* recovery to be expressed because *L. latifolium* is well-suited to site conditions. While glyphosate offered some degree of control, it also raised the possibility of perpetual and destructive treatments.

My findings indicate that pepperweed responds differently to subtle combinations of factors, which means control decisions must be dynamically matched to the situation at hand. *Lepidium latifolium* is adapted to conditions ranging from fresh to saline, but with increasing salinity, distribution becomes restricted by flooding. Limitations are born out at every major life stage, from viability through seed production. Control of this species should account for the ecology of the site, the propagule pool present in the plant community, and the likelihood of successful control.