

# *Lepidium latifolium* reproductive potential and seed dispersal along salinity and moisture gradients

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**Abstract** *Lepidium latifolium* is an aggressive plant species that is invading both wetlands and uplands across a wide range of salinities. This study examined how salinity and moisture gradients influence the potential for invasion by *L. latifolium*. Three sites in the San Francisco Bay Delta with varying salinity and moisture levels were chosen as research sites. These sites corresponded to a dry (18.32‰) freshwater (3.88‰) site, a wet (40.53‰) brackish (23.16‰) site, and a moderately wet (38.33‰) saline (32.33‰) site. Our results showed that inflorescence number and height were unaffected by salinity or soil moisture. Seed production was significantly affected by salinity ( $P = 0.0297$ ) and moisture levels ( $P = 0.0004$ ). Seed production at the high salinity site was reduced by 29% from the freshwater site. Seed production at the wettest site had an 87% reduction from the driest site. Seed viability was also reduced by both salinity ( $P < 0.0001$ ) and soil moisture ( $P < 0.0001$ ). Viability at the highest salinity site was reduced by 49% from freshwater sites and was reduced by 8% from the wettest to driest sites. Mean seed dispersal distance

was 0.23 m greater at the freshwater site, which was not statistically significant ( $P = 0.1815$ ). The deleterious effects of salinity and moisture resulted in reduced *L. latifolium* densities in high salinity and moisture locations, but only at the highest salinity site. With increased seed production and viability, drier freshwater sites experience greater propagule pressure, resulting in an increased invasion potential. Therefore, variability along salinity and soil moisture gradients serve as useful metrics for prioritizing control and eradication efforts of *L. latifolium*.

**Keywords** *Lepidium latifolium* · Perennial pepperweed · Salinity · Soil moisture · Invasion · Landscape susceptibility · Dispersal · Viability · Reproductive potential

## Introduction

*Lepidium latifolium*, commonly known as perennial pepperweed, is an increasingly common invasive plant species found widely throughout the western United States. A native of southern Europe and western Asia, *L. latifolium* was first introduced to the United States in the early part of the twentieth century (Bellue 1936; Robbins et al. 1941; Lantz and Simon 1998; DiTomaso and Healy 2003). Since introduction, *L. latifolium* has invaded wetlands and riparian zones and continues to spread.

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In early spring *L. latifolium* develops as a rosette of basal leaves. As the season progresses, *L. latifolium* stems bolt, producing multiple inflorescences 0.5–2.0 m tall (Blank and Young 2002; Blank et al. 2002; DiTomaso and Healy 2003; Whitson et al. 2004). Typical specimens produce three to eight inflorescences each season, with seed dispersal beginning in mid-summer and continuing throughout the winter, even after senescence.

Although, seed production has not been explicitly studied, *L. latifolium* is commonly known as a prolific seed producer. One unpublished account suggests that *L. latifolium* may produce as many as 8,000 seeds per inflorescence (Young et al. 1995, 1997; Blank and Young 1997). Stem counts per square meter have been observed exceeding 150 per square meter (Blank and Young 1997; Blank and Derner 2004; Renz and Blank 2004). Seeds are highly viable, and under favorable conditions germination exceeds 90% (Miller et al. 1986). From these accounts, annual seed production in dense infestations equates to more than one million viable seeds per square meter. Such a high rate of reproductive potential can result in significant colonization by *L. latifolium*, even if establishment from seed is rare.

Once established, *L. latifolium* spreads vegetatively forming dense patches which exclude native vegetation. It has been known to grow from a single plant into a dense patch several meters in diameter within 2 years (Blank and Young 2002; Blank et al. 2002). As a long-lived perennial, *L. latifolium* can persist in an area indefinitely and continue to spread.

Infestations of *L. latifolium* are notoriously difficult to control. Mowing, grazing, and tilling have been shown to reduce above-ground biomass (Young et al. 1998; Williams et al. 2002), but eradication has been ineffective because *L. latifolium* readily resprouts from small root fragments. Roots are known to grow to depths of 3 m or more (DiTomaso and Healy 2003) further undermining eradication by mechanical means.

The use of herbicides to treat *L. latifolium* infestations has also yielded mixed results. Chlorsulfuron has consistently been shown to be effective in treating infestations (Young et al. 1998). Unfortunately, chlorsulfuron is a persistent herbicide and its use is limited to upland locations. Since *L. latifolium* is typically located near water few viable options are available to effectively control infestations.

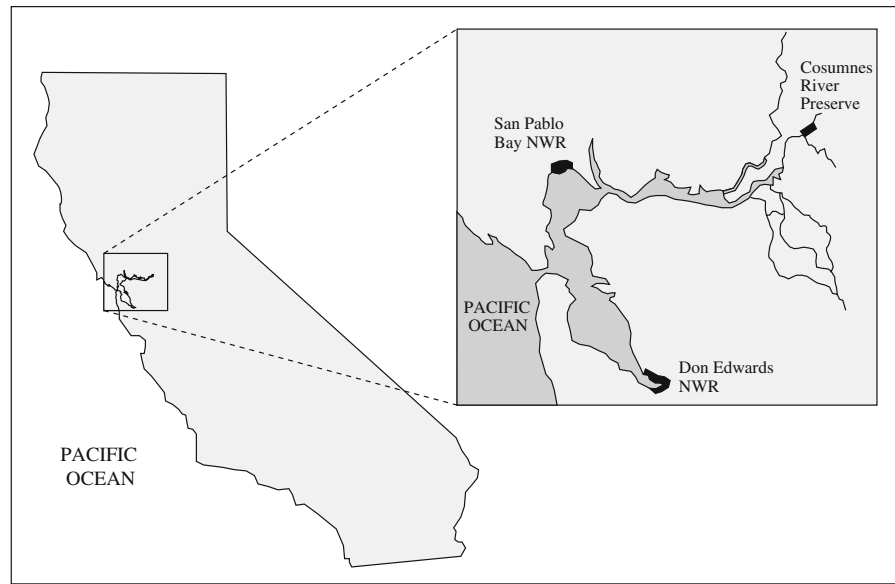
Due to the highly competitive nature of *L. latifolium* and difficulty in controlling infestations, the best strategy is to prevent invasion from occurring. This requires a more thorough understanding of *L. latifolium* invasion dynamics. Since *L. latifolium* has such high rates of viable seed production, it is important to understand how the dispersal of these seeds influence its invasion dynamics (Bullock and Clarke 2000; Neubert and Caswell 2000; Caswell et al. 2003). It is also important to consider the fate of dispersed seeds, and their relative persistence in the seed bank.

Key factors affecting seed dispersal are seed production, seed viability, inflorescence height, inflorescence number, and dispersal distance. It is also important to understand how environmental conditions influence each of these factors. Seed production, viability, and inflorescence number are important to dispersal because they dictate the number of propagules available. Plant height is an important factor because it determines the height of seed release, which can greatly influence seed dispersal distances (Bullock and Clarke 2000; Nathan et al. 2001; Tackenberg 2003).

*Lepidium latifolium* has exhibited plasticity related to varying environmental conditions (Chen et al. 2002, 2005). Stresses due to flooding have been shown to adversely affect growth and survival (Mitsch and Gosselink 2000; Chen et al. 2002, 2005; Chen and Qualls 2003). The deleterious effect of increased salinity has also been well-documented (Lambers et al. 1998; Mitsch and Gosselink 2000; Zedler et al. 2003; Larson and Kiemnec 2005). If salinity and moisture stresses have variable effects on *L. latifolium*, then these variations may be used to assess the relative susceptibility of a site to invasion. Therefore understanding the response of *L. latifolium* to these gradients is a critical first step toward prioritizing control efforts to prevent and slow invasion. Ultimately this information may lead to the development of more effective and efficient management practices.

This study focused on three major aspects of *L. latifolium* invasion dynamics to determine their invasion potential. First it focused on evaluating the effects of salinity and soil moisture on adult physiological characteristics of *L. latifolium*. Second it determined the reproductive potential of *L. latifolium* in response to changes in salinity and soil moisture.

**Fig. 1** Map of *Lepidium latifolium* study site locations in California, USA



Lastly, this study focused on determining the distance and rate of seed dispersal of *L. latifolium*, and the post-dispersal persistence of seeds. These components provide a framework for evaluating the invasive potential of *L. latifolium* along salinity and soil gradients and thereby allow sites to be characterized in terms of their relative susceptibility to invasion.

We hypothesized that high salinity and soil moisture would adversely affect the reproductive potential of *L. latifolium* by reducing (1) the inflorescence number per plant, (2) seed production, and (3) seed viability. We also hypothesized that increased levels of salinity and soil moisture would adversely influence dispersal by decreasing (1) the inflorescence height, (2) the mean dispersal distance, and (3) increase the mortality of dispersed seed. Finally, we hypothesized that a reduction in reproductive potential and reduced expansion would result in lower densities of *L. latifolium* at wetter, more saline sites.

## Methods

To determine how salinity and moisture influence *L. latifolium* invasion dynamics this study was broken into three principal phases encompassing adult plant responses, viable seed production, and dispersal. Three study sites were established within the San Francisco Bay Delta in California, USA. These sites

were located at Cosumnes River Preserve (N38°16', W121°26'), San Pablo Bay National Wildlife Refuge (N38°07', W122°26'), and Don Edwards National Wildlife Refuge (N37°30', W122°06') (Fig. 1). These sites correspond to three different salinity and soil moisture regimes. Cosumnes River Preserve is a drier freshwater site, San Pablo Bay NWR is a brackish marsh with nearly saturated soils, and Don Edwards NWR has wet soils and high salinity. At each study site, 16 one square meter study plots were established to examine the effects of salinity and soil moisture on *L. latifolium* characteristics. Half of the 16 plots were low density plots (<40% *Lepidium* cover), and the other half consisted of high density plots (>70% *Lepidium* cover).

In each study plot, the number of inflorescences and maximum inflorescence height was recorded. Study plots were monitored four times between May 2004 and May 2005. In 2004, seed production was measured by bagging one average sized inflorescence from each study plot after flowering had waned, but prior to seed dispersal. This allowed for pollination while still preventing seed loss from dispersal. The bagged inflorescences were later collected, and seeds were cleaned and counted.

Soil salinity samples were collected nine times between March 2004 and October 2005 at each of the study plots. Soil moisture samples were collected seven times during the same period. Soil samples were taken at three depths of 0–33 cm, 33–66 cm,

and 66–100 cm. The soil moisture was calculated gravimetrically, by weighing 20 g of wet soil and drying it in an oven at 105°C until it reached constant weight. The dry soil was then reweighed. Percent water was calculated by subtracting the dry weight from the wet weight, and then dividing by the wet weight. Soil salinity was measured by saturating soils with deionized water and then extracting the water using a centrifuge. The salinity for each sample was then measured using a refractometer.

To assess the effects of salinity and soil moisture on *L. latifolium* seed viability and persistence, seed was collected from Cosumnes River Preserve, San Pablo Bay NWR, and Don Edwards NWR. Fifty seeds were then placed in small nylon bags. The bags were sealed and secured for later retrieval. The bags had a 0.2 mm mesh width which allowed for water and gas exchange but prevented seed loss. In March 2005 four bags were buried 2–3 cm deep in the soil at each of the 16 plots at the three study sites. One bag from each plot was then collected from the field in April, June, August, and October of 2005. Only seeds collected from the study site were used at that site. This consistency was employed to preclude any potential translocation of genetic material.

Seed viability was examined through a combination of germination and tetrazolium testing. Upon collection from the field, seeds were counted and rinsed with deionized water. Twenty seeds were selected at random from each of the bags and placed in a Petri dish lined with filter paper. The filter paper was then moistened with deionized water. The dishes were covered and placed in a greenhouse with a daily temperature range between 15°C and 27°C. The seed remained in the greenhouse for 7 days. After 7 days, all of the seeds that germinated were removed and the remaining seeds were then scarified to break any dormancy. Seeds were scarified by carefully cutting longitudinally between the cotyledons and the radicle. The scarified seeds were then allowed to germinate for three additional days.

Seeds that failed to germinate in the greenhouse were then treated with tetrazolium red (2,3,5-triphenyl-2H-tetrazolium chloride) following standardized procedures established by the Association of Official Seed Analysts (Peters 2000). The tetrazolium red solution stains living tissue and seeds were considered viable as long as the radicle, hypocotyl, and at least 50% of the cotyledons were shown to be viable. The data from

the germination and tetrazolium phases were then combined to provide a complete picture of seed viability.

Concurrent germination and viability trials were also performed on lab stored seed during each collection period to assess the effects of field exposure. Five sets of 20 lab stored seeds from each of the three source sites were germinated alongside the field exposed seeds at each collection period.

To determine the distance and rate of seed dispersal, five dispersal plots were established in addition to the 16 study plots at each site. At each site five plants were targeted. Preference was given to isolated plants so that the source of dispersing seeds could be ensured. All other *L. latifolium* plants within 10 m of the target plants had their inflorescences removed to prevent additional seed dispersal into the study area. Surrounding plants were monitored for regrowth throughout the duration of the experiment, and all new inflorescences were removed as needed.

Three transects were established radiating out from each target plant. Each transect consisted of 11 plywood trap platforms evenly spaced from 0 to 5 m from the target plant in half meter intervals (Fig. 2). The traps consisted of an arc with its length scaled to the dispersal distance such that the percent area being sampled remained consistent with distance. Trap widths were fixed at 10 cm. The resulting traps sampled 3.8% of the total area at each distance. This consistent scaling provided an even sampling intensity with distance from the target plant, and thereby precluded any potential bias that may result from



**Fig. 2** Dispersal plot at Cosumnes River Preserve taken in late summer 2004

differing sampling intensities (Barrowclough 1978). Transects were established along directions of least topographical change. Traps consisted of a piece of plastic sheeting cut to size that was stapled down to each trap platform. The traps were then covered with a thin layer of sticky adhesive known as Tangle-Trap<sup>®</sup>. *L. latifolium* seeds that fall on the Tangle-Trap<sup>®</sup> become adhered to the dispersal traps. The traps were left in the field for 2 weeks each month.

After 2 weeks in the field the dispersal traps were covered with clear cellophane to prevent seed loss during transport and were then removed from the platforms. *L. latifolium* seeds was counted and recorded for each trap collected from the field. Traps were replaced after 2 weeks to determine dispersal rates throughout the growing season. Trap collections were carried out eight times between July 2004 and December 2004. At the end of December, any seed left remaining on the target plants were collected to estimate total seed production.

Statistical analysis was carried out using SAS Version 8 for Windows (SAS Systems). A significance level of  $P = 0.05$  was used for all tests. A Shapiro-Wilk test was used to ensure normality. This was done for all continuous variables including salinity, soil moisture, seed production, seed viability, inflorescence number per plant, maximum inflorescence height, and inflorescence number per square meter. Summary statistics were calculated for each variable. Site wise comparisons were made for each plant metrics using analysis of variance grouped by site. Means were separated using a Duncan's multiple range test if significant.

Soil salinity and moisture where evaluated using analysis of variance for repeated measures. These metrics included site, depth, and density, and date as the repeated measure. Means for significant class variables were separated using a Duncan's multiple range test.

Linear regression was used to assess salinity and soil moisture effects on continuous plant metrics. Regressions were carried out for seed production, seed viability, inflorescence number per plant, maximum inflorescence height, and inflorescence number per square meter against both salinity and soil moisture. The relative influence of salinity and moisture on each of the plant metrics was then assessed based on the slope of the regression line and the percent change along each gradient.

Dispersal data was limited to only the dry freshwater site and the moderately wet saline site. Due to phenological differences between sites, statistical analysis was limited to seasonal totals. Mean dispersal distance was analyzed using a *t*-test by site.

## Results

The analysis of the soil samples taken from each of the study plots revealed that salinity and soil moisture were distinct for many of the variables tested. Results also showed that salinity and soil moisture varied over the course of the season.

Salinity was statistically significant to each of the plot metrics studied. Site ( $P < 0.0001$ ), depth ( $P < 0.0001$ ), density ( $P = 0.0001$ ), and date ( $P < 0.0001$ ) were all statistically significant to salinity. A number of two and three way interactions were also significant (Table 1).

Analysis of the moisture data revealed that site ( $P < 0.0001$ ), density ( $P = 0.0004$ ), and date ( $P < 0.0001$ ) were significant, while depth had no significant effect ( $P = 0.0813$ ). There were also a number of significant two and three way interactions effecting moisture (Table 1).

The means separation for salinity by site revealed that each of the three study sites were distinctly different. The summary statistics and mean separation defined Cosumnes River Preserve as the freshwater site (3.88‰), San Pablo Bay NWR as the brackish site (23.16‰), and Don Edwards NWR as the most saline site (32.33‰) (Table 2).

Mean separation of the moisture data also demonstrated that each site was distinct. Cosumnes River preserve was the driest site (18.32%), followed by Don Edwards NWR (38.33%), and San Pablo Bay NWR (40.53%).

Salinity was also distinctly different at each of the three depths. Salinity tended to increase with depth. This effect was muted at the lower salinity sites particularly at Cosumnes River Preserve where the salinity gradient was narrow. Conversely, the high salinity plots at Don Edwards NWR exhibited the greatest disparity between salinities at high and low depths. Averaged across all sites, salinity in the deepest soils was 8‰ higher than the soils closest to the surface (Table 2).

**Table 1** Statistical significance summary table for salinity and soil moisture

Variable	Salinity			Moisture		
	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>
Date	8	308.23	<0.0001	5	222.55	<0.0001
Density	1	15.46	0.0001	1	13.32	0.0004
Depth	2	19.05	<0.0001	2	2.55	0.0813
Site	2	1257.11	<0.0001	2	268.75	<0.0001
Date × density	8	1.35	0.2148	5	4.67	0.0004
Date × depth	16	24.81	<0.0001	10	1.15	0.3218
Site × date	16	32.38	<0.0001	10	145.00	<0.0001
Depth × density	2	0.55	0.5762	2	0.06	0.9426
Site × density	2	20.75	<0.0001	2	23.43	<0.0001
Site × depth	4	5.18	0.0006	4	0.40	0.8068
Date × depth × density	16	1.22	0.2434	10	1.27	0.2465
Site × date × density	16	3.47	<0.0001	10	5.54	<0.0001
Site × date × depth	30	5.64	<0.0001	20	1.21	0.2414
Site × depth × density	4	0.43	0.7845	4	2.25	0.0666

**Table 2** Summary data for salinity and moisture broken down by each class variable. Note that each site is distinct in terms of its salinity and moisture. Also note that increasing depth resulted in increasing salinity and moisture, higher density plots were typically drier and less saline. Salinity tended to increase over the course of the year, while moisture decreased. Variables with the same group distinction are statistically similar. Group distinctions were obtained using Duncan's multiple range test

Variable	Salinity				Moisture			
	<i>n</i>	Mean (‰)	SE	Group	<i>n</i>	Mean (‰)	SE	Group
<i>Site</i>								
Cosumnes River Preserve	280	3.88	0.21	A	192	18.32	0.35	A
San Pablo Bay NWR	430	23.16	0.38	B	287	40.53	0.89	B
Don Edwards NWR	406	32.33	0.44	C	268	38.33	0.74	C
<i>Depth</i>								
0–33 cm	431	18.32	0.66	A	283	31.21	0.91	A
33–66 cm	374	21.57	0.69	B	248	34.22	0.95	B
66–100 cm	311	26.41	0.65	C	216	37.52	1.01	C
<i>Density</i>								
Greater than 70% <i>L. latifolium</i> cover	570	19.78	0.54	A	382	31.56	0.73	A
Less than 40% <i>L. latifolium</i> cover	546	23.62	0.57	B	365	36.62	0.83	B
<i>Date</i>								
March 4, 2004	125	14.99	1.03	A	–	–	–	–
April 23, 2004	116	17.92	1.06	B	–	–	–	–
July 22, 2004	115	23.99	1.15	C	112	41.33	1.36	A
October 2, 2004	126	23.88	1.14	C	–	–	–	–
March 15, 2005	136	16.00	1.02	D	136	37.48	1.16	B
April 15, 2005	124	34.76 <sup>a</sup>	1.15	E	126	39.63	1.35	C
June 15, 2005	131	18.37	1.08	B	131	37.63	1.35	B
August 15, 2005	125	23.18	1.14	CF	124	26.59	1.24	D
October 15, 2005	118	22.55	1.04	F	118	20.99	0.47	E

<sup>a</sup> Anomalous readings were systematic and likely due to a miscalibrated refractometer

When soil moistures were compared with depth, we observed that deep soils held more than 6% more moisture than shallow soils (Table 2), but this difference was not statistically significant ( $P = 0.0813$ ).

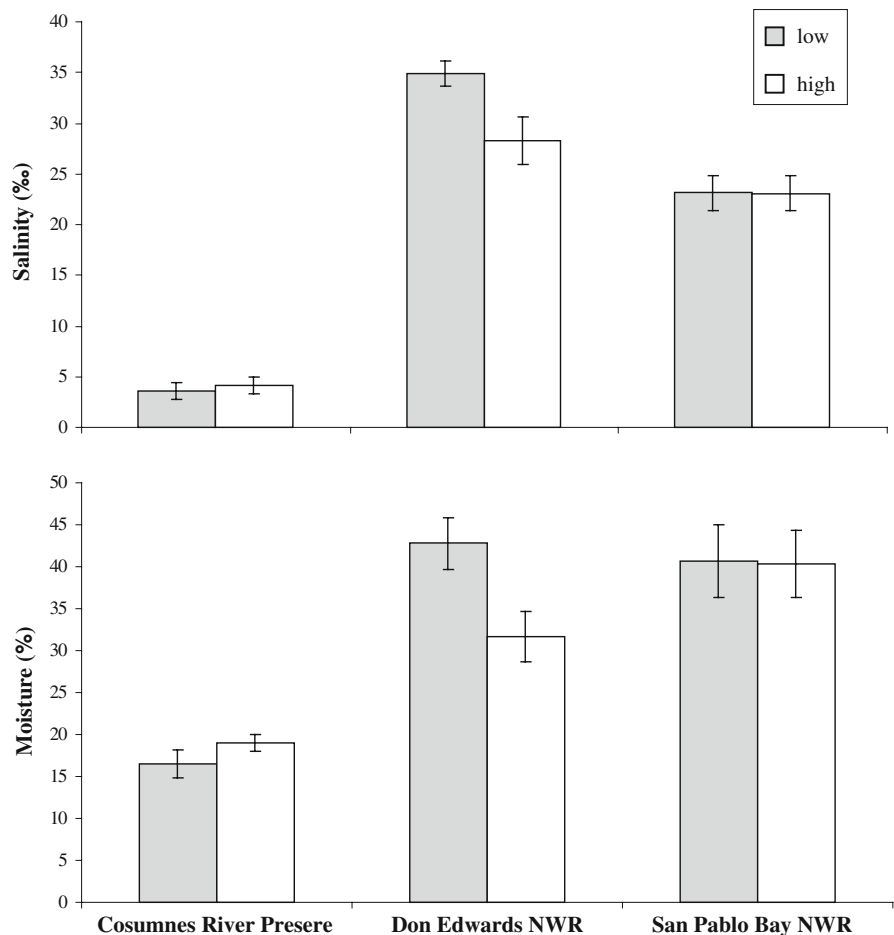
High and low densities of *L. latifolium* had differing salinity levels. High density *L. latifolium* stands had 3.84‰ lower salinity levels than low density stands (Table 2). Dense *L. latifolium* plots also had drier soils compared to low density plots. This equated to a 5.06% decrease in soil moisture between high and low density plots.

When salinities were broken down by site and density, analysis revealed that density differences were only significant ( $P < 0.0001$ ) at the high salinity site, Don Edwards NWR (Fig. 3). No significant differences were observed at either the freshwater site ( $P = 0.5422$ ), or the brackish site ( $P = 0.9967$ ). The same relationship was observed for moisture. At Don Edwards moisture levels were

significantly ( $P < 0.0001$ ) lower in high density plots compared to low density plots, but the same was not true for the freshwater ( $P = 0.3184$ ) and brackish sites ( $P = 0.8994$ ).

When salinity was analyzed by date we found that early spring salinities tended to be lower and increased gradually from March into June as the season progressed. In both 2004 and 2005 March had the lowest observed salinity. Summer and early fall salinities from July through October tended to be grouped together, and were generally the highest for the season. April of 2005 was the only observation period that failed to follow this trend and showed anomalously high salinities (Table 2). Observed salinities for April 2005 were more than 15‰ above April 2004 estimates, as well as both March and June estimates for 2005. These anomalous readings were systematic across plots at all three sites and were likely the result of an incorrectly calibrated refractometer.

**Fig. 3** Salinity and soil moisture effects on density (note that significant density effects were only found at Don Edwards NWR, where high density is associated with lower salinity and moisture)



Moisture levels by date were highest for the lone 2004 sample taken in July. In the 2005 samples, moisture tended to be highest in early spring, drying out steadily as the season progressed. Peak moisture levels in 2005 occurred in April, with the driest conditions occurring in October (Table 2).

The seasonal trends of both salinity and soil moisture were most clearly revealed when the data was converted into percent differences from the mean. When these percentages were graphed against the date they showed a steady increase in salinity and decrease in soil moisture over the course of the growing season (Fig. 4).

Evaluation of the specific plant metrics demonstrated a number of similarities between sites. Assessment of average inflorescence heights showed that Cosumnes River Preserve average 116 cm, Don Edwards NWR averaged 115, and San Pablo Bay NWR had 104 cm (Table 3). Inflorescence heights were not significantly different ( $P = 0.2708$ ) between sites.

Inflorescence height was significantly different between high and low density at Cosumnes River

Preserve ( $P = 0.0003$ ), Don Edwards NWR ( $P < 0.0001$ ), and San Pablo Bay NWR ( $P = 0.005$ ). High density plots had consistently taller inflorescences than lower density plots.

The number of inflorescences per square meter tended to be lower at the drier sites, but this was not statistically significant ( $P = 0.4992$ ). Inflorescence number per square meter was lowest at Cosumnes River Preserve with an average of 34, followed by Don Edwards NWR with 35, and San Pablo Bay NWR at 45 (Table 3).

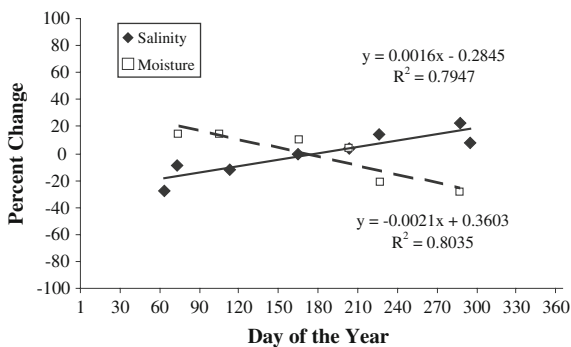
Inflorescence number per plant was also not significantly different between sites ( $P = 0.5354$ ), with Cosumnes River Preserve averaging 3.5, Don Edwards NWR averaging 4.1, and San Pablo Bay NWR with 4.6 (Table 3).

Seed production differed significantly from one site to another ( $P < 0.0001$ ). Cosumnes River Preserve averaged 3,244 seeds per inflorescence, San Pablo Bay NWR averaged 424 seeds, and Don Edwards NWR averaged 2,297 seeds (Table 3). The most productive site at Cosumnes River Preserve produced on average less than half of the 8,000 seeds per inflorescence that is commonly cited from an unpublished source (Young et al. 1995, 1997; Blank and Young 1997).

The maximum number of seed produced on a single inflorescence in this study was 6,611 at Cosumnes River Preserve. The minimum number of seed produced was four on an inflorescence bagged at San Pablo Bay NWR.

These results illustrate a 29.2% reduction in seed production along the salinity gradient between the fresh water site and the high salinity site. Along the moisture gradient there was an 86.9% reduction between the driest and wettest sites.

Seed germination and viability varied between seed sources. Over the course of the study, Cosumnes



**Fig. 4** Seasonal percent change of salinity and soil moisture at all three sites

**Table 3** Plant characteristics and seed viability at three sites in the San Francisco Bay Estuary

Variable	Cosumnes River Preserve			San Pablo Bay NWR			Don Edwards NWR		
	<i>n</i>	Mean	SE	<i>n</i>	Mean	SE	<i>n</i>	Mean	SE
Inflorescence per meter square	16	56.08	9.57	16	66.50	15.30	16	47.27	8.22
Inflorescence per plant	16	3.46	0.44	16	4.57	0.85	16	4.07	0.73
Maximum inflorescence height (cm)	16	115.84	6.44	16	101.19	8.75	16	115.16	5.87
Seed produced <sup>a</sup>	16	3243.94	333.90	13	424.46	132.00	16	2297.25	491.64
Seed viability (%)	16	95.63	1.01	16	87.19	1.31	16	45.47	3.09

<sup>a</sup> Seed produced per inflorescence



River Preserve had an average germination rate of 95.63%, Don Edwards NWR averaged 45.47%, and San Pablo Bay NWR averaged 87.19% (Table 3). Tetrazolium tests of viability demonstrated little to no observed seed dormancy. Less than 1% of nongermminating seed were shown to be viable.

When field exposure were analyzed, there was no difference in the germination and viability rates between seeds at time zero and those exposed to 7 months of field conditions at any salinity or moisture level. There was also no significant difference in viability between field exposed seeds and those stored under lab conditions. No differences in viability were observed between high density or low density *L. latifolium* plots and lab stored seed. Since seed viabilities demonstrated no effects from field exposure, the seed viabilities were averaged across all sampling periods for each plot. These averages were then used for all subsequent data analysis.

Seed source significantly influenced seed viability ( $P < 0.0001$ ). Soil moisture effects on seed viability were muted with only an 8.44% decrease from the driest to the wettest sites. Seed viability was highest at the freshwater site but declined by 50.16% at the high salinity site.

Linear regressions revealed the relative influence of salinity and moisture on continuous plant metrics. Since each of the plant metrics were taken only once a year, salinity and soil moisture values were averaged by date. Salinity and soil moisture were also averaged across all three depths because salinity differences by depth were muted in freshwater plots and because moisture levels were not significantly different with depth. This also simplified the analysis and interpretation by providing a single salinity and soil moisture value for each study plot.

Linear regression revealed that the average salinity had a statistically significant influence on seed number ( $P = 0.0297$ ) and seed viability ( $P < 0.0001$ ). Salinity had no significant effect on inflorescence height ( $P = 0.4685$ ), inflorescence number per plant ( $P = 0.8530$ ), or inflorescence number per square meter ( $P = 0.6326$ ).

The regression of salinity and seed number was negative with a slope of  $-48.81$ , and had a weak coefficient of determination ( $R^2 = 0.1043$ ). Salinity and seed viability also demonstrated a negative slope of  $-1.50$ , but had a higher coefficient of determination ( $R^2 = 0.5971$ ).

Soil moisture regressions also showed that seed number ( $P = 0.0004$ ) and seed viability ( $P < 0.0001$ ) were statistically significant. Inflorescence height ( $P = 0.2253$ ), inflorescence number per plant ( $P = 0.9898$ ), and inflorescence number per square meter ( $P = 0.9072$ ) were not significant.

The regression of moisture to seed number has a slope of  $-86.99$  and a relatively low coefficient of determination ( $R^2 = 0.2821$ ). The slope of the moisture and seed viability regression also had a negative slope ( $-1.01$ ) and low coefficient of determination ( $R^2 = 0.2327$ ).

Seed dispersal profiles were obtained for Cosumnes River Preserve and Don Edwards NWR. Unfortunately, dispersal traps at San Pablo Bay NWR were severely disturbed by tidal inundation in each sampling period and therefore were abandoned.

Seed production was estimated from the dispersal traps and served as an estimate of capture efficacy. Captured seed totals were scaled up to encompass 100% of the dispersal area out to 5 m. Estimated seed production was also scaled up to account for 100% of the time between the first and final sampling periods.

The estimated seed number per inflorescence based on the dispersal traps at Cosumnes River Preserve totaled 3,810, while Don Edwards NWR totaled 1,987 (Table 4). The values estimated for Cosumnes River Preserve differed 14.9% from those observed from the bagged inflorescence (3,244). Estimates for Don Edwards NWR were 13.5% lower than those observed from the bagged inflorescences (2,297).

At both sites, the number of captured seeds was highest for the dispersal trap located 1 m from the target plant. Mean dispersal distance calculations based on the trap data showed that Cosumnes River Preserve averaged 117 cm, while Don Edwards NWR averaged 94 cm (Table 4). Mean dispersal distances were highly variable between plots, and the observed differences were not statistically significant ( $P = 0.1815$ ). Overall seed dispersal profiles were nearly identical at both Cosumnes River Preserve and Don Edwards NWR (Fig. 5).

Seed dispersal tended to peak early in autumn and tapered off as the season progressed (Fig. 6). Seed dispersal rates at Cosumnes River Preserve peaked during the second sampling period in September, whereas rates at Don Edwards NWR were highest in the first sampling period. The high dispersal in the

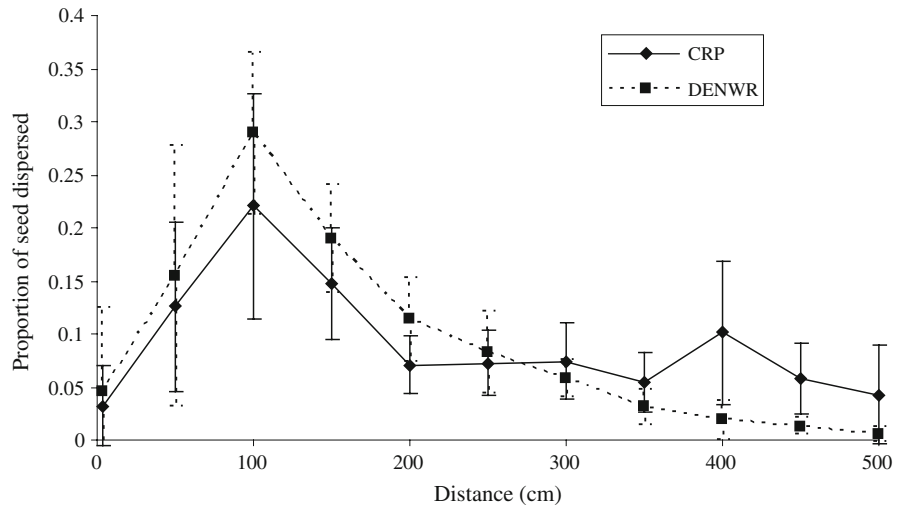
**Table 4** Mean dispersal and seed production from dispersal plots

Variable	Cosumnes River Preserve			Don Edwards NWR		
	<i>n</i>	Mean	SE	<i>n</i>	Mean	SE
Mean dispersal distance (cm)	5	116.70	19.33	5	93.70	14.53
Estimated seed production <sup>a</sup>	5	3809.96	1357.21	5	1986.74	884.61
Persistent seed <sup>b</sup>	5	545.20	355.15	5	19.60	6.61

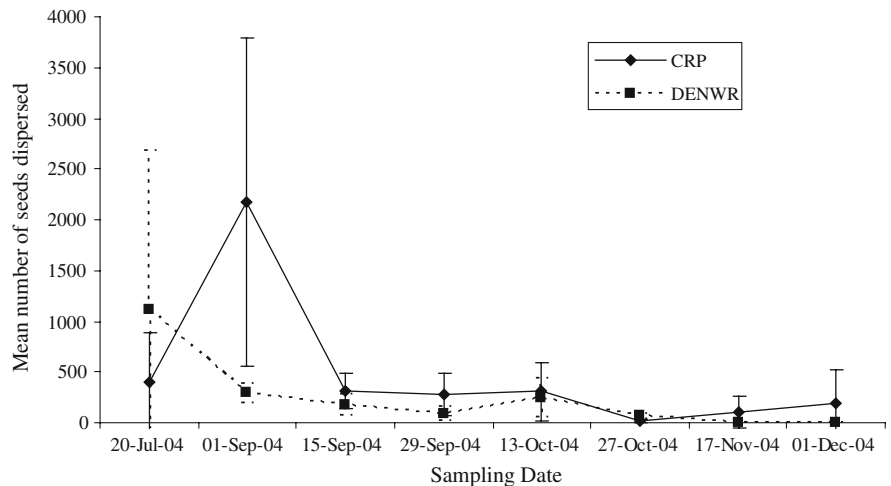
<sup>a</sup> Seed production estimated from dispersal data corrected for time and area

<sup>b</sup> Seed remaining on the plant after December 2005

**Fig. 5** Seasonal proportion of seed dispersed with distance



**Fig. 6** Rate of seed dispersal over the field season. CRP stands for Cosumnes River Preserve, while DENWR stands for Don Edwards NWR



first observation at Don Edwards NWR suggests that some seed may have been dispersed prior to plot establishment. At both sites seed dispersal continued through the culmination of the study in December 2005.

Some seed remained persistent on the plant through the culmination of the study. Seed persistence was much higher at Cosumnes River Preserve with an average of 545 seeds per inflorescence or 14.1% of seed remaining on the inflorescence in

**Table 5** Estimated reproductive potential of *Lepidium latifolium* at each site

Study site	Number of viable seed produced per inflorescence	Number of viable seed produced per plant	Number of viable seed produced per square meter
Cosumnes River Preserve	3102	10734	173970
San Pablo Bay NWR	370	1691	24611
Don Edwards NWR	1045	4251	49376

December. Don Edwards NWR averaged only 20 seeds per inflorescence (Table 4) or 1.0% of seed remaining on the inflorescence.

The overall reproductive potential of *L. latifolium* was reduced by increases in both salinity and soil moisture. When the number of viable seeds per inflorescence was calculated for each site, this study found that Don Edwards NWR produced only 33.7% of the seed produced per inflorescence at Cosumnes River Preserve, while San Pablo Bay NWR produced only 11.9%. Similar percentages were obtained when production was scaled up per plant or per square meter (Table 5).

## Discussion

Salinity and soil moisture clearly are important factors affecting the invasion dynamics of *L. latifolium*, but these effects appear to be focused primarily on the earliest life stages. Salinity and soil moisture showed no significant impact on adult characteristics such as inflorescence number or inflorescence height.

Although, our results showed no reduction in inflorescence height, Chen et al. (2002) showed a 52% reduction in stem biomass with 50 days of continuous flooding. The moisture levels at our study sites were only periodically flooded. Conditions at the wettest site at San Pablo Bay NWR were frequently near saturation, but flooded only during high tide events to depths of 0.5 m. The intermittent flooding at our sites likely ameliorated conditions compared to those described in Chen et al. (2002) allowing *L. latifolium* to maintain its inflorescence height and number.

The consistent stature of *L. latifolium* observed in this study resulted in no reduction in reproductive potential based on inflorescence number. The consistent inflorescence height also maintained a high release point that is often critical to defining the seed

dispersal profile (Bullock and Clarke 2000; Nathan et al. 2001; Tackenberg 2003).

Even though salinity and moisture had no significant effect on adult plant characteristics they did reduce the reproductive potential of *L. latifolium*. Seed production was reduced by 86.9% along the soil moisture gradient. In some instances this reduction was nearly complete with fewer than ten seeds being produced per inflorescence. This reduction was recognizable in the field and manifested itself as a withering of inflorescences. This withering occurred after flowering and only in the wettest of locations. During flowering there were no apparent differences between the sites.

Chen et al. (2005), found similar results under flooded conditions but observed reduced flowering as well as a reduction in seed production. Even though the highest moisture levels observed in this study occurred at or near the time of flowering, we observed no reduction in flowering at the site. Soil moisture effects were only apparent post-flowering during seed set.

Salinity also resulted in a slight reduction in seed production, but this effect was small when compared to soil moisture. Although significant, the relative effect was minimal compared to that observed along the moisture gradient. Although percent changes provide a means of assessing the effect of salinity and soil moisture, the combined effect of these two variables remains unclear.

Stresses from salinity and soil moisture adversely affected not only the quantity but also the quality of *L. latifolium* seed produced. Seed viability declined sharply with salinities greater than 25‰. This decline in seed quality was evident upon close inspection of the seed. Seed produced under high salinities were frequently characterized by a slightly dimpled seed coat. By comparison, seed from freshwater and brackish sites were consistently full and smooth. This suggests that seed may experience some

desiccation during seed set at high salinities. Viability also appears to decrease with increasing moisture, although this effect was not as strong. This reduction in seed viability and seed production suggests that *L. latifolium* is more susceptible to stresses during seed development and maturation.

Since salinity and moisture stresses adversely affect the number and quality of *L. latifolium* seed produced, they have a major impact on its reproductive potential. Of the three sites studied, the wettest location at San Pablo Bay NWR had the lowest overall reproductive potential (Table 5). Even at this low production site, the number of seeds produced per inflorescence averaged 370, equating to more than 24,000 viable seeds per square meter. This prolific seed production even under high stress conditions suggests that there are more than enough propagules present for continued colonization, even if establishment from seed is rare.

Although salinity and soil moisture reduced the reproductive potential of *L. latifolium*, seed dispersal showed very little change from one source to another. *L. latifolium* seed have no specialized structures to aid in dispersal, therefore the potential distance a seed can be dispersed is dictated primarily by the height of the inflorescence. Since inflorescence height was unaffected, little to no differences in dispersal would be expected.

The similarities in dispersal between both sites were immediately apparent when comparing the two dispersal profiles (Fig. 5). Even though dispersal was quite variable, the two profiles show remarkable agreement. Therefore, even though salinity and soil moisture have negative impacts on the quantity and quality of seed being dispersed, there appears to be no difference between these seeds in terms of their dispersal distances or profiles.

The onset of dispersal tended to be much earlier at Don Edwards NWR compared to Cosumnes River Preserve (Fig. 6). This divergence was due primarily to phenological differences between the two sites, which were also mirrored in flowering times at each site. These phenological differences most likely are the result of climatic differences between the two sites.

Don Edwards NWR is characterized by a mediterranean climate with mild summers (Köppen classification Csb), while Cosumnes River Preserve lies at a transition between a mediterranean climate with hot summers (Csa) and a semi-arid warm steppe

(Bsh) (Kesseli 1942). When phenological differences were accounted for by matching peak dispersal, the rates were very similar, and were characterized by peak dispersal early in the season tapering off as the season progressed.

Phenological differences between sites are also likely responsible for the difference in the number of persistent seed remaining on the plant at the culmination of the study. The inland site at Cosumnes River Preserve, had 12.5% of the seed produced remaining on the plant, while at Don Edwards less than 1.0% persisted. Unfortunately, due to logistic constraints the study was terminated in late December. Therefore, it is unknown whether the persistent seed at Cosumnes River Preserve would have continued dispersing in the same manner as that observed at Don Edwards NWR.

Seed production values obtained from dispersal data estimates were in very close agreement with seed production numbers from bagged inflorescences at Cosumnes River Preserve. Unfortunately because dispersal rates at Don Edwards NWR were highest in the first observation, some dispersal may have gone unobserved. Therefore, dispersal estimates may underestimate the total number of seed produced at Don Edwards NWR. That aside, seed production from bagged inflorescence and those extrapolated from the dispersal plots are in close agreement and suggest that the methods used for seed capture were effective.

The post-dispersal fate of seeds is critically important to the invasion success of *L. latifolium*. The field exposure portion of the viability study demonstrated that seeds suffer no ill effects from salinity and soil moisture even after 7 months of exposure. Previous research has shown that *L. latifolium* germination requires a light cue and wet soils (Miller et al. 1986; Larson and Kiemnec 2005; Laubhan and Shaffer 2006). Germination can occur under low to moderate salinities up to 25‰ (Laubhan and Shaffer 2006; Spent et al. 2006).

Seedling survival and establishment from seed is rare under saline conditions, but in controlled experiments establishment has been observed in salinities as high as 20‰ (Spent and Foin 2006). Under these conditions salinity stresses are quite high. Establishment under such conditions is likely ameliorated by microsite variability or episodic freshwater flushing of surface soils by rain, fog, or dew. Irregardless of the

mechanisms responsible it is clear that *L. latifolium* is able to establish in this high salinity environment, as evidenced by the acres of infestation within the tidal marsh flats.

While salinity and soil moisture adversely affect the reproductive potential of *L. latifolium*, this study also found that this stress has an effect on the density of *L. latifolium* stands. At Don Edwards NWR where soils are wet and salinity is high, *L. latifolium* tended to have higher densities in drier, less saline conditions (Fig. 4). At Cosumnes River Preserve and San Pablo Bay NWR we see no significant difference in salinity or soil moisture between low and high density locations. This suggests that even though viable seed production is lowest at San Pablo Bay NWR *L. latifolium* colonization is not inhibited within the gradient range observed at each site. This implies that the reduction in reproductive potential is not strong enough to inhibit colonization at San Pablo Bay NWR. At Don Edwards NWR where viable seed production is almost three times higher, we see a density effect. This indicates an establishment bottleneck occurring at Don Edwards NWR, which limits the rate of colonization at that site.

The reduced rate of colonization observed at Don Edwards NWR, may also be the result of reduced vegetative growth and expansion. The additive stresses of both anoxia and salinity on established *L. latifolium* plants at Don Edwards NWR may limit vegetative expansion. It is likely that some individuals became established in marginal habitats, which become ecologically important only under high stress conditions like those observed at Don Edwards NWR.

Overall, the results of this study demonstrate complex interactions between salinity and soil moisture and specific plant metrics at each site. The specific effects of salinity and moisture do not exert uniform stress across all *L. latifolium* life stages, or at each site.

The deleterious effects of salinity and soil moisture instead exert varying stresses upon plant metrics given specific site conditions. For example, conditions at San Pablo Bay NWR were least favorable when only considering reproductive potential, yet we saw no differences between high and low density *L. latifolium* plots. At Don Edwards NWR, we saw nearly three times as many viable seeds produced, but *L. latifolium* densities were reduced by salinity and soil moisture.

The deleterious effects of salinity and moisture on growth and development of *L. latifolium* provide

added insight into its invasion dynamics. The physiological responses of *L. latifolium* to varying intensities of salinity and moisture allow specific sites to be characterized in terms of their relative susceptibility to invasion, which serves as a potential tool for prioritizing control and eradication efforts.

For example at Cosumnes River Preserve, *L. latifolium* is prevalent and appears to follow no discernable distribution pattern. *L. latifolium* patches at this site are widespread and disparate. Since salinity and flooding stresses are muted, *L. latifolium* has no barriers to invasion and spreads indiscriminately via its abundant seed.

At San Pablo Bay NWR, the reproductive potential of *L. latifolium* is drastically reduced, and establishment is limited by excessive flooding. At this site *L. latifolium* has invaded by colonizing slightly elevated portions of the marsh. These elevated patches serve as sources for vegetative spread into the lower marsh. Colonization from seed may also occur in the lower marsh following extended periods of low moisture. Because site conditions are variable spread of *L. latifolium* is not completely inhibited, but the rate of invasion at San Pablo Bay NWR will be slow relative to Cosumnes River Preserve.

*Lepidium latifolium* populations at Don Edwards NWR are strongly associated with disturbed areas that are elevated above the open marsh. These disturbed elevated areas lack strong competitors and experience episodic freshwater inputs following heavy rains. These sites are elevated enough that tidal inundation occurs intermittently. At this site, colonization into the lower marsh appears to be limited. Colonization instead appears to occur only along the margins where salinity and moisture stresses are ameliorated. This site appears to be the least susceptible to invasion, compared to both San Pablo Bay NWR and Cosumnes River Preserve.

From a management perspective site characterization allows for control efforts to be prioritized. This prioritization invariably increases efficiency and efficacy by focusing control and eradication efforts toward sites most susceptible to invasion.

Overall this study has shown that salinity and soil adversely affect the reproductive potential and establishment of *L. latifolium*, by reducing the number of viable propagules available for dispersal. Dispersal is unaffected by salinity and soil moisture, and seeds can persist in high salinity and moisture conditions for at

least one growing season. Salinity and soil moisture stresses further reduce establishment of *L. latifolium* beyond reducing reproductive potential by preventing establishment or curtailing vegetative spread, resulting in reduced densities under high stress conditions.

The deleterious effects of salinity and soil moisture may impart some sites with an inherent resistance to *L. latifolium* invasion. Wet locations like San Pablo Bay NWR, have such reduced seed production that invasive spread at these sites will be much slower when compared to dry freshwater sites such as Cosumnes River Preserve. Other sites like Don Edwards NWR have reduced reproductive potential as well as establishment stresses that slow or inhibit colonization.

By analyzing the effects of salinity and moisture on the key components of *L. latifolium* biology, this study has served to deepen our understanding of the underlying mechanisms guiding its spread. This study has quantified many aspects of *L. latifolium* biology that were previously unknown, including seed production, seed dispersal, and effects of salinity and soil moisture on adult plant characteristics. In so doing, this study has deepened our understanding of *L. latifolium* invasion biology which provides a framework for the development of more effective management practices.

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