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Potential for Spread of Algerian Sea Lavender (*Limonium ramosissimum* subsp. *provinciale*) in Tidal Marshes

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We investigated the potential for an invasive sea lavender, *Limonium ramosissimum* subsp. *provinciale* (Algerian sea lavender; LIRA) to spread in San Francisco Estuary (SFE) tidal marshes by testing how two determinants of tidal marsh plant distribution, salinity and inundation, affect LIRA dispersal, germination, growth, and reproduction. Simulating dispersal in 0, 15, and 30 parts per thousand (ppt) salinity water, we found seeds remained afloat similarly regardless of salinity, and seed viability after floatation was high (88%); however, seeds in 0 ppt aquaria germinated after just 4 d, suggesting shorter dispersal distances in fresh than in brackish or saline water. Next, we compared LIRA and native halophyte seed germination in 0, 15, 30, and 45 ppt water. Percentage of germination was similar between species after 3 wk, but LIRA germinated faster in fresh water than all native species (90% vs. 5% germination after 4 d), suggesting a possible establishment advantage for LIRA at low salinities. Finally, we grew LIRA under crossed salinity and inundation levels in a tidal simulator for a growing season. LIRA growth and seed production increased when either salinity or inundation was reduced. We conclude that spread could be greatest among salt marshes due to high potential for seed dispersal in saline water, yet spread within marshes may be greatest in relatively lower salinity conditions where growth and reproduction are maximized.

Nomenclature: Algerian sea lavender, *Limonium ramosissimum* (Poir.) Maire subsp. *provinciale* (Pignatti) Pignatti.

Key words: Dispersal, germination, halophyte, inundation, *Jaumea*, life history transitions, propagule pressure, *Salicornia*, salinity gradient, transition zone.

Algerian sea lavender (*Limonium ramosissimum* [Poir.] Maire subsp. *provinciale* [Pignatti] Pignatti; hereafter, LIRA), is one of several invasive sea lavenders from the western Mediterranean (Devillers-Terschuren and Devillers-Terschuren 2001) that have invaded salt marshes and tidal lagoons across California (Barbour et al. 2007; Consortium of California Herbaria 2012). Where studied in California salt marshes, LIRA has been found to spread rapidly within high marsh and transition zone habitats and to reduce cover of native halophytes (Archbald and Boyer 2014; M Page, personal communication). In the San Francisco Estuary (SFE), LIRA was only recently discovered, but has already invaded approximately 15,000 m^2 (3.7 ac) of saline tidal marshes in Central and South San Francisco Bay (Archbald and Boyer 2014). However, factors influencing LIRA's potential for further spread within the SFE were largely unknown.

In general, species are more likely to establish when an increase in resources, such as space, light, and nutrients, coincides with the arrival of a seed source (Davis et al. 2000). As a result, wetlands are frequently invaded because they concentrate seeds from surrounding watersheds and are periodically disturbed by wrack, sediment deposition, and scour (Zedler and Kercher 2004), Tidal marshes in the SFE have undergone significant anthropogenic disturbance (e.g., Atwater et al. 1977; Josselyn 1983) which encourages invasion by decreasing seed supply and cover of native plants, and, therefore, native biotic resistance (Belote et al. 2008; Hobbes and Huenneke 1992). A rapid increase in marsh restoration projects, too, may have the unintended consequence of increasing resources (e.g., space and light) for invading plants. In SFE, for example, the invasion of hybrid smooth cordgrass (*Spartina alterniflora* Loisel. X *Spartina foliosa* Trin) in marsh and mudflat habitats has likely been accelerated by an increase in available habitat via

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Management Implications

Information regarding the potential for newly introduced nonnative species to invade wildland ecosystems is needed for resource managers to prioritize responses to multiple simultaneous plant invasions. Management decisions, such as which species or populations to prioritize for eradication or seed suppression, are aided by research that addresses how variation in environmental conditions affects a species' spread. This is true in tidal marshes of the San Francisco Estuary (SFE) where several invasive plants have been identified as priorities for management action because of their rapid spread and impacts, and where new nonnative species continue to establish, many with unknown potential for widespread invasion. This research provides timely information regarding how the spread of an invasive plant recently found in the SFE, Algerian sea lavender, is affected by two key environmental factors that vary within and among tidal salt marshes: salinity and inundation. Investigating the effects of these variables on key life history stages of Algerian sea lavender (dispersal, germination, growth and reproduction) permitted characterization of conditions where Algerian sea lavender propagule pressure will be greatest, and may serve as a model for predicting spread of other nonnative plants across a complex environmental gradient.

marsh restoration (P. Olofson, personal communication). LIRA, too, has invaded both disturbed and restored marshes in the SFE (Archbald and Boyer 2014).

In addition to an availability of resources, propagule pressure (or invader supply) is a key indicator of which species will establish and spread (Eschtruth and Battles 2009; Kolar and Lodge 2001). Frequent delivery of individuals to new habitats increases the probability that species will overcome mortality events and establish new populations (Simberloff 2009). The importance of propagule pressure to influence species composition has been shown in a number of marsh systems (Morzaria-Luna and Zedler 2007; Rand 2000) including the SFE, where seed rain was found to be an important driver of species composition in restored marshes (Diggory and Parker 2011). As a result, how physical factors affect plant growth, as well as seed output, dispersal, and viability, plays a strong role in determining an invader's potential for spread (Kolar and Lodge 2001).

Salinity and frequency of tidal inundation affect the growth and reproductive output of halophytes (Flowers and Colmer 2008; Ryan and Boyer 2012; Schile et al. 2011; Seliskar 1985), and ultimately the distribution of estuarine marsh plants (Hinde 1954; Mahall and Park 1976; Watson and Byrne 2009). Landscape-scale gradients in salinity occur along an estuary's axis and gradients in both salinity and inundation occur within tidal marshes (Atwater et al. 1977; Mitsch and Gosselink 2000). Therefore, predicting spread in SFE marshes relies, in part, on understanding the effects of both factors (Grossinger et al. 1998). Prior research has investigated these factors to predict invasive plant spread in the SFE (e.g., perennial pepperweed [*Lepidium latifolium* L.; Leininger and Foin 2009; Reynolds and Boyer 2010; Spenst 2006] and hybrid smooth cordgrass [Callaway and Josselyn 1992; Collins 2002]).

We conducted three experiments to measure LIRA's response to a range of salinity and inundation levels during dispersal, germination, growth, and reproduction. To evaluate dispersal potential, we tested seed floatation over time across a range of water salinities typically found in the SFE, from fresh to saline (Atwater and Hedel 1976; Grossinger et al. 1998). Since low-salinity events (e.g., rainfall) trigger halophyte seed germination in salt marshes (Gul et al. 2013; Noe and Zedler 2001), we germinated seeds in fresh water following removal from aquaria to simulate the effect of reduced salinity upon seeds after arrival at a suitable substrate. We hypothesized that LIRA seeds would float in water at all salinities (Elsey-Quirk et al. 2009). However, since halophyte seeds often remain dormant in high-salinity water (Gul et al. 2013), we hypothesized floating seeds would remain ungerminated (and thereby retain the capacity to germinate upon arrival) longer in higher-salinity aquaria. In the second experiment, we assessed salinity effects on LIRA seed germination in comparison to common native halophytes. We expected seed germination of all species to be highest in fresh conditions (Khan and Gul 2006; Ungar 1995). However, since we have observed LIRA recruiting in otherwise barren, hypersaline soils in SFE marshes, we predicted LIRA would have a higher percentage of seed germination than common native marsh plants in hypersaline water (> 35 ppt). In the third experiment, we investigated growth and seed production of LIRA under crossed inundation and salinity treatments. Field studies of LIRA in the SFE indicated that plant size and seed production are highest in relatively dry, low-salinity soil (Archbald and Boyer 2014); however, whether salinity or inundation is responsible was unknown. We hypothesized that inundation stress is the primary driver of the differential growth and reproduction observed in the field because many *Limonium* species in the Mediterranean region occupy high-salinity, dry habitats (e.g., wave-spray–fed cliffs and hypersaline, interior basins subject to extreme summer drying [Devillers-Terschuren and Devillers-Terschuren 2001]).

We interpret findings to inform understanding of LIRA's ability to spread within and among marshes of varying salinity. As invasive sea lavender is continuing to spread within SFE and to other marshes throughout California, such information could be critical to early detection and control.

Materials and Methods

Study Location. Experiments were carried out at San Francisco State University's Romberg Tiburon Center for

Environmental Studies (RTC) located at the edge of San Francisco Bay in Tiburon, CA (37.889°N, 122.446°W). Experiments utilized RTC's outdoor flow-through bay water system and its greenhouse, a Plexiglas-roofed structure with open, screened walls.

Seed Collection. We collected LIRA inflorescences bearing mature achenes (one-seeded indehiscent fruits; hereafter, seeds) throughout the plant's elevational distribution at Sanchez Marsh, in the city of Burlingame, CA, in October of 2007 and 2008. At the same location, we collected seeds of the native halophytes perennial pickleweed (*Salicornia pacifica* Standl; hereafter, SAPA), marsh jaumea (*Jaumea carnosa* (Less.) A. Gray; hereafter, JACA), and a native sea lavender, marsh rosemary (*Limonium californicum* (Boiss.) A. Heller; hereafter, LICA) in the summer and fall of 2008. Seeds were stored at room temperature prior to experiments.

Dispersal Potential at Estuarywide Salinity Levels. We simulated LIRA seed dispersal and tested the effect of salinity and time on both seed floatation and potential for subsequent establishment. We placed 120 seeds in replicate 0-, 15-, and 30-ppt salinity aquaria ($n = 5$) for 2 wk, monitored buoyancy, then removed and germinated seeds using fresh water. Set-up involved arranging 15 37.9-L (10-gal) tanks (aquaria) within a large, round outdoor fiberglass tank (1.8 m diam by 0.85 m deep) equipped with drainage and supplied with flow-through bay water such that aquaria were partially submersed to regulate temperature. Fresh water and Marine Labs Instant Ocean Sea Salt® (Instant Ocean, United Pet Group, 3001 Commerce St., Blacksburg, VA USA, 24060-6671) were used to prepare salinity treatments, which were randomly assigned to aquaria. Aeration was supplied individually to each aquarium using air bubblers to simulate field conditions by reducing water surface tension.

The experiment was begun by placing seeds, each still enclosed by a dry flower, into aquaria in June 2008. As a control for floatation and salinity, 15 seeds were germinated indoors between filter paper wetted with fresh water in each of five petri dishes. The numbers of seeds afloat in aquaria were recorded on days 1, 2, 3, 7, 9, 10, and 14. After 1, 2, 4, 7, and 14 d, 15 seeds were removed from each treatment, rinsed, then germinated between two layers of filter paper with deionized water. Seeds that sank were removed first from aquaria so that seed removal would not disturb on-going floatation counts. Between day 4 and day 7, nearly all seeds in 0 ppt salinity aquaria germinated while afloat, precluding subsequent seed germination testing following floatation (see Results). Aquaria water salinity and temperature were monitored daily and water was added to compensate for evaporation. Germination was determined by the emergence of a radicle and was monitored until 1 wk past the last date seeds were removed from aquaria.

Seed floatation data did not meet parametric test assumptions. Therefore, we tested the effects of aquaria salinity and time (days in aquaria) and their interaction on the percent of seeds afloat using the Scheirer-Ray-Hare (S-R-H) extension of the Kruskal-Wallis test. The S-R-H test is a nonparametric alternative to the two-way ANOVA (Dytham 2011). We evaluated differences (post-hoc) between individual treatment levels of interest using separate Kruskal-Wallis tests. We tested the effects of aquaria salinity on percentage of seed germination following floatation using repeated measures ANOVA on the first four dates that seeds were removed from the aquaria only (days 0, 1, 2, and 4), as seeds from the freshwater aquaria could not be tested for germination after that. All statistical tests were conducted with PASW Statistics 18 (SPSS, International Business Machines Corporation, 1 New Orchard Road, Armonk, NY USA 10504-1722).

Germination of LIRA Compared to Native Halophytes. We tested LIRA germination under a range of simulated soil salinities (0, 15, 30, and 45 ppt) relative to native halophytes that commonly co-occur with LIRA in the SFE: SAPA, JACA, and LICA (Archbald and Boyer 2014). To prepare seeds for germination, we removed flower husks from LIRA and LICA seeds (with tweezers) and probed JACA seeds in husks to verify their presence. SAPA seeds, enclosed by a translucent fruit coat, were checked under a dissecting scope to verify seed presence. Seeds of all species were surface sterilized with 10% Clorox (0.52% sodium hypochlorite) for 1 min (following Khan and Weber 1986) then rinsed two or three times with deionized water. Saline treatments were prepared by mixing Marine Labs Instant Ocean Sea Salt with deionized water; the 0 ppt treatment consisted of deionized water. In March 2009, we placed 15 seeds of each species between two sheets of filter paper in replicate petri dishes ($n = 4$) in the greenhouse at RTC. Germination was identified by the emergence of a radicle and was monitored seven times over the 49-d experiment. Salinity treatments were maintained throughout the experiment by flushing petri dishes using spray bottles with appropriate salinity treatments every few days. Percentage of germination data could not be transformed adequately; therefore, we evaluated these results descriptively and graphically.

Effect of Salinity and Inundation on Growth and Reproduction. We tested how inundation and salinity affect early growth and reproduction of LIRA by growing plants from seedlings through flowering under crossed salinity (0, $\cong$ 15, and $\cong$ 30 ppt) and inundation treatments (once per day, twice per week, and twice per month). We planted 20 LIRA seeds per pot in round (21 cm [8.3 in] diam by 22 cm deep) nursery pots 2 cm below soil surface in a high-clay terrestrial soil (American

Soil and Stone, San Rafael, CA) in November 2008 and watered pots with fresh water for 3 wk. Following seedling emergence, we placed each pot into a larger plastic pot (26 cm diam by 23 cm deep) situated on water tables in the RTC greenhouse. Each outer, larger pot was fed by irrigation tubing delivering nine unique inundation by salinity treatment combinations in randomized blocks. Three treatment lines were fed by RTC's filtered flow-through bay water system to deliver water at near-oceanic salinities, three were from fresh water plumbing, and three were via aquaria pumps drawing water from an outdoor fiberglass mesocosm tank (1.8 m diam by 0.85 m) used for mixing and storage of brackish water. Brackish water was prepared by delivering equal volumes of fresh water and flow-through bay water into the storage tank. During treatment, outer pots were filled for 2 h, submerging the soil surface of inner pots 4 cm and overflowing onto water tables. After constant flow ended, water drained out over 2 h from a small hole drilled in the bottom of each outer pot. The 15- and 30-ppt treatments varied with the salinity of San Francisco Bay water at RTC during the course of the study (December 2009 to September 2010), with an average of 14.7 ppt ± 0.6 (SE) and 29.5 ppt ± 0.4, respectively. Salinity of treatments was monitored with a refractometer during weekly and bimonthly inundation treatments. The frequencies of inundation treatments were chosen to approximate the range of average annual inundation frequencies LIRA experiences in the field. This was determined by counting the number of high tides per year in 2008 predicted by tidesandcurrents.noaa.gov (NOAA Tides and Currents 2008) to reach or exceed three elevations at Coyote Point Marina, San Mateo, CA, corresponding to average high, medium, and low sections of LIRA's vertical range. LIRA's range was established by surveying an invaded marsh near Coyote Point Marina using a Topcon laser level (Topcon Positioning Systems, 7400 National Drive, Livermore, CA USA 94550) relative to the high tide waterline on a single, calm day with a known predicted high tide.

We monitored mortality (the number of individuals that died per pot) and number of leaves per rosette approximately every 2 mo over the 255-d study and recorded number of flowers and height of inflorescences approximately every 2 wk during flowering from June through August. When flowering had largely ended (in September), we clipped inflorescences, then dried, weighed, and counted seeds from a subset of pots in order to estimate the number of seeds produced in the remaining pots through regression ($y = 0.0014x + 0.0042$, where x = grams of seeds with encapsulating flowers and y = number of seeds; $R^2 = 0.988$). We measured vegetative tissue biomass by clipping plants at soil level, then rinsing, drying, and weighing rosettes. To measure belowground biomass we submersed soil with roots in water, agitated by hand to loosen soil, rinsed roots through a 1-mm (0.039 in) sieve (repeating three times per pot), and dried and weighed the combined live and dead roots. Number of leaves, above- and belowground biomass, mortality, number of inflorescences, and number of seeds per inflorescence were analyzed by two-way ANOVA (factors: salinity, inundation, and their interaction) following transformations to meet parametric test assumptions.

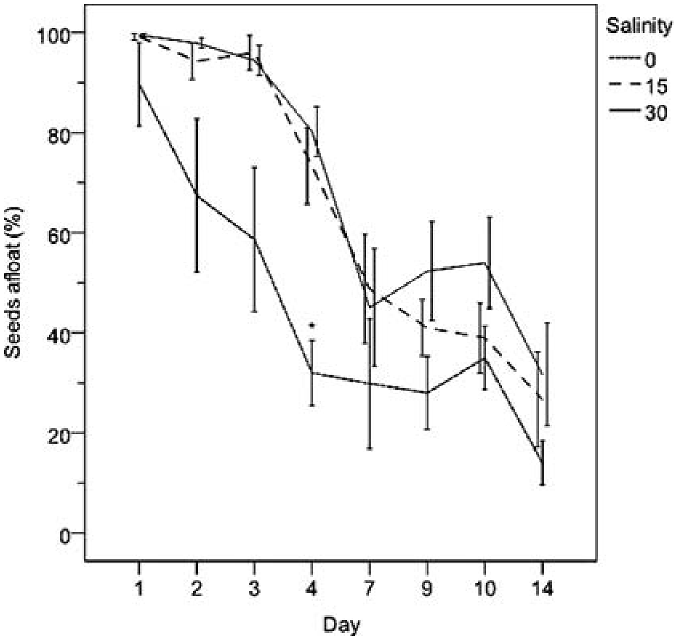

Figure 1. Effects of salinity (0, 15, and 30 parts per thousand) and time on floatation of Algerian sea lavender seeds. Error bars represent ± 1 SE. Asterisk (*) represents a significant effect of salinity. Points offset to increase visibility.

Results

Dispersal Potential at Estuarywide Salinity Levels. Seeds sank over time in all salinity aquaria. Approximately 50% of all seeds sank by day 6 and approximately 75% of all seeds sank by day 14. However, fewer seeds remained afloat in fresh (0 ppt) than in brackish (15 ppt) or fully saline (30 ppt) water (Figure 1). Both time ($P < 0.001$) and salinity ($P = 0.002$) significantly affected the percentage of seeds afloat (no interaction, $P = 0.99$). Post-hoc tests found that salinity's effect on floatation was significant on day 4 only ($P = 0.008$), though there was also a trend toward a negative effect of 0 ppt salinity on floatation on days 2 ($P = 0.063$) and 3 ($P = 0.059$). On average, across salinities, seeds sank according to a negative logarithmic function ($R^2 = 0.94$; $y = -28.597\ln(x) + 103.09$ where y = percentage of seeds remaining afloat and x = number of days of floatation). On day 4, major germination of seeds in fresh aquaria began. Of the seeds that were removed

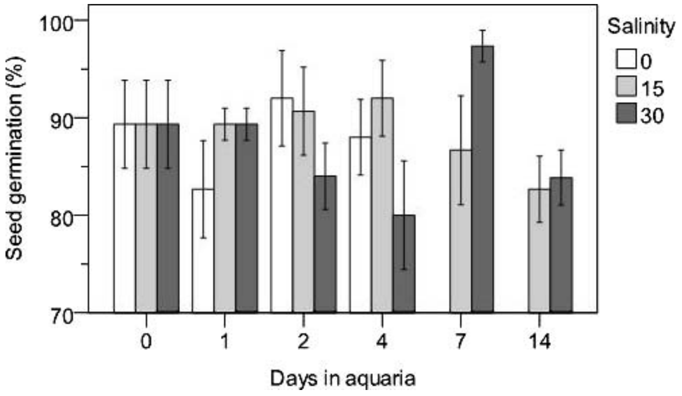

Figure 2. Effect of floatation in 0, 15, and 30 parts per thousand (ppt)salinity water on subsequent Algerian sea lavender seed germination in fresh water. Note 0 ppt treatment not shown after day 4 when seed germination in fresh water aquaria began; n = 15, error bars represent ± 1 SE.

from tanks and exposed to fresh water (i.e., seeds in 0 ppt aquaria removed through day 4 and all seeds in 15 and 30 ppt aquaria), 88% of seeds germinated, averaged across time and salinity treatments, as compared with 89% of seeds that germinated in the control. Salinity mattered little to germination after floatation. Repeated measures ANOVA across salinity treatments for the first four dates only (because germination could not be tested for the freshwater treatment after this) showed no significant differences or interactions, nor were there obvious patterns in germination among the 15 and 30 ppt treatments across dates (Figure 2).

Germination of LIRA vs. Native Plants. LIRA was the first to germinate when exposed to the 0 ppt salinity treatment (Figure 3). Five days after being exposed to fresh water, 90% of invasive sea lavender seeds had germinated compared to only 14% of LICA and 0% of JACA or SAPA seeds. By day 21 at 0 ppt, LICA and JACA reached similar levels of germination as LIRA with 97% and 85%,

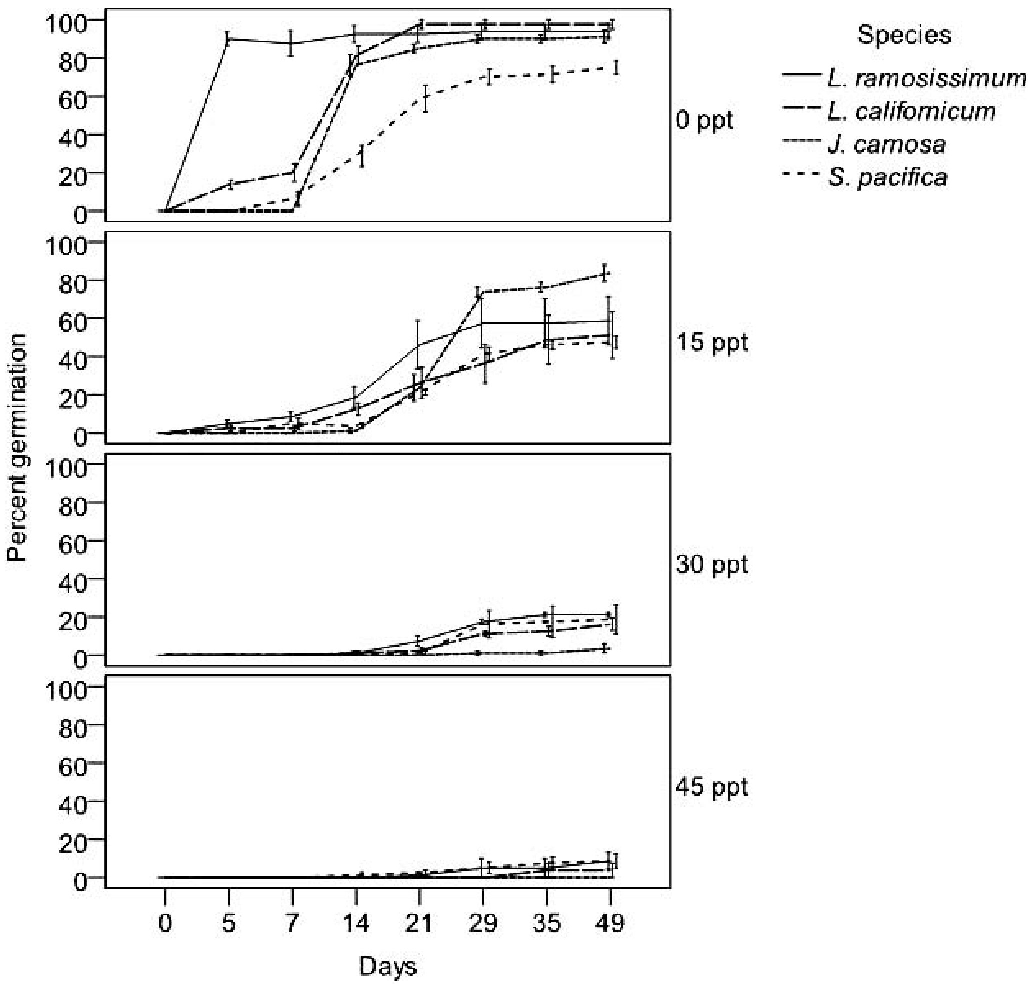

Figure 3. Percentage of germination of jaumea, marsh rosemary, Algerian sea lavender and pickleweed over time in petri dishes with 0, 15, 30, and 45 parts per thousand salinity. n = 4; error bars represent ± 1 SE.

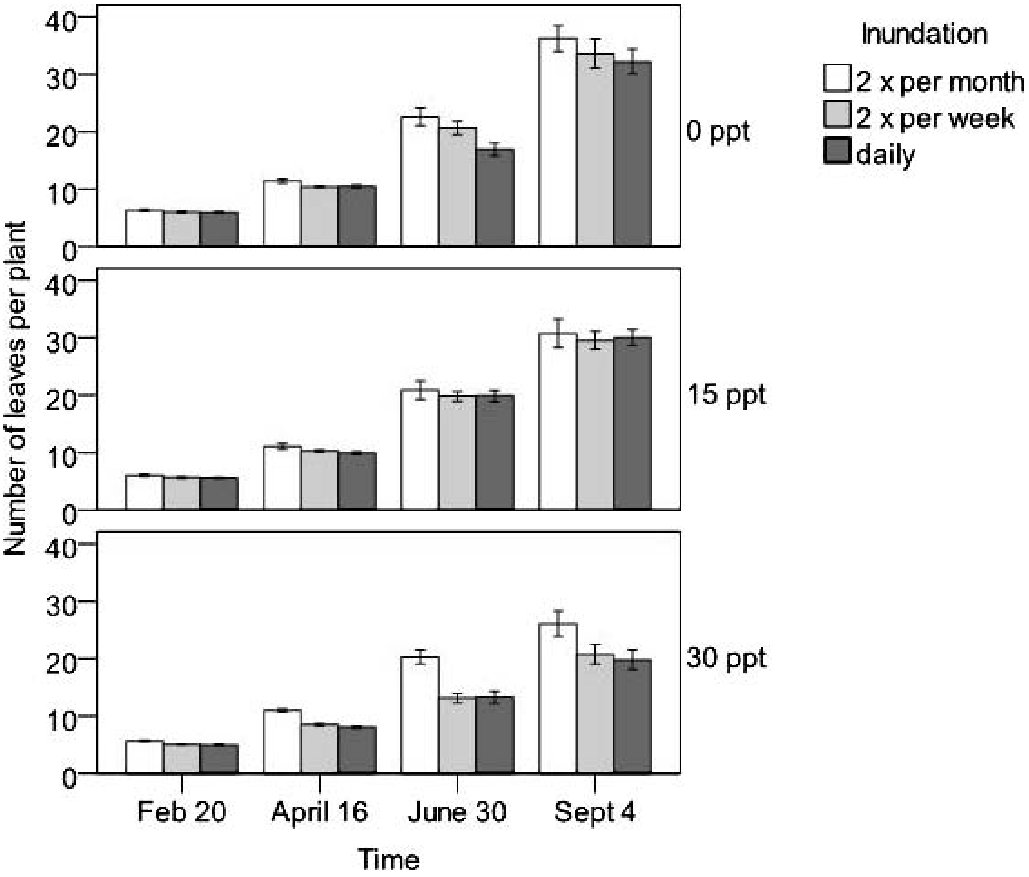

Figure 4. Effect of salinity and inundation on number of leaves per plant, averaged by pot, on Algerian sea lavender after 255 d of growth in a tidal simulator. $n = 7$; error bars represent ± 1 SE.

respectively. Germination of SAPA after 49 d of exposure to 0 ppt trended lower than all three other species at 75%.

LIRA percentage of seed germination at 15, 30, and 45 ppt salinity treatments after 49 d appeared similar to the other species. Seed germination of all species declined and germination took longer at progressively higher salinities (Figure 3).

Effect of Salinity and Inundation on Growth and Reproduction. Experimentally increasing salinity had significant negative effects on growth and reproductive characteristics, including leaf abundance, aboveground biomass, inflorescences per plant, and seeds per inflorescence (Figures 4–6; Table 1). Increased inundation also significantly reduced aboveground biomass and seed production, and tended to reduce leaf abundance and inflorescences per plant (Figures 4–6; Table 1). There was a significant interaction among treatments on root mass owing to the stronger effect of inundation at low- vs. high-salinity treatments (Figure 5; Table 1). In general, the lowest inundation frequency combined with the lowest salinity produced the most favorable conditions for growth and reproduction. Notably, for a few measures (aboveground biomass and seed production), reduced inundation (two times per month) minimized negative effects of moderate to high salinity levels.

Entering the tidal simulator with between 16 and 20 individuals per pot, a very small proportion died by the end of the experiment. There were no significant effects of salinity or inundation on mortality (Table 1), but there tended to be greater mortality at 30 ppt (0.43 individuals) than at 0 ppt (0.04 individuals), and at high inundation frequency (0.67 individuals) compared to the lowest frequency (0.14 individuals).

Discussion

LIRA populations have been found in both saline and brackish tidal marshes in the SFE (totaling 15,144 m^2; Archbald and Boyer 2014). Our findings suggest LIRA is well adapted to invade additional saline marshes, with seeds able to float at least 2 wk in saline water, germinate at high salinities on par with native plants, and produce prolific seed when grown in saline conditions. However, we also found that reducing salinity stress increases LIRA growth and seed output, suggesting LIRA spread may occur most

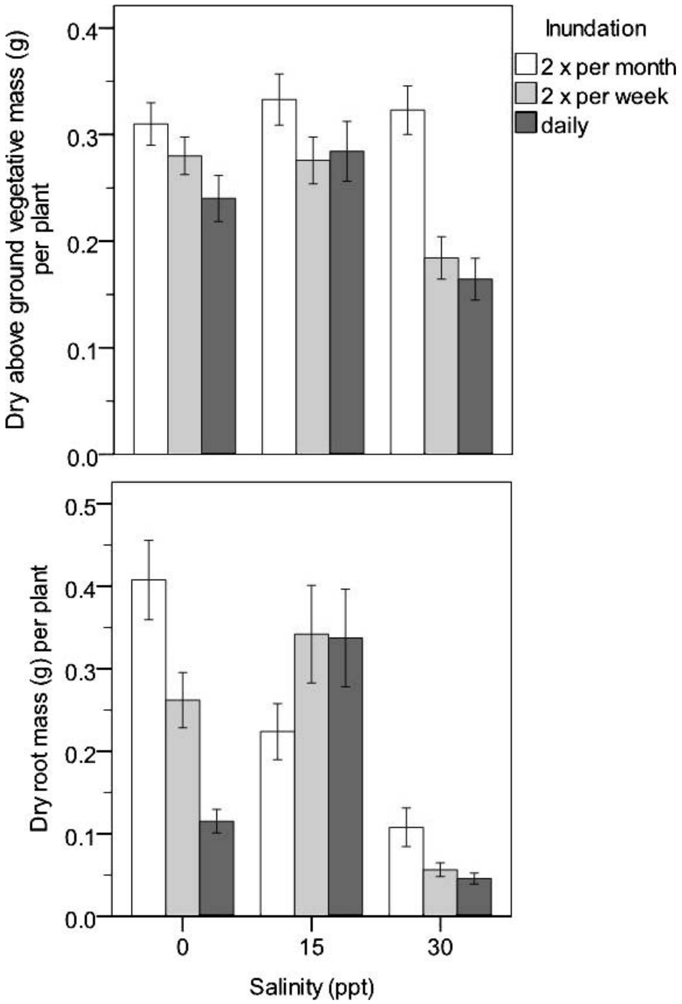

Figure 5. Effect of salinity and inundation on above- and belowground dry mass of Algerian sea lavender after 255 d of growth in a tidal simulator. $n = 7$; error bars represent ± 1 SE.

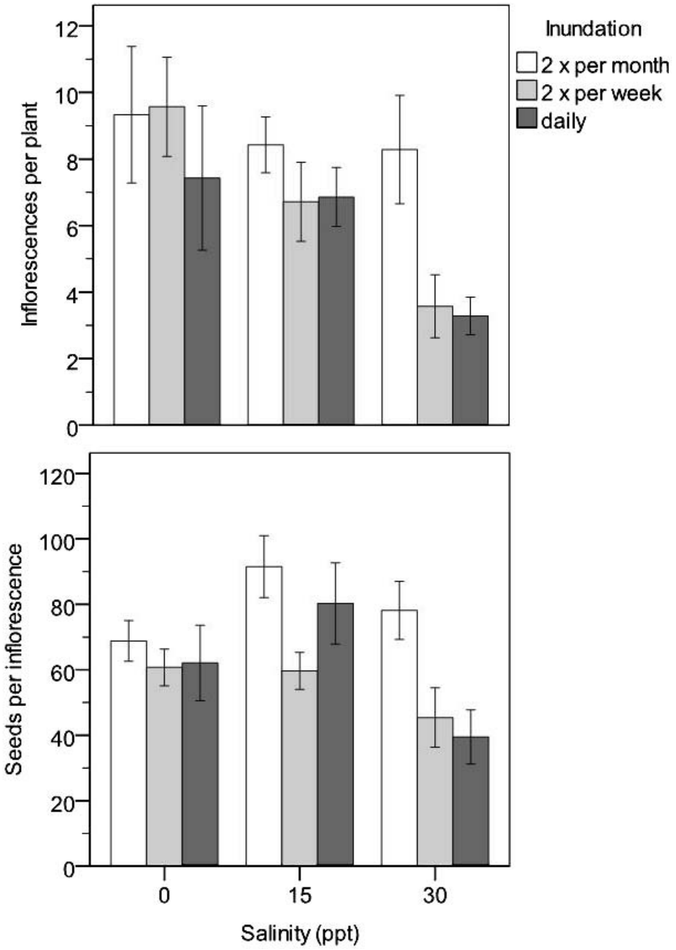

Figure 6. Inflorescence and seed production of Algerian sea lavender after 255 d of growth under crossed salinity and inundation treatments. $n = 7$; error bars represent ± 1 SE.

rapidly within brackish and fresh marshes, and in less saline locations within salt marshes.

Our finding that LIRA seeds can float regardless of water salinity and, furthermore, that seeds can float and then germinate with high viability, fits with results of similar experiments of halophyte seed dispersal in saline waters (Elsey-Quirk et al. 2007; Hubbard and Page 1997; Ungar 1991). In contrast, LIRA seed germination after just a few days of simulated dispersal in fresh water may greatly limit seedling establishment (but see Huiskes et al. 1995 for evidence that some halophyte seeds can germinate during aquatic transport and then establish). Our study indicates that LIRA can likely disperse greater distances in saline than in fresh reaches of the SFE since seeds in saline water can longer retain the capacity to germinate in an appropriate substrate.

Our measures of seed floatation can be used to roughly estimate seed dispersal distances in fresh vs. saline water. One study simulating estuarine seed dispersal using drift cards released from within the SFE and other Pacific estuaries found most cards made landfall less than 25 km (16 mi) away from the release site 1 to 6 d after release (Morgan and Sytsma 2013). This finding suggests 25 km is a reasonable upper limit of dispersal distance in fresh conditions where LIRA seeds germinate after a few days afloat. Morgan and Sytsma (2013) also found most drift cards released near the mouth of the SFE (at Crissy Field in San Francisco), traveled out of the estuary and both northward (predominantly) and southward along the coast at up to 16 km d^{-1}, suggesting that, over the 2 wk we found LIRA seeds float, dispersal by ocean waters could be up to 224 km. Understanding how currents and wind drive seed dispersal in the SFE would help us to understand where populations are most likely to spread from existing LIRA populations (Archbald and Boyer 2014). Further, understanding dispersal patterns would be aided by genetic studies that determine relatedness of existing populations.

Table 1. Results of two-way ANOVA on salinity and inundation effects on growth, mortality, and reproduction of Algerian sea lavender after 255 d of growth in a tidal simulator.

Factor	F	df	P[a]
Number of leaves per plant			
Salinity	26.308	2	**< 0.0001**
Inundation	2.849	2	0.067
Salinity × inundation	.544	4	0.704
Dry aboveground vegetative mass (g) per plant			
Salinity	9.016	2	**< 0.0005**
Inundation	15.049	2	**< 0.0001**
Salinity × inundation	2.489	4	0.054
Dry root mass (g) per plant (cube root)			
Salinity	62.236	2	**< 0.0001**
Inundation	7.707	2	**0.001**
Salinity × inundation	8.268	4	**< 0.0001**
Inflorescences per plant (natural log)			
Salinity	5.215	2	**0.008**
Inundation	3.134	2	0.052
Salinity × inundation	1.040	4	0.395
Seeds per inflorescence			
Salinity	5.000	2	**0.010**
Inundation	6.162	2	**0.004**
Salinity × inundation	1.445	4	0.232
Change in number of living plants (mortality)			
Salinity	0.647	2	0.514
Inundation	3.069	2	0.055
Salinity × inundation	1.294	4	0.284

[a] Bold indicates significance at $\alpha = 0.05$.

Table 2. Seed production of selected native and nonnative salt marsh species in the San Francisco Estuary.

Status	Species	Seed production m^{-2}
Native	*Distichlis spicata*	5,124 ± 19 (SE)[a]
	Grindelia stricta var. *angustifolia*	27, 287 ± 1,749 (SE)[a]
	Jaumea carnosa	14,164 ± 210 (SE)[a]
	Salicornia pacifica	80,755 ± 168 (SE)[a]
Nonnative	*Lepidium latifolium*	49,376–173,970[b]
	Limonium duriusculum	360–11,400[c]
	Limonium ramosissimum subsp. *provinciale*	≅ 36,400–132,600[d]

[a] Diggory and Parker (2011).

[b] Leininger and Foin (2009). Range of viable seed counts at marsh sites along a salinity gradient in the San Francisco Estuary.

[c] Hubbard and Page (1997). Range of seed counts from low to mid-high elevations across *L. duriusculum*'s vertical range at Carpinteria Marsh, Santa Barbara, CA.

[d] Estimated from range of average seeds per inflorescence, inflorescences per plant (Archbald and Boyer 2014) and plants m^{-2} (Archbald, unpublished data) from low to high elevations across vertical range of *Limonium ramosissimum* subsp. *provinciale* in a tidal salt marsh in south San Francisco Bay.

Contrary to our hypothesis that LIRA may be uniquely well adapted to germinate in high salinity conditions, such as those found in hypersaline bare patches (Bertness and Shumway 1992), our study found similar percentages of germination after 49 d, regardless of salinity, between LIRA and common native marsh plants, including the dominant plant species in California salt marshes, SAPA; a common high marsh plant, JACA; and the only native *Limonium* species in California tidal marshes, LICA. However, we also found LIRA reaches maximum germination approximately 2 wk prior to these native species when exposed to fresh water. Assuming ungerminated LIRA and native seeds were present at the same time (e.g., via dispersal or, possibly, in an existing seed bank), this could confer a competitive establishment advantage for LIRA. These findings also suggest LIRA germination may be favored over SAPA, JACA, and LICA following short-duration, low-salinity events (e.g., infrequent rainfall). Our observation, therefore, that LIRA occupies hypersaline patches in the absence of other species, may instead be due to its greater seed output (Table 2), rapid germination, or, perhaps, salinity tolerance in later stages.

Our tidal simulator study found that LIRA's growth and seed production increased when either inundation frequency or salinity were reduced. These results explain why LIRA growth and reproductive output are highest in salt marshes at the upper end of LIRA's elevation range where salinity and inundation are both relatively low (Archbald and Boyer 2014). Furthermore, they suggest that, in marshes with low salinity, LIRA growth and seed production are likely to be relatively more prolific at low elevations where the combination of salinity and inundation stress lower LIRA growth and reproductive output in saline marshes. As a result, we predict that in fresh marshes, spread will be more rapid and populations will deliver more propagules to nearby marsh habitat than in more saline marshes.

Other studies have also found that inundation and salinity reduce the growth and seed output of *Limonium* species. A transplant study of *Limonium duriusculum* (Girard) Fourr. (no common name; initially misidentified as Algerian sea lavender (*Limonium ramosissimum* (Poir.) Maire; D. Kelch; personal communication) at Carpinteria Marsh in Santa Barbara, CA, resulted in total mortality when plants were transplanted lower than their natural range, demonstrating sensitivity to more frequent inundation. Furthermore, plants grew largest in the high marsh where inundation stress was lowest, but flowering and percent cover was highest within the midmarsh where salinity stress was relatively low during summer months (Hubbard and Page 1997). In another study, common sea lavender (*Limonium vulgare* Mill.) was grown under crossed inundation and salinity treatments. Both seedlings and mature plants were most sensitive when exposed to inundation and saline water simultaneously (Boorman 1971). These experiments support a view of *Limonium* as a genus that is inhibited by frequent inundation at high salinity and less so as salinity decreases.

Other invasive SFE tidal marsh plants are more sensitive to inundation at higher salinities. For example, the native Pacific cordgrass (*Spartina foliosa* Trin.) grows lower in elevation as salinities decrease (Atwater and Hegel 1976), as does hybrid smooth cordgrass (Collins 2002). Invasive perennial pepperweed seed production varies with salinity and inundation; a 29% seed reduction was found along a salinity gradient from fresh to saline whereas there was an 86% seed reduction from the driest to wettest sites (Leininger and Foin 2009). In light of these trends, in addition to increased reproductive output in fresher conditions, it is possible that LIRA's vertical range may be larger, or shift lower, at low-salinity marshes.

Increased propagule pressure by LIRA is likely to affect the composition of restored marshes. A study in the SFE found seed production to be a key factor predicting which species are likely to establish after tidal marsh restoration (Diggory and Parker 2011) and LIRA, under optimal conditions, produces from approximately 50% to over an order of magnitude more seeds per square meter than common native high-marsh species (Table 2). LIRA's ability to produce prodigious, viable seed and disperse long distances is likely to lead to additional LIRA invasions in high marsh and salt marsh–terrestrial ecotone habitats (i.e., the transition zone) of restored marshes. Transition zone habitats have been disproportionately lost to development (Collins and Grossinger 2004) yet provide critical high tide refugia habitat for native species including the endangered (federal and California state listed) salt marsh harvest mouse (*Reithrodontomys raviventrus*) and California clapper rail (*Rallus longirostris obsoletus*) and provide habitat for rare plants including Point Reyes bird's beak (*Chloropyron maritimum* [Nutt. Ex Benth.] A. Heller subsp. *palustre* [Behr] Tank & J.M. Egger) and California seablight (*Suaeda californica* S. Watson). Therefore, control of nonnative *Limonium* in the SFE may be important to maintaining native species diversity in SFE salt marshes.

Propagule pressure is increasingly recognized as a driver of species invasions and has been found to be more important than both competition and abiotic factors in determining the success of new invaders (Holle and Simberloff 2005). However, a dominant paradigm in salt marsh ecology is that species that are successful in high-salinity environments (e.g., LIRA), are often outcompeted in low-salinity habitats (Crain et al. 2004; Pennings and Callaway 1992). In the SFE, the invader *Spartina alterniflora* × *foliosa*, for example, is dominant under saline conditions but outcompeted in low-salinity conditions by *Schoenoplectus* (formerly *Scirpus*) species. Similarly, SAPA may be outcompeted by the less common saltgrass (*Distichlis spicata* [L.] Greene) under low-salinity conditions (Ryan and Boyer 2012). The competitive ability of LIRA relative to native plants under low-salinity conditions is unknown. However, the sheer acreage of marsh habitat being restored (over 5,600 ha [14,000 ac] of wetlands in the San Francisco Bay Area as of 2011 and over 10,900 ha slated for restoration in the future; SFEI 2011) suggests periods of low competition associated with habitat creation will increase the importance of physical factors on propagule pressure and broader invasion dynamics.

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