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Spread Dynamics of Perennial Pepperweed (*Lepidium latifolium*) in Two Seasonal Wetland Areas

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Perennial pepperweed is an invasive plant that is expanding rapidly in several plant communities in the western United States. In California, perennial pepperweed has aggressively invaded seasonal wetlands, resulting in degradation of habitat quality. We evaluated the rate and dynamics of population spread, assessed the effect of disturbance on spread, and determined the biotic and abiotic factors influencing the likelihood of invasion. The study was conducted at eight sites within two wetland regions of California. Results indicate that in undisturbed sites, spread was almost exclusively through vegetative expansion, and the average rate of spread was 0.85 m yr^{-1} from the leading edge. Spread in sites that were disked was more than three times greater than in undisturbed sites. While smaller infestations increased at a faster rate compared with larger populations, larger infestations accumulated more newly infested areas than smaller infestations from year to year. Stem density was consistently higher in the center of the infestations, with about 2.4 times more stems per square meter compared with the leading edge at the perimeter of the population. The invasion by perennial pepperweed was positively correlated with increased water availability but was negatively correlated with the cover of perennial and annual species. Thus, high cover of resident vegetation can have a suppressive effect on the rate of invasion, even in wetland ecosystems. On the basis of these results, we recommend that resident plant cover not be disturbed, especially in wet areas adjacent to areas currently infested with perennial pepperweed. For infested areas, management efforts should be prioritized to focus on controlling satellite populations as well as the leading edge of larger infestations first. This strategy could reduce the need for costly active restoration efforts by maximizing the probability of successful re-establishment of resident vegetation from the adjacent seedbank.

Nomenclature: Perennial pepperweed, *Lepidium latifolium* L. LEPLA.

Key words: Wetlands, riparian, spread dynamics, invasion, spatial spread, population growth.

Perennial pepperweed (*Lepidium latifolium* L.) is an herbaceous perennial native to temperate portions of Europe, central and southwestern Asia, and the Mediterranean region (Lyeik 1989). It was accidentally introduced into the United States in the 1930s as a contaminant of sugarbeet seed (Robbins et al. 1951). In North America, perennial pepperweed has invaded higher elevation rangelands, riparian habitats, mountain meadows, alkaline sinks, coastal marshes, and seasonal wetlands, particularly in the western United States (Leininger and Foin 2009; Reynolds and Boyer 2010; Weber 1989; Young et al. 1995a, 1995b, 1997). Within these areas, it is an aggressive colonizer, often forming dense populations that displace many native species (DiTomaso and Healy 2007; Renz 2005).

Perennial pepperweed can allocate 60% of its biomass to belowground tissues (Renz et al. 1997). Although 85% of root biomass is present in the top 60 cm of soil, roots have been observed many meters deep along the capillary fringe of water tables (Gardner 2002; USDA 1997). This growth pattern allows plants to avoid water stress during dry periods and likely contributes to their competitiveness in seasonally dry habitats. Stems of perennial pepperweed typically emerge from either semiwoody crowns or perennial roots in early spring, and stem densities can reach 170 stems m^{-2} [17 stems ft^{-2}]) by summer in older, well-established populations (Renz and DiTomaso 2001).

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Management Implications

Perennial pepperweed is one of the most important invasive plants of wetland areas in the western United States. In several undisturbed plots at two locations, we showed that its spread was almost exclusively through vegetative expansion along the perimeter of the infestation at an average of 0.85 m yr^{-1}. By comparison, the spread rate was three times greater in a site that was disked, which can explain why disking is not recommended for perennial pepperweed control. Stem densities were nearly 2.5 times higher in the interior of the infestations compared with the leading edge. Because of the reduced stem density, the perimeter of the patch is considered to be easier to control compared with the denser patch centers. Small infestations expanded at a faster rate compared with larger patches, but larger patches added more newly infested areas. We determined that the expansion of perennial pepperweed was more closely correlated with increased water availability but was negatively correlated with resident plant cover. Thus, we conclude that the most appropriate strategy for managing perennial pepperweed is to minimize disturbance of plant cover and control both the rapidly expanding satellite infestations and the perimeter of larger infestations. Concentrating management efforts on the densely stemmed, more difficult to control, and highly thatched regions at the center of the infestation might not be cost effective. These areas also have less resident vegetation. Furthermore, the ability of desirable resident vegetation to re-establish from the adjacent seedbank at the perimeter of the infestation could also prevent the need for expensive active restoration programs when focusing on the center of large infestations.

Fully expanded inflorescences can form dense canopies that block light to the understory vegetation and create near monotypic populations (Renz 2005). Reproduction occurs both by seeds and by creeping perennial roots. Although plants are known to produce more than 16 billion seeds ha^{-1} (6.5 billion seeds ac^{-1}) annually, few seedlings are observed in the field, particularly in well-established populations (Young et al. 1997).

The increased expansion of perennial pepperweed is of concern to federal and state resource managers in California and other western states (Renz 2005). Plant communities displaced by perennial pepperweed are often dominated by native species that provide important wildlife habitat. For example, dense perennial pepperweed stands threaten pickleweed [*Sarcocornia pacifica* (Standl.) A. J. Scott] habitat, which is critical to the survival of the endangered salt marsh harvest mouse (*Reithrodontomys raviventris* Dixon) (Trumbo 1994). Seasonal wetlands in many state Wildlife Areas and National Wildlife Refuges provide productive nesting and feeding habitat for waterfowl and other wildlife. Such sensitive wetland areas are particularly vulnerable to perennial pepperweed invasion (Chen et al. 2002; Laubhan and Shaffer 2006).

In an alkali flat, Blank and Young (1997) found perennial pepperweed expansion to occur clonally along the edge of an invasion. However, little is known of the dynamics of spread in other habitats, particularly wetland communities, or how disturbance by nonchemical management techniques can affect populations of perennial pepperweed. The objectives of this study were to determine the rate of spread of perennial pepperweed infestations in two seasonal wetland regions in California, to assess the effect of management techniques on spread, to evaluate the biotic and abiotic factors that influence the likelihood of further spread in these seasonal wetlands, and to use this information to develop more effective recommendations for the revegetation of perennial pepperweed–infested wetlands.

Materials and Methods

Site Description. The study sites were located at the Colusa National Wildlife Refuge in the Central Valley bioregion (39°10.130′N, 122°02.535′W) and the Grizzly Island Wildlife Area (38°08.327′N, 121°57.881′W) in the San Francisco Bay Area bioregion. The elevation at both sites was below 15 m (50 ft). Average maximum and minimum temperature patterns are similar at the two sites, however the summers were slightly cooler and the winters slightly warmer at Grizzly Island (Table 1). Accumulated degree days (accumulated degrees C of maximum daily temperature above 15 C [59 F]) were 4,667 at Colusa compared with 3,376 at Grizzly Island during the course of the experiment.

Site Selection. Eight sites total were selected at Colusa (five sites) and Grizzly Island (three sites). Selected sites were isolated from other populations of perennial pepperweed by > 100 m and had similar vegetation and topography. A 50 by 50-m plot was established in the center of each site. Each plot contained one to three isolated patches (15 total), in circular shapes of varying sizes and densities (< 2,500 m^2). Patches were separated from each other by > 5 m. Perennial pepperweed patch expansion rates and patch dynamics were measured over a 3-yr period in each plot. The plots included a mix of perennial pepperweed and other resident plant species, both native and nonnative (Table 2).

Management at Sites. All sites were managed using standard practices for waterfowl and other ground-nesting birds. At Colusa, land managers conducted a prescribed burn on two sites (nos. 1 and 2) in December 1999, and at Grizzly Island, managers disked one site (no. 3) in the fall of 1999. No active management occurred in any of the other sites throughout the course of the experiment.

Density, Area, and Perimeter of Infestations. Each 50- by 50-m plot was established in 1998–1999 and divided into 2,500, 1-m^2 subplots using a squared grid system (Figure 1). This temporary grid system allowed measurements of

Table 1. Characteristics of study sites at Colusa National Wildlife Refuge and Grizzly Island Wildlife Area.[a]

Site parameters	Colusa	Grizzly Island
Soil type	Willow silty clay	Valdez silty clay loam
Perennial pepperweed growing season	February–October	Year round
Accumulated degree days (> 15 C) from 1999 to 2001	4,667	3,376
30-yr average annual precipitation (mm)	435	337
1999 annual precipitation (mm)	278	253
2000 annual precipitation (mm)	406	337
2001 annual precipitation (mm)	317	275

[a] Climatological data were summarized from the University of California IPM Online website for weather stations (http://www.ipm.ucdavis.edu/WEATHER/wxretrieve.html).

perennial pepperweed stem densities within each subplot. Perennial pepperweed stem counts were recorded between June and August of every year (1999, 2000, and 2001), when the majority of bolted stems were at the flower bud to flowering stages. The initial area and perimeter of each pepperweed patch was determined and populations mapped with data obtained from the grid evaluations. Comparisons between years were used to calculate the rate and area of

Table 2. Plant species composition, species richness, and dominant species measured in 2001 in each plot at Colusa National Wildlife Refuge and Grizzly Island Wildlife Area. Measurements were taken of species cover only for uninfested areas surrounding each nascent focus (≤ 3 m from infested patch) within each plot. Standard deviations are indicated in parentheses.

			Cover						
Site	Plot no.	Disturbance	Native annual dicots	Nonnative annual grasses	Native perennial monocots	Native perennial dicots	Bare ground	Species richness	Dominant plants[a]
			%					avg. no. plants m^{-2}	
Colusa[b]	1	Burned	30 (23)	46 (22)	0 (0)	16 (9)	8	4 (1)	*Lolium multiflorum* (I), *Hordeum marinum* (I), *Grindelia camporum* Greene (N)
	2	Burned	3 (4)	77 (10)	0 (0)	13 (8)	7	4 (1)	*Lolium multiflorum* (I), *Hordeum marinum* (I)
	3	Undisturbed	8 (12)	72 (23)	10 (14)	4 (5)	6	3 (2)	*Lolium multiflorum* (I)
	4	Undisturbed	10 (9)	82 (11)	0 (0)	0 (2)	8	3 (1)	*Lolium multiflorum* (I), *Malvella leprosa* (Ortega) Krapov. (N)
	5	Undisturbed	21 (14)	65 (16)	2 (7)	1 (3)	11	4 (1)	*Lolium multiflorum* (I), *Hordeum marinum* (I)
Grizzly Island[c]	1	Undisturbed	7 (13)	56 (24)	4 (11)	25 (28)	8	4 (1)	*Hordeum marinum* (I), *Sarcocornia pacifica* (N)
	2	Undisturbed	7 (7)	88 (12)	0 (0)	0 (1)	5	2 (1)	*Lolium multiflorum* (I)
	3	Disked	8 (8)	79 (15)	0 (2)	1 (4)	12	3 (1)	*Lolium multiflorum* (I), *Hordeum marinum* (I)

[a] Dominant plants averaged 10% or more cover within the site. I, nonnative introduced species; N, native species.

[b] Sample size (*n*) to calculate plant cover for each plot was 364, 380, 351, 964, and 381 for Colusa nos. 1, 2, 3, 4, and 5, respectively.

[c] Sample size (*n*) to calculate plant cover for each plot was 208, 284, and 523 for Grizzly Island nos. 1, 2, and 3, respectively.

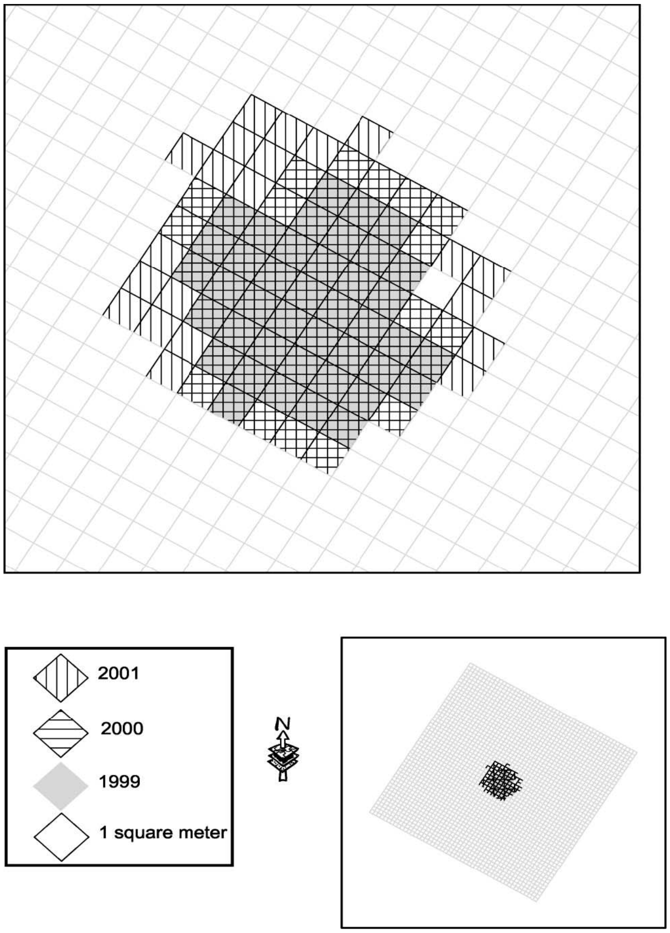

Figure 1. Example of grid with 1-m^2 quadrats used to evaluate rate of population spread and stem density. A different pattern of grid boxes was used to monitor change in infestation size from 1999 to 2001.

patch expansion from 1999 to 2000, 2000 to 2001, and the 2-yr period, 1999–2001.

To evaluate the changes in density within an infestation, subplots were classified as along the edge or in the center of the patch. Center patch subplots were surrounded on each side by subplots also containing perennial pepperweed, whereas edge subplots had at least one adjacent subplot that contained no perennial pepperweed. Plant density was averaged for each class (edge or center), and comparisons were made within years and sites and after combining all years and all sites using *t* tests.

Species Composition and Environmental Variables. To determine the resident vegetation surrounding perennial pepperweed patches, as well as the vegetation within the infested patches, relative percent bare ground and cover of individual plant species was visually estimated annually within a subset of the subplots at each site between June and July at Colusa and between July and August at Grizzly Island in 1999, 2000, and 2001. Visual cover estimates were recorded within each invaded subplot, and all uninvaded subplots within 3 m of the invaded patch. Cover was estimated at 1% intervals between 0 and 10% and at 5% intervals between 10 to 100%. The cover values for uninfested subplots are presented in Table 2 as an estimate of the resident vegetation adjacent to infested patches. Only data from 2001 are presented. Cover values in uninfested subplots were compared with species cover in infested subplots for all years in the canonical correspondence analysis (CCA) and discriminant analysis (DA) evaluations.

Soil samples were randomly taken in one-third of the subplots evaluated for cover. Soil cores were 3 cm in diameter and 20–30 cm deep. The soil core was removed and placed in a sealed bag, weighed, dried for 48 hr in an oven at $>$ 50 C, and reweighed to determine soil moisture. A soil moisture, temperature, and salinity meter (Aquaterr ECC-300 Digital Soil Moisture, Temperature, and Salinity Meter, Aquaterr Instruments & Automation LLC, 1685 Babcock Street, Costa Mesa, CA 92627) was inserted into the hole created by the probe and depressed 30–40 cm to measure electrical conductivity.

CCA and DA. CCA using CANOCO software and DA using the SAS DISCRIM procedure were performed to assess biotic and abiotic factors potentially influencing the invasion of a particular subplot (Der and Everitt 2002; ter Braak and Šmilauer 2002). Both analyses used data collected from the 84 subplots for the 2000 and 2001 assessment dates. The segment length ($>$ 4 SD) from a detrended correspondence analysis using CANOCO software indicated that a unimodal approach such as CCA was warranted (Lepš and Šmilauer 2003). All data were log(y + 1)–transformed to remedy the highly skewed species cover values. The quantitative environmental variables measured on subplots were soil moisture levels, soil temperature, species richness, total perennial grass cover, total annual dicot cover, percent cover of nonnatives, percent cover of natives, percent bare ground, and soil electrical conductivity (Table 3). A Monte Carlo permutation test was run to construct a model containing only the environmental variables that explained a significant portion ($P < 0.05$) of species variation. A CCA biplot depicting species scores and environmental variables was assessed for whether plant cover classes were related to the density of perennial pepperweed and the environmental variables. A stepwise DA was used to develop the best discriminant function using the STEPDISC procedure in SAS, which distinguishes between the subplots invaded by perennial pepperweed from those not invaded (i.e., perennial pepperweed presence/absence) (Der and Everitt 2002). Significance level to keep or eliminate variables at each step was set to $P < 0.15$ (SAS Version 9.1, SAS Institute Inc., 100 SAS Campus Drive, Cary, NC 27513). The CCA was

Table 3. Variables included in the canonical correspondence (CCA) and discriminant analysis (DA).

Variable	Description	DA	CCA[a]
anngrass	Annual grass cover	X	X
anndicot	Perennial broadleaf cover	X	X
pergrass	Perennial grass cover	X	X
perdicot	Perennial broadleaf cover	X	X
bare	Bare-ground cover	X	X
natives	Native species cover	X	X
nonnativ	Nonnative species cover	X	X
speciesn	No. of plant species	X	X
PPWdensi	Perennial pepperweed density		X
PPWpres	Perennial pepperweed presence	X	
year	Year data was taken	X	X
burned	Burn status	X	X
watersoi	Percent water : soil weight	X	X
EC	Soil electrical conductivity	X	X
ASTSU	*Aster subulatus* Michx. var. *ligulatus* Shinners cover		X
ATRIP	*Atriplex* spp. cover		X
CRETR	*Cressa truxullensis* Kunth cover		X
DISSP	*Distichlis spicata* (L.) Greene cover		X
FRASA	*Frankenia salina* (Molina) I. M. Johnst. cover		X
GRICA	*Grindelia camporum* Greene cover		X
HORMA	*Hordeum marinum* cover		X
LOLMU	*Lolium multiflorum* cover		X
LOTCO	*Lotus corniculatus* L. cover		X
MALLE	*Malvella leprosa* (Ortega) Krapov. cover		X
PLAST	*Plagiobothrys stipitatus* (Greene) I. M. Johnst. cover		X
RUMCR	*Rumex crispus* L. cover		X
SALSU	*Sarcocornia pacifica* cover		X

[a] Although the CCA included the cover of all individual species in each subplot, the species presented in Figure 3 and this table only include the 13 species with the highest average cover in subplots evaluated ($n = 84$).

exploratory for all species associations and their abundance along the environmental gradients in a single analysis. By comparison, the DA was intended to quantify the effects attributable to the functional groupings of species (e.g., annual dicots, annual grasses, etc.) and environmental variables that made a subplot more or less likely to become invaded by perennial pepperweed. This form of the discriminant function provides land managers a generalized predictive tool whereby they would input the percent cover of the plant functional groups growing on their lands and estimate the risk of invasibility by perennial pepperweed. The DA generated a discriminant function from which a z score, $z(i)$, was computed for each subplot i by:

$$z(i) = -z_{\text{critcal}} + \sum_{j=1}^{n} a_j x_j \qquad [1]$$

where a_j is the discriminant coefficient for variable j, and x_j is the observed value for variable j. The critical z value, z_{critical} is computed as the mean of the average z score for all subplots where perennial pepperweed was absent and the average z score for all subplots where perennial pepperweed was present. The exact F tests used to assess the overall model of variables selected in the stepwise DA were Wilks' Lambda, Pillai's Trace, Hotelling–Lawley Trace, and Roy's Greatest Root with a total sample size of $n = 84$. The main assumption with these multivariate analyses was that subplots not invaded by perennial pepperweed had adequate exposure to infestation but the biotic and abiotic conditions were not suitable for a successful invasion.

Results and Discussion

Vegetative Composition of Uninfested Sites. Although unique plant communities occurred at each site, the adjacent noninfested areas at both the Colusa and Grizzly Island study areas were dominated by nonnative annual grasses (Table 2), particularly Italian ryegrass [*Lolium multiflorum* Lam.; = *L. perenne* L. ssp. *multiflorum* (Lam.) Husnot] and Mediterranean barley [*Hordeum marinum* Huds. ssp. *gussonianum* (Parl.) Thellung]. Species richness ranged from 2 to 4 species m^{-2} at both sites, but

Table 4. Total area and percent increases in the area infested by perennial pepperweed at Colusa National Wildlife Refuge and Grizzly Island Wildlife Area from 1999 to 2001. Sample size (*n*) was annually 2,500 for each plot.

Plot no.	Disturbance	Area infested (m^2) 1999	2000	2001	Total area increase from 1999–2001	Increase between years 1999–2000	2000–2001	1999–2001	Average expansion per year from leading edge
		m^2				%			m
Colusa									
1	Burned	208	195	223	15	−6	14	7	0.15
2	Burned	38	59	87	49	55	47	129	0.88
3	Undisturbed	32	56	73	41	75	30	128	0.80
4	Undisturbed	247	293	356	109	19	22	44	0.90
5	Undisturbed	38	52	87	49	37	67	129	0.88
Grizzly Island									
1	Undisturbed	41	57	78	37	39	37	90	0.70
2	Undisturbed	52	86	113	61	65	31	117	0.98
3	Disked	62	125	331	269	102	165	434	2.90

few native plants dominated (> 10% cover) these sites. Overall, the percent cover of native plants averaged 21% among all plots and sites but varied widely within and between the two sites, ranging from a low of 7% in the undisturbed plot 2 at Grizzly Island to a high of 46% in the burned treatment of plot 1 at Colusa.

Expansion of Infestations. Perennial pepperweed patches expanded by 44 to 129% of their initial areas from 1999 to 2001 in the undisturbed plots at Colusa (nos. 3, 4, and 5) and Grizzly Island (nos. 1 and 2) (Table 4). Although rates of patch expansion varied within each plot, all plots increased in total infested area over the 2 yr of growth. During the 3 yr of evaluation, patch spread was entirely through vegetative expansion from existing populations, and no new patches were discovered that persisted. Only six perennial pepperweed seedlings were observed between 1999 and 2001, with none surviving to maturity. All infestations consisted of discrete circular patches of various sizes. Calculating the total difference in area infested between 1999 and 2001, the average distance of expansion from the leading edge of the patch was very similar among the undisturbed plots, ranging from 0.70 to 0.98 m yr^{-1} (Table 4). Blank and Young (1997) found a similar spread distance of approximately 1 m yr^{-1}, with values never exceeding 3 m yr^{-1}. In another study, Andrew and Ustin (2010) found perennial pepperweed spread to average 3 to 6 m yr^{-1} but found some plants invaded locations > 100 m from known infestations. They attributed the higher spread rate to the high amount of disturbance that occurs within this habitat.

The two Colusa plots that were burned in the winter of 1999 had varying results. After one year (1999 to 2000), burning reduced the infested area at Colusa no. 1 by 6%, but increased the infested area at Colusa no. 2 by 55% (Table 4). The difference in spread after a 2-yr period (1999 to 2001) was even more pronounced, with Colusa nos. 1 and 2 increasing the perennial pepperweed–infested area by 7 and 129%, respectively. In Colusa no. 2, the average annual expansion distance from the leading edge (0.88 m) was similar to undisturbed plots, but in Colusa no. 1, it was far less, at only 0.15 m yr^{-1}. Although we only had two burned plots, Wilson et al. (2008) also reported burning to be ineffective for control of perennial pepperweed. Compared with an untreated area, they showed that prescribed burning had no effect on the cover of perennial pepperweed. The difference between these two sites may be dependent on other factors, such as fire intensity, which was greater at Colusa no. 1 compared with Colusa no. 2 (D. Gilmer, personal observation). Higher burn intensity may have caused increased damage to perennial pepperweed root crowns near the surface, which could have resulted in higher root crown mortality and a slower rate of spread from the leading edge.

Although unreplicated, the disking treatment at Grizzly Island (no. 3) in fall 1999 led to the greatest increase in perennial pepperweed spread among the three management strategies (undisturbed, burning, disking), resulting in a 434% increase in the area of infestation over the 2-yr period (Table 4). Although no other patch at either site expanded from the leading edge by more than 1 m a year, patches within the disked plot averaged 2.9 m of expansion per year. This rapid spread is hypothesized to be due to the effect of disking on perennial root and crown fragmentation and transport of these segments by the equipment to a distance greater than would be possible by natural

Table 5. Comparison of the density between the center and edge of perennial pepperweed infestations in the Grizzly Island Wildlife Area and the Colusa National Wildlife Refuge. Number in parentheses represents number of replicates within each classification area or combined area or year. Bold *t* test values represent significant difference between stem densities in center and edge plants at $P \leq 0.05$, and NS indicates no significant difference. No subplots were categorized as center plots at Colusa no. 2 in 1999. For total of years, plots within Grizzly Island and Colusa, and both sites combined, each quadrat measurement was treated as a separate replicate.

	1999			2000			2001			All years combined		
Plot	Center	*t* test	Edge	Center	*t* test	Edge	Center	*t* test	Edge	Center	*t* test	Edge
	stems/m^{-2}		——— m^{-2} ———			——— m^{-2} ———			——— m^{-2} ———			stems/m^{-2}
Grizzly Island												
1	38.3 (14)	**0.0004**	10.6 (27)	31.3 (25)	**0.0002**	6.3 (32)	26.2 (37)	**0.0032**	11.7 (41)	28.6 (76)	**< 0.0001**	9.7 (100)
2	4.2 (6)	NS	4.9 (46)	13.4 (23)	**0.0008**	4.9 (63)	17.8 (32)	**0.0001**	7.7 (81)	14.8 (61)	**< 0.0001**	6.1 (190)
3	5.0 (1)	—	3.6 (61)	21.5 (11)	**0.0002**	3.8 (114)	14.8 (68)	**< 0.0001**	5.2 (263)	15.6 (80)	**< 0.0001**	4.6 (438)
Total	28.1 (21	**0.0002**	6.4 (134)	22.5 (59)	**< 0.0001**	4.5 (209)	18.6 (137)	**< 0.0001**	6.4 (385)	20.5 (217)	**< 0.0001**	5.7 (728)
Colusa												
1	12.3 (41)	NS	11.8 (125)	20.0 (89)	**< 0.0001**	9.3 (106)	13.6 (95)	**< 0.0001**	6.8 (128)	15.9 (225)	**< 0.0001**	9.3 (359)
2	—	—	5.9 (38)	25.6 (5)	**0.0503**	4.5 (54)	16.3 (15)	**0.0103**	6.3 (72)	18.6 (20)	**0.0467**	5.6 (164)
3	23.0 (3)	NS	6.0 (29)	24.8 (10)	**0.0099**	6.8 (46)	22.0 (20)	**0.0001**	6.6 (53)	22.9 (33)	**< 0.0001**	6.5 (128)
4	34.8 (65)	**< 0.0001**	12.3 (182)	31.5 (73)	**< 0.0001**	15.0 (219)	34.3 (108)	**< 0.0001**	18.6 (248)	33.6 (246)	**< 0.0001**	15.6 (649)
5	14.1 (7)	0.0600	4.6 (31)	21.4 (9)	**0.0020**	6.9 (43)	21.1 (23)	**< 0.0001**	5.5 (64)	19.9 (39)	**< 0.0001**	5.7 (138)
Total	25.3 (116)	**< 0.0001**	10.5 (405)	25.0 (186)	**< 0.0001**	17.9 (468)	23.6 (261)	**< 0.0001**	11.7 (565)	24.4 (563)	**< 0.0001**	11.1 (1,438)
Total for both sites	23.0 (137)	**< 0.0001**	9.2 (539)	24.4 (245)	**< 0.0001**	9.0 (677)	21.6 (398)	**< 0.0001**	9.6 (950)	22.7 (780)	**< 0.0001**	9.3 (2,166)

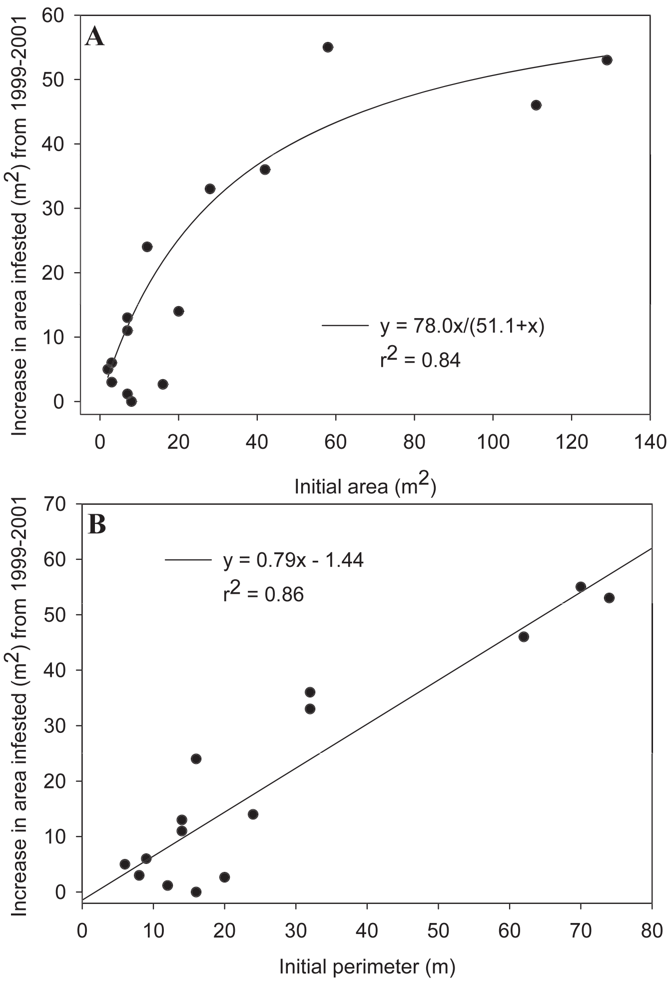

Figure 2. Increase in spread of 15 individual perennial pepperweed patches at Colusa and Grizzly Island from 1999 to 2001. Expansion is represented as (A) increase in area relative to initial area, and (B) increase in area relative to initial perimeter. The rectangular hyperbola (A) and linear regression (B) describe the predicted solid lines.

expansion. As in the case with burning, Wilson et al. (2008) also reported disking to be ineffective for perennial pepperweed control when used as a sole management strategy. Although they did not monitor the spread of perennial pepperweed, they reported no reduction in cover between the untreated and disked areas.

Stem Density. Perennial pepperweed stem densities along the leading edge of the patches were nearly always significantly less than stem densities at the center of the patch at all sites over all 3 yr (Table 5). When data were combined for years, plots within each site, and both sites, the density of perennial pepperweed stems in the center of the patch were always significantly higher, ranging from 1.4 to 5.0 times more stems compared with subplots at the edge of the patch. For all data combined, the density in the patch centers was 2.4 times greater, with 22.7 stems m^{-2} compared with 9.3 stems m^{-2} at the edge of the patch. This has important consequences in developing management strategies because stem density can greatly influence the effectiveness of perennial pepperweed control (Eiswerth et al. 2001; Renz and DiTomaso 2001, 2004, 2006).

Perennial pepperweed is most effectively controlled when herbicide applications are made to plants in the flower-bud to early flowering stages (Young et al. 1998). However, few herbicide options can effectively control perennial pepperweed in wetland areas. Although glyphosate formulations can be used in aquatic environments, Renz and DiTomaso (2006) demonstrated that infestation by perennial pepperweed at a high stem density (170 stems m^{-2}) could not be controlled with glyphosate. However, at a far lower stem density (15 stems m^{-2}), glyphosate gave over 90% control of perennial pepperweed. Reduced glyphosate efficacy at high stem density was attributed to less spray deposition at the base of the plant, which was shown to decrease glyphosate translocation to the belowground reproductive structures (Renz and DiTomaso 2004). In contrast, lower stem densities had greater spray deposition on the lower leaves and higher glyphosate translocation to the belowground structures. Thus, edge populations would theoretically be easier to control with foliar or wick-applied herbicides, such as glyphosate, compared with higher stem density infestations in the center of the patches. Imazapyr is also labeled for use in wetland areas, and limited research has shown it to be effective at controlling perennial pepperweed (Boyer and Burdick 2010). However, the residual activity of imazapyr has prevented adoption by land managers because native plants did not increase in cover after perennial pepperweed treatment (Boyer and Burdick 2010).

Relationship between Size and Spread. As previously discussed, the total rate of patch expansion from 1999 to 2001 ranged between 44 and 129% in the undisturbed plots at the two sites (Table 4). This wide range in expansion rate could be explained by differences in the initial area or perimeter of patches. To examine this, we compared the expansion rate of 15 individual undisturbed patches of varying sizes among the different plots and sites.

A rectangular hyperbolic relationship existed between initial infested area and the new area of patch expansion (Figure 2A). Small patches expanded at a greater rate compared with larger initial patches. This observation is consistent with other research on spread of perennial pepperweed (Andrew and Ustin 2010). Consequently, high priority should be given to controlling new satellite infestations. The reduction in the expansion rate of patches with larger areas is due to the clonal method of spread, which limits expansion to the perimeter of the patch. Additionally, larger patches reproduce new stems within

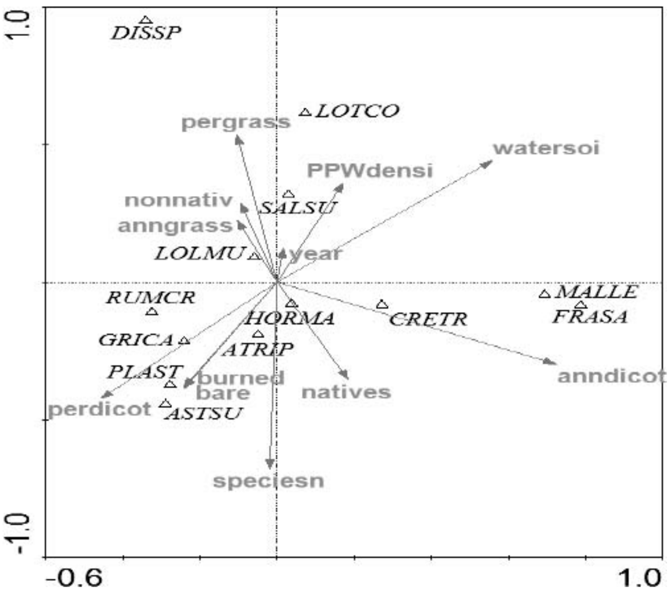

Figure 3. Canonical correspondence analysis biplot depicting the correspondence among species (hollow triangles) and quantitative environmental variables (arrows) for all years from 1999 to 2001. The angle between quantitative environmental arrows is indicative of positive ($< 90°$), negative ($> 90°$), or no ($= 90°$) correlation. The arrows point in the direction of maximum change of that variable, and their length is proportional to their correlation with the ordination axis and thus their relation to pattern of community variation. Perpendicular projection of species score onto an environmental arrow (or its extensions) corresponds to the ranking of the weighted averages (and thus optimal response) of the species with respect to that variable. Distance between species scores approximates the chi-square distance between the species distributions, indicative of association.

the interior of the population, which increases their stem density in the center. Despite the increased rate of expansion in the smaller patches, a positive linear relationship occurred between the initial perimeter of the patch and the total area of increased spread (Figure 2B). Thus, the increase in total area infested is directly related to the initial perimeter length, and larger patches increased the total amount of infested area more than smaller patches. A similar pattern of spread has been observed in crown vetch (*Coronilla varia* L.) (Losure et al. 2009) and hoary cress [*Cardaria draba* (L.) Desv.] (Selleck 1961). We conclude that focusing management efforts only on new satellite populations, while leaving larger patches unmanaged, could lead to an increase in net expansion of perennial pepperweed into previously uninvaded areas. A more appropriate management strategy should consider controlling the expansion of perennial pepperweed in both small satellite populations and the expanding edges of larger infestations.

Factors Associated with Invasion and Species Composition. The CCA and DA found consistent correlations for species and environmental variables that might explain factors that facilitate or inhibit perennial pepperweed invasion. This was true even though the CCA used perennial pepperweed density (a quantitative metric), whereas DA used perennial pepperweed presence or absence (a binomial metric). Both analyses found that the significant effects did not depend on year. The first two axes of the CCA biplot of species–environmental variables explained 24.5% of the variance in the species data and 47.3% of the variance in the weighted averages and class totals of the species with respect to the environmental variables over the 1999 to 2001 assessment dates (Figure 3). All correlations represented were extracted from the correlation matrix weighted by sample totals; consequently, there can be no correlations greater than 0.70 (ter Braak and Šmilauer 2002). The weight of water as a percent of soil weight (watersoi) was found to be most consistently correlated with the pattern of community variation based on its arrow length on the first two CCA axes ($r_{\text{watersoi-CCA1}} = 0.51$ and $r_{\text{watersoi-CCA2}} = 0.41$) and the Monte Carlo permutation test (P = 0.002). Most of the variables found to be significant by permutation test had negative correlations with perennial pepperweed density from most negatively correlated ($r = -0.16$) to least ($r = -0.12$): percent bare soil (bare), percent cover by perennial dicots (perdicot), burn status (burned), and species numbers (speciesn). One rare exception was the positive correlation that percent water weight of soil had with perennial pepperweed density ($r_{\text{watersoi-PPWdens}} = 0.07$). Therefore, the positive values on the first two CCA axes, which account for the most variation in species cover of all assessed axes, corresponded to subplots that had low species numbers, high incidence of perennial pepperweed, and high soil moisture. In addition to perennial dicot cover, the other functional species assemblages that were found to be significant explanatory variables ($P < 0.05$) in terms of species associations by permutation test were percent cover of annual dicots (anndicot), annual grasses (anngrass), perennial grasses (pergrass), native plants (natives), and nonnative plants (nonnative). These later species assemblages were, however, not found to be correlated with perennial pepperweed density based on their perpendicular orientation to the perennial pepperweed density (PPWdens) arrow in the CCA diagram. In general, as vegetative cover and soil moisture increased, the likelihood of perennial pepperweed density increased, whereas increased perennial dicot and bare-ground cover was associated with a reduced pepperweed density. The benefit of increased soil moisture on perennial pepperweed spread has also been shown by Andrew and Ustin (2010). They found that increased spring precipitation was correlated with enhanced spread. The CCA found negative relationships between perennial pepperweed density and species diversity (species number, speciesn). This negative

Table 6. Plant community functional groups and the abiotic variable (watersoi) affecting the potential for perennial pepperweed infestation as determined from stepwise discriminant analysis (DA) with coefficient estimates for variables included in the final discriminant function ($n = 177$). The z score can be computed to determine the potential for perennial pepperweed invasion for an area of unknown threat using Equation 1, where $z_{critical} = 5.3335$, by inputting the values observed for each of the selected variables, j. A computed z score less than 0 would be indicative of an increased potential for perennial pepperweed infestation. Any variable with a negative coefficient is indicative of an increased potential for invasion as the value of that variable increases.

Variable	Description	P value	Coefficient a_j
anndicot	Annual broadleaf cover	< 0.0001	0.1386
perdicot	Perennial broadleaf cover	< 0.0001	0.1146
anngrass	Annual grass cover	< 0.0001	0.0768
natives	Percent native cover	0.024	−0.0238
watersoi	Percent water : soil weight	0.013	−6.5331

correspondence is greatest for the native broadleaf species *Atriplex* spp. and *Aster subulatus* Michx. var. *ligulatus* Shinners [=*Symphyotrichum divaricatum* (Nutt.) G. L. Nesom], and the nonnative *Rumex crispus* L. based on the ordering of the weighted average species scores along the perennial pepperweed density eigenvector (Figure 3). Furthermore, the CCA reveals a high correspondence between perennial pepperweed and the natives *Frankenia salina* (Molina) I. M. Johnst. and *Malvella leprosa* (Ortega) Krapov., as well as the nonnative perennial dicot, *Lotus corniculatus* L.

The stepwise discriminant analysis found four plant species groupings and a soil moisture variable that could be used to predict the potential for perennial pepperweed invasion with a significant ($P < 0.0001$) multivariate exact F test for the overall model (Table 6). The misclassification rate, classifying a subplot as invaded by perennial pepperweed when it really was not and vice versa, by the resubstitution and cross-validation methods on a calibration data set was 29% and 32%, respectively.

Like the CCA permutation tests, the DA found that the percentage of soil weight that was water (watersoi) had a very high negative coefficient and, thus, was the most significant abiotic environmental variable that could predict perennial pepperweed invasion (Table 6). Among the biotic variables, the DA also found perennial broadleaf vegetative cover to be significantly negatively correlated with perennial pepperweed presence (Table 6). Like the CCA, the DA also found the same strong negative relationship between perennial pepperweed presence and the perennial broadleaf group (perdicot) (Table 6). The DA found both broadleaf and grass annual species cover (anndicot and anngrass) to be significant predictors resulting in reduced potential for perennial pepperweed invasion on the basis of their positive DA coefficients. Thus, the presence of these species functional groups adjacent to the perennial pepperweed patches might have provided some level of invasion resistance. Specific functional groups of vegetation have been widely shown to reduce invasibility (e.g., James et al. 2010; Wilson et al. 2009). The functional native species grouping had a significant negative DA coefficient, indicating susceptibility to invasion into plots in which plant cover comprised native species.

Management Implications. At both the Colusa and Grizzly Island locations, perennial pepperweed spread was primarily through vegetative expansion along the perimeter of the patch at an average of 0.85 m yr^{-1} in the undisturbed sites. This rate of expansion did not appear to be related to the initial size of the patch. As was reported by Wilson et al. (2008), disking is not an acceptable control strategy when used alone and is likely to lead to an increased rate of population growth. Although seeds do not appear to be the major method of perennial pepperweed expansion, they might play a key role in the occasional establishment of new nascent foci populations. Thus, the release of seed-feeding insects as a sole method for biological control would be unlikely lead to an effective long-term management strategy for perennial pepperweed.

In determining how and where to prioritize management efforts, it is important to consider that although smaller satellite infestations expand at a faster rate per unit area compared with larger infestations, larger populations accumulate more newly infested total area than smaller infestations from year to year. The amount of new expansion is directly related to the increased perimeter length in the larger patches.

Not only will unmanaged infestations continue to expand, but an increased proportion of the patch will be in the center and, thus, will have higher stem density compared with the leading edge. Higher stem density of perennial pepperweed will be more difficult to control (Renz and DiTomaso 2001, 2004) and can have reduced resident native or desirable vegetation (Boyer and Burdick 2010). Even if control is possible by using an herbicide in these near monotypic stands within the center regions of an infestation, the area could be devoid of recovering vegetation because of a thick litter layer and lack of residual plant diversity and corresponding seedbanks in the soil

(Wilson et al. 2008). Excessive litter can block light penetration to the soil and suppress the recovery of other desirable species. These areas might require tillage or burning to break up the thatch layer, followed by expensive active revegetation efforts to achieve the desired plant community (Renz and DiTomaso 2001, 2006; Wilson et al. 2008).

When financial resources are limited, it might be more cost effective to manage perennial pepperweed by prioritizing control efforts on the rapidly expanding satellite populations as well as the leading edge of the larger patches, while avoiding treatment to the center of the larger patches. These treatment areas would have lower stem density, higher resident desirable vegetation, less litter accumulation, lower carbohydrate reserves stored belowground, and less time to alter soil attributes (Renz and Blank 2004). All these factors would increase the likelihood of successful control and re-establishment of resident vegetation, particularly native broadleaf species, from adjacent areas. Such a management plan may prevent the need for expensive active restoration programs.

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