Biology, Ecology and Control of
Perennial Pepperweed (*Lepidium Latifolium* L.)

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ABSTRACT

Perennial pepperweed is an invasive weed spreading throughout the western United States. Its biology, ecology and control are poorly understood. The objectives of this dissertation were to study aspects of perennial pepperweed growth and spread and to develop and test control methods across habitats. It was found that integration of mowing with herbicides enhanced effectiveness of certain herbicides in controlling perennial pepperweed. Mechanisms responsible were also investigated.

At three sites in California, perennial pepperweed infestations spread clonally 1 to 2 m per year, expanding 44% to 129% over 2 years. Disking or burning did not reduce the rate of spread at any of the sites. Efficacy of several systemic herbicides were evaluated; chlorsulfuron (0.104 kg ai/ha) reduced biomass of perennial pepperweed in dense infestations by $\geq$ 74% one year after treatment. Mowing alone did not reduce perennial pepperweed biomass, but mowing followed by chlorsulfuron (0.052 kg ai/ha) or glyphosate (3.33 kg ae/ha) reduced perennial pepperweed biomass in dense, established infestations by $\geq$ 90% one year after treatment. Mowing did not result in increased herbicide efficacy in young, less-dense infestations. However, following control, resident plant species reestablished poorly in dense infestations, but extensively in young, less-dense sites.

Several factors account for the synergistic effect of integrating mowing and herbicides. Mowing altered the vertical distribution of leaf area, which affected deposition of spray solution. In mowed plants most herbicide landed in the basal one-third of the canopy, compared to the middle and top third of the canopy in unmowed plants. In greenhouse studies, 6.7% of ^{14}C-glyphosate applied to basal leaves of mowed plants was translocated into belowground tissue, compared to 0.37% of ^{14}C-glyphosate applied to unmowed plants. Moreover, field studies demonstrated that mowing removed strong sinks in the upper canopy and delayed herbicide applications to allow plants to resprout, thereby maximizing translocation to belowground tissues.

In this research, effective techniques for perennial pepperweed control were developed and demonstrated in several habitats. Investigation of the synergism between mowing and herbicide application elucidated factors involved in herbicide efficacy which may assist in managing other perennial weeds.

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CHAPTER 1

Early season mowing improves the effectiveness of chlorsulfuron and glyphosate for control of perennial pepperweed (*Lepidium latifolium* L.)

AUTHORS: MARK J. RENZ and JOSEPH M. DITOMASO

ABSTRACT

Perennial pepperweed is an invasive noxious weed spreading rapidly throughout a wide range of habitats in the western United States. This study was established to test whether incorporating mowing with systemic herbicides would provide control of perennial pepperweed within a high desert, roadside and floodplain habitat. Chlorsulfuron alone at 0.104 kg ai/ha reduced biomass from 74 to 100% and density from 78 to 100%, while 2,4-D and glyphosate alone at 2.11 kg ae/A and 3.33 kg ae/A, respectively, were inconsistent and did not significantly reduce biomass at two of the sites. Mowing alone did not reduce perennial pepperweed biomass or density, but mowing followed by herbicide treatments to resprouting plants significantly reduced biomass 57 to 67%. Combinations of mowing and chlorsulfuron at 0.052 kg ai/ha or glyphosate at 3.33 kg ae/A significantly reduced perennial pepperweed biomass by ≥ 99% and ≥ 91%, respectively. The effectiveness of glyphosate in combination with mowing provides land managers with an effective perennial pepperweed control option in areas where chlorsulfuron is not registered for use.

INTRODUCTION

Perennial pepperweed (*Lepidium latifolium* L.) is a highly invasive herbaceous perennial that is expanding its range throughout the west (Young et al. 1998) and has the ability to establish large monospecific infestations throughout a wide range of habitats. Although it is most frequently associated with riparian areas, marshes, estuaries, irrigation channels, wetlands and floodplains, perennial pepperweed can also infest roadsides, native hay meadows, alfalfa fields, and rangelands. Its ability to survive in a diverse range of habitats is speculated to be due several factors including the production of a large perennial root system that has a high capacity to store carbohydrate reserves for future growth, root growth deep into the soil profile to access soil moisture not available to other plants, and a high tolerance to salinity (Young et al 1997)**.**

Successful control of perennial pepperweed was previously reported with chlorsulfuron at 0.104 kg ai/ha (Young et al. 1998). However, chlorsulfuron is not registered for use in many areas where perennial pepperweed invades, particularly areas in or adjacent to water. The compounds that are registered within these areas (e.g. 2,4-D, glyphosate) have only shown limited effectiveness in controlling perennial pepperweed (Trumbo 1994, Young et al. 1998). As a result, few if any options are available for perennial pepperweed management within riparian, floodplain, seasonal wetland, and marsh habitats in California, and other areas of the western United States.

Field observations indicated that early season mowing followed by applications of systemic herbicides to resprouting shoots dramatically improved control of perennial pepperweed. This study was conducted to quantitatively evaluate the effectiveness of integrating mowing and systemic herbicides for control of perennial pepperweed. The goal is to provide options for perennial pepperweed control in sensitive habitats where management options are limited.

MATERIALS AND METHODS

Experiments were initiated in a native hay meadow in the high desert (Susanville, CA 1996), a roadside area (Woodland, CA 1997), and a floodplain habitat (Woodland, CA 1998). All three sites had dense, monospecific infestations of perennial pepperweed with > 85% cover (Table 1). Treatments consisted of mowing, herbicide applications, or a combination of the two. At all sites, mowing was conducted when flowerbuds were present on the main shoot and shoots from axillary buds. Shoots were mowed to a 2 to 5 cm height from the soil surface with a weed whacker or sickle bar mower and cut portions were removed from plots. Herbicide treatments were applied to unmowed plots the following day. The flowerbud stage was reported to be optimal for systemic herbicide application on perennial pepperweed (Young et al. 1998). After mowing, not all resprouting shoots bolted, but many remained as rosettes for the remainder of the season. Herbicide treatments were applied to mowed plants when shoots that bolted resprouted to the flowerbud stage. Herbicide treatments and rates varied depending upon the site (Table 2 & 3). Herbicide treatments were applied in a 3 meter swath with a backpack sprayer propelled with $C0_2$ at 45 psi delivering a solution at 382 L/ha with 8004 nozzles.

The high desert and floodplain experiments were split plot designs with mowing as the main plot and herbicide treatment as the sub-plot. Treatments were replicated 3 times in the high desert site and 4 times in the floodplain site. The roadside experiment was a randomized complete block design with 4 replications. Subplots (high desert and floodplain) or plots (roadside) were 3 meters wide and 9 meters long.

Plant biomass and plant density were collected one year after treatments by randomly placing a 0.25 m^2 quadrat into the plot, avoiding the edges of the plot. Data were analyzed by performing an analysis of variance for each site followed by a Fisher's protected LSD for biomass and density of each mowing treatment separately (not mowed or mowed). A t-test was then used to compare the effectiveness of mowing between specific herbicide treatments. Additional analyses of variance were performed to determine if mowing improved herbicide effectiveness in controlling perennial pepperweed. To test this, untreated control plots were excluded, and herbicide treatments were combined for mowed and unmowed treatments. Analysis of variance was then performed followed by a Fisher's protected LSD to separate means. Equality of variances was checked prior to all analyses and appropriate transformations were made to data if necessary. All data is presented in the untransformed form. Due to the small area sampled within each plot and the large degree of variability of biomass and density within the infestations, p values < 0.1 were considered significantly different.

RESULTS AND DISCUSSION

Although sites varied considerably, mowing alone did not significantly reduce perennial pepperweed biomass or density one year after treatment (Table 2 & 3). When herbicide treatments were combined, treatments including mowing showed enhanced control with significant reductions in perennial pepperweed biomass and density compared to areas not mowed (Table 4). Although biomass and density varied between sites, biomass significantly decreased 57 to 67% across all sites, and density decreased by 33 to 50% in the roadside and floodplain site (high desert site was not significantly different) (Table 4). These indicate that an initial mowing can significantly improve the efficacy of systemic herbicides across varying habitats.

Herbicide treatments alone

Of the herbicides applied alone, chlorsulfuron provided the most consistent control of perennial pepperweed. Reductions in biomass ranged from 74 to 99% at 0.052 kg ai/ha to 100% at 0.104 kg ai/ha (Table 2). Plant density was also reduced with chlorsulfuron from 35 to 99% at 0.052 kg ai/ha and 100% at 0.104 kg ai/ha. These results support those of Young et al. (1998), indicating chlorsulfuron is very effective for control of perennial pepperweed in a wide range of habitats. Results with 2,4-D and glyphosate were inconsistent one year after treatment. Some reduction in perennial pepperweed biomass occurred with 2,4-D and glyphosate compared to untreated plots, but decreases were only statistically significant at the high desert site. In the floodplain site, glyphosate applications to unmowed areas at both 1.67 and 3.3 kg ae/ha increased biomass one year after treatment (Table 2). The variability among sites may be partially explained by the environmental and geographic variability between sites such as soil moisture, depth of watertable, El Nino, and soil type. Young et al. (1998) observed no difference in vegetative cover of perennial pepperweed one year after treatment with glyphosate at 0.6 kg ai/ha. Glyphosate or 2,4-D applications may provide moderate suppression when used alone, but the level of control appears to be too inconsistent and highly sensitive to other environmental and/or physical factors.

Mowing and herbicide combinations

Shoots quickly resprouted after mowing, resulting in a dense stand of rosette plants. The majority of these shoots remained rosettes throughout the season. As a result, canopy architecture was opened and stem height was reduced at the time of herbicide application in mowed plots compared to plots not mowed.

While mowing alone is not an effective control method, it improved the control of perennial pepperweed when used in combination with systemic herbicides (Table 2, 3 & 4). Mowing before applications of chlorsulfuron at 0.052 kg ai/ha significantly reduced the biomass of perennial pepperweed by > 99% in all three sites. In the floodplain site, perennial pepperweed biomass was reduced 99% or more with either rate of chlorsulfuron regardless of whether the herbicide treatment occurred alone or following mowing. Glyphosate at 3.33 kg ae/A reduced perennial pepperweed biomass at the roadside and floodplain sites by 81 and 98% respectively (Table 2). While similar trends were seen with plant density, only chlorsulfuron at 0.052 kg ai/ha at the high desert site and roadside site, and glyphosate at 3.33 kg ae/A at the roadside site, had significantly less plants than the same treatments without mowing (Table 3). The incorporation of mowing with 2,4-D did not significantly reduce the biomass of perennial pepperweed across all sites. These data indicate that mowing can enhance the efficacy of glyphosate and chlorsulfuron on the control of perennial pepperweed.

Potential mechanisms

Mowing has been shown to increase the effectiveness of other herbicides in controlling several perennial weed species including tropical soda apple (*Solanum viarum*; author Mislevy et al. 1999), Canada thistle (*Cirsium arvense*; authors Hunter 1996, and Beck and Sebastian 2000) and common reed (*Phragmites australis*; author Monteiro et al. 1999). Mislevy et al. (1999) found that a 1.1 kg ai/ha triclopyr application to tropical soda apple 60 days after a pre-herbicide mowing significantly increased effectiveness 38% compared to plants mowed but not treated. These researchers also demonstrated that mowing reduced the biomass and percent total nonstructural carbohydrates of below ground storage organs in tropical soda apple (Mislevy et al. 1999), and speculated that this reduced the lethal dose of herbicide required to translocate to below ground storage organs. Hunter (1996) successfully controlled Canada thistle by integrating an initial tillage followed by glyphosate applications to resprouted rosettes. He hypothesized that tillage changed the canopy architecture of the infestation. In this case, resprouting plants remained rosettes compared to untilled areas where stems elongated and flowered. Fewer active meristems were present in the shoots of plants resprouting after tillage, thus greater herbicide contact can occur on the lower leaves in conjunction with increased herbicide translocation and accumulation in the below ground vegetative reproductive structures. In support of this hypothesis, he found a 4 times more ^{14}C-glyphosate in the roots of rosette plants compared to plants at the flowerbud stage, and 7 times more ^{14}C-glyphosate in the shoots of plants at the flowerbud stage compared to rosettes.

Beck and Sebastian (2000) showed mixed results when integrating mowing with systemic herbicides. They applied several herbicide treatments after mowing Canada thistle 1, 2 or 3 times at two sites. At one site they found significantly less cover of Canada thistle one year after mowing was incorporated with fall applications of 2,4-D and chlorsulfuron (0.14-0.28 kg ai/ha and 0.75-1.46 kg ai/ha respectively). While at another site, mowing significantly reduced the cover of Canada thistle only when combined with dicamba at 2.24 kg ai/ha. They postulated that inconsistent results between sites was due to differences in initial density of the infestation, rate of increase/decrease of density over the experiment, and soil moisture. Mowing may also influence other physiological, biological and/or anatomical characteristics of the plant, thus altering herbicide deposition patterns, absorption, and/or translocation rate on or in resprouting shoots.

Regardless of the mechanism(s) responsible, our results indicate that mowing consistently enhanced the effectiveness of glyphosate and chlorsulfuron in controlling perennial pepperweed one year after treatment. More importantly, incorporating an initial mowing increased the effectiveness of glyphosate at 3.33 kg ae/A to a level where it can be considered an effective control option. Since glyphosate is registered for use near water, land managers now have an effective method to manage perennial pepperweed in these sensitive habitats.

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Table 1. Site and treatment information.

	High desert (Susanville, CA)	**Roadside** (Woodland, CA)	**Floodplain** (Woodland, CA)
Coordinates	40° 21.28 N 120° 20.10 W	38° 39.03 N 121° 45.50 W	38° 40.63 N 121° 40.35 W
Elevation (meters)	1298	19	19
Soil type	Humboldt silty clay loam	Sycamore silty clay loam, flooded	Sacramento soils, flooded
Previous management techniques	None	Annual mowing	Seasonal flooding and biannual disking
Precipitation the year of application	479.1 mm	461.3 mm	805.8 mm
Precipitation the year after application	529.1 mm	805.8 mm	377.6 mm
30 year average annual rainfall	387.5 mm	496.1 mm	496.1 mm
Date of mowing & herbicide treatments made in unmowed plots	6/15/1996	4/29/1997	5/22/1998
Date of herbicide treatments in mowed plots	7/23/1996	5/28/1997	7/24/1998
Date of biomass and density measurements	6/30/1997	7/3/1998	7/30/1999

Annual precipitation was calculated starting July 1st of the previous year to June 31st of the current year.

Table 2. Impact of treatments on perennial pepperweed biomass one year after applications.

			Biomass (g dry wt/m^2)[b]			% reduction[c]	
Site	Herbicide	Rate (kg ai or ae/ha)	Not mowed	(t-test)	Mowed	Not mowed	Mowed
High desert	2,4-D[a]	2.11	267 b		86 b	73.5	91.5
	glyphosate	1.67	166 b		127 b	83.5	87.4
	glyphosate	3.33	-		-	-	-
	chlorsulfuron[a]	0.052	211 b	*	4 c	79.1	99.6
	chlorsulfuron	0.104	-		-	-	-
	control	-	1008 a		1028 a	-	-2.0
Roadside	2,4-D	2.11	747 ab		786 a	13.0	8.5
	glyphosate	1.67	-		-	-	-
	glyphosate	3.33	583 ab	**	13 b	32.1	98.5
	chlorsulfuron	0.052	220 b	*	1 b	74.4	99.9
	chlorsulfuron	0.104	-		-	-	-
	control	-	859 a		976 a	-	-13.6
Floodplain	2,4-D	2.11	677 c		450 bc	42.2	62.2
	glyphosate	1.67	1688 a	**	721 ab	-41.6	39.5
	glyphosate	3.33	1426 ab	**	231 c	-19.6	80.6
	chlorsulfuron	0.052	11 d		2 d	99.1	99.8
	chlorsulfuron	0.104	0 d		0 d	100	100
	control	-	1192 bc		860 a	-	27.9

[a] Silicone based surfactant added at 0.1 % v:v at all sites and rates.
[b] Letter indicate significant differences ($p<0.10$) within site and mowing regime only.
[c] % reduction compared to unmowed control.
* Significant difference using a t-test $p<0.1$
** Significant difference using a t-test $p<0.05$

Table 3. Impact of treatments on perennial pepperweed density one year after applications.

			Density (Shoots/m^2)[b]			% reduction[c]	
Site	Herbicide	Rate (kg ai or ae/ha)	Not mowed	t-test	Mowed	Not mowed	Mowed
High desert	2,4-D[a]	2.11	35 c		49 c	63.2	53.7
	glyphosate	1.67	80 ab		82 b	15.8	13.7
	glyphosate	3.33	-		-	-	-
	chlorsulfuron[a]	0.052	62 bc	*	4 d	34.7	95.8
	chlorsulfuron	0.104	-		-	-	-
	control	-	95 a	*	155 a	-	-63.2
Roadside	2,4-D	2.11	114 a		168 a	29.2	-4.3
	glyphosate	1.67	-		-	-	-
	glyphosate	3.33	170 a	***	15 b	-5.6	90.7
	chlorsulfuron	0.052	35 b	*	4 b	78.3	97.5
	chlorsulfuron	0.104	-		-	-	-
	control	-	161 a		201 a	-	-24.4
Floodplain	2,4-D	2.11	92 c		70 b	45.9	58.8
	glyphosate	1.67	247 a		174 a	-45.3	-2.4
	glyphosate	3.33	123 bc		64 b	27.6	62.4
	chlorsulfuron	0.052	2 d		5 c	98.8	97.1
	chlorsulfuron	0.104	0 d		0 c	100	100
	control	-	170 ab		163 a	-	4.1

[a] Silicone based surfactant added at 0.1 % v:v at all sites and rates.

[b] Letter indicate significant differences ($p<0.10$) within site and mowing regime only.

[c] % reduction compared to unmowed control.

* Significant difference using a t-test $p<0.1$

** Significant difference using a t-test $p<0.05$

*** Significant difference using a t-test $p<0.01$

Table 4. Influence of mowing on the effectiveness of herbicides in controlling perennial pepperweed one year after treatment. Control plots without herbicide treatments were excluded from this analysis.

Site	Biomass (g dry wt/m^2)		Density (stems/m^2)	
	Not mowed	Mowed	Not mowed	Mowed
High desert	215	72	59	45
LSD[a] (0.1)	121		ns	
Roadside	536	228	105	52
LSD[a] (0.05)	305		38	
Floodplain	701	282	85	57
LSD[a] (0.1)	324		20	

[a] Fisher's protected LSD was used to separate means within each site.

CHAPTER 2

Mechanism for the enhanced effect of mowing followed by glyphosate to resprouts of perennial pepperweed

AUTHORS: MARK J. RENZ and JOSEPH M. DITOMASO

ABSTRACT

Herbicides currently registered for use near water have been ineffective for control of perennial pepperweed. Previous research has demonstrated that mowing followed by an application of glyphosate at 3.33 kg ae/ha applied to resprouting tissue can enhance the control of perennial pepperweed (Chapter 1). The objectives of this study were to determine the mechanism(s) responsible for the enhanced effectiveness of glyphosate in combination with mowing. Mowing plants altered the location of leaf area within the canopy. In mowed areas, the majority of leaf area was in the basal third of the canopy, whereas the bulk of the leaf area was in the top third of the canopy in unmowed areas. This change in plant architecture affected the deposition pattern of the spray solution. Unmowed plants retained 49 – 98% and 42 – 83% of a dye solution within the middle and top thirds of the canopy at the Colusa and Woodland sites respectively, and only 1.9 – 6.0% dye deposited on the basal third of the canopy at both sites. In contrast, mowed plants had 18 – 34% and 26 – 70% of the dye retained in the basal third of the canopy at the Colusa and Woodland sites, respectively. Greenhouse studies showed ^{14}C-glyphosate applied to basal leaves of mowed plants translocated significantly more to below ground tissue. Unmowed plants accumulated 0.37% ^{14}C-glyphosate in below ground tissue 48 hours after labeling. In contrast, mowed plants accumulated 6.7% ^{14}C-glyphosate in the below ground tissue. Within the field, estimates of seasonal translocation rates utilizing TNC pools indicate that mowing did not change the translocation rate. However the delay in application timing to allow plants to resprout appeared to synchronize applications with maximal translocation of carbohydrates to below ground structures. We hypothesize that the change in the canopy structure of

perennial pepperweed after mowing results in fewer above ground sinks and greater deposition of herbicide to basal leaves where it can preferentially be translocated to the root system. Furthermore, a delay in herbicide application following mowing allows plants to resprout, thus synchronizing maximal below ground translocation rates among the exposed shoots. These factors all appear to be involved in the enhanced control of mowing and glyphosate.

INTRODUCTION:

Perennial pepperweed (*Lepidium latifolium* L.) is a deep-rooted herbaceous perennial weed that is currently invading wildland areas throughout the western United States. Perennial pepperweed can exist in a wide range of habitats, but preferentially establishes in areas near water (wetland, floodplain, riverbank, and riparian areas) where limited tools exist for its control. Management of perennial pepperweed infestations have been evaluated with approved herbicides for use in these areas (e.g. 2,4-D, glyphosate), but have not been effective (Young et al. 1998, Chapter 1).

We have demonstrated that mowing followed by an application of glyphosate at 3.33 kg ae/ha applied to resprouting tissue can effectively control perennial pepperweed (Chapter 1). Integrating mowing and herbicides has been utilized to enhance control of several other perennial species (Mislevy et al. 1999, Hunter 1996, Beck and Sebastian 2000, Monteiro et al. 1999). Several mechanisms have been postulated to explain the improved control. Mislevy et al. (1999) speculated enhanced control of tropical soda apple (*Solanum viarum* Dunal) occurred from depletion of below ground biomass and enhanced basipetal translocation. Hunter (1996) suggested that mowing changes the herbicide deposition pattern due to canopy architecture changes in Canada thistle (*Cirsium arvense* L. Scop.). They hypothesized that this was partially responsible for increased accumulation of herbicide in below ground tissue and enhanced long-term control. While data exist supporting these hypotheses (Mislevy et al. 1999, Hunter 1995, Hunter 1996, O'Sullivan and Kossatz 1984, McIntyre et al. 1978), no detailed studies have been conducted to determine the specific mechanism(s) responsible for improved effectiveness of systemic herbicides applied to any plant species resprouting from mowing.

Mowing can alter many physiological and morphological processes in plants (Briske and Richards 1995). Physiological or morphological changes in perennial pepperweed incurred from mowing can affect the amount of glyphosate deposited on plant tissue, deposition patterns of glyphosate within the canopy, absorption of glyphosate into the foliage, or translocation and accumulation of glyphosate into roots of perennial pepperweed. Any of these factors could be responsible for the observed enhanced effectiveness of glyphosate following an initial mowing. The objective of this study was to determine the mechanism(s) responsible for improved control of perennial pepperweed using a combination of mowing followed by an application of glyphosate to resprouted shoots. Specifically we evaluated the influence of mowing on a) the amount and location of spray solution deposition, b) the absorption and accumulation of glyphosate, and c) seasonal translocation rates into roots of perennial pepperweed plants.

MATERIALS & METHODS

Leaf area and dye deposition

Glyphosate deposition patterns were estimated at a seasonal wetland and floodplain site (Colusa and Woodland California, respectively) in 1999 utilizing a water-soluble dye (Hi-Lite Blue™). Both experiments were designed as randomized complete block experiments with four replications. Treatments consisted of plants that were not mowed, mowed at the flower bud stage, or mowed at the full flower stage. A 1% v:v dye solution was applied to unmowed plants at the flower bud, full flower, or fruiting stages while mowed areas received treatments when plants resprouted to rosette (24-32 days after mowing), flower bud (48-59 days after mowing), or fruiting stages (83-99 days after mowing). Plots were 3 meters wide and 9 meters long. All treatments were applied in a 3 meter swath with a backpack sprayer propelled with 310 kPa of $C0_2$ delivering a solution at 382 L/ha with six 8004 nozzles.

The spray solution was allowed to dry before three sub-samples of shoots were randomly harvested from a 625 cm^2 area within each plot. Sub-samples were separated into basal, middle and top thirds of the canopy. Canopy levels were determined by separating tissue into thirds based on the average stem height within each sample. If no stems were present, all tissue was considered in the basal portion of the canopy. Dye was removed by washing plant tissue with 500 mL of 0.01% v:v Triton X-100 in water. Previous experiments indicated that >95% of dye was repeatedly recovered with this method (data not shown).

Quantification of dye on each canopy level was determined with a spectrophotometer[1] utilizing a peak absorbance wavelength for the dye (630 nm). A standard curve was established for known dye concentrations, and the equation describing this curve was utilized to determine the concentration of dye in the sub-sample solutions. To eliminate the influence of contaminants, untreated plant tissue from the basal, middle, and top third of the canopy at each stage of application were also collected from each sampling period and washed as described above. Absorption values obtained from untreated samples were subtracted from values for each treated sample.

To account for differing amounts of bareground present within treated areas, the amount of dye applied per unit area was determined on bareground areas adjacent to

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[1] DU-64 Spectrophotometer Beckman Instruments Inc.., Palo Alto, CA 94304

infestations on four occasions. Seven petri dishes (9.1 cm in diameter) covered with tin foil were placed in areas adjacent to infestations and dye applications were made using techniques as described above. After the dye dried, tinfoil was removed and the amount of dye recovered was determined using the same techniques described above, except the rinsate volume was 200 ml. The total amount of dye recovered per unit area was calculated and concentrations for each plant sub-sample were divided by this value to give the percentage of dye sprayed within a specific area recovered on perennial pepperweed plant tissue. After dye removal, leaf area was measured from each sample utilizing a licor LI-3100 leaf area meter.

Data were analyzed by both parametric and nonparametric methods. Total leaf area and total dye, as well as leaf area and dye present within each canopy level were each analyzed separately by analysis of variance (ANOVA). For each variable, normality and homogeneous variance were checked and appropriate transformations were made as necessary. Due to a highly significant difference ($p< 0.01$) between sites, each was analyzed separately (data not shown).

Since the response of the plant canopy to specific treatments was of interest, we also analyzed the difference between leaf area and percent dye recovered throughout canopy levels utilizing multiple response permutation procedure (MRPP). MRPP is a nonparametric analysis that tests for significant differences between groups of variables for each treatment (in our case leaf area or percent dye recovered within the basal, middle, and top third of the canopy) (Mielke et al. 1981). We compared the differences between plants not mowed at the flower bud stage to plants that had been either mowed at the flower bud or full flower stage and had been given ample time to resprout to the flower bud stage. If no stems were present in samples, values of 0 were given for leaf area, as well as percent dye recovered for the middle and top thirds of the canopy.

^{14}C-Glyphosate absorption and translocation

Plants were grown from 1.0 – 1.5 g fresh weight root fragments obtained from plants that had been chilled (8 °C) for at least 1 month prior to planting. Segments were planted in cone-shaped pots (656 mL capacity, 6.4 cm diameter, 25 cm depth) to facilitate ample vertical root formation. Plants were sub-irrigated with water containing ample nutrients so that plant growth was not limited throughout the experiment. This experiment was a randomized complete block design with three treatments each replicated six times. Blocks consisted of plants initiated and grown at the same time. Treatments consisted of plants at the flower bud stage, plants mowed at the flower bud stage and allowed to resprout for 30 days, and plants at the fruiting stage (grown for 30 days after the flower bud stage). Shoots of mowed plants were cut at the soil surface at the flower bud stage and allowed to resprout for 30 days before treatments were applied. Although longer periods were required for plants to resprout to the flower bud stage after mowing in the field (48-59 days after mowing), treatments were made 30 days after mowing in the greenhouse due to the advanced maturation of plants growing under these conditions.

Applications were made to leaf pairs for all treatments. On unmowed plants (flower bud and fruiting stage), applications were made to the 6th and 7th leaves subtending the inflorescence (counting from the shoot apex down). Mowed plants remained in the rosette stage. Therefore, applications were made to the two largest leaves present 30 days after mowing. Applications consisted of four, 1 uL drops of ^{14}C-glyphosate (glyphosate-phosphonomethyl-2-^{14}C)[2] (2.035 MBq/mL and 88.8 MBq/mmol) with 0.5% v:v R-11 surfactant applied to a 1 cm^2 area of selected leaves. The four drops were spread over the entire 1 cm^2 area to maximize absorption and standardize surface area covered.

Plants were harvested after 48 hours of exposure to ^{14}C-glyphosate. Treated leaves were detached and washed with 10 mL of water to remove unabsorbed ^{14}C from the leaf surface (White et al. 2000). Liquid scintillation spectrometry was used to determine dpm from 10 uL aliquots of washes. Wash solution was added to 5 mL of scintillation cocktail[3], placed into the scintillation counter[4], and counted for 5 minutes. Background samples were measured and subtracted from wash samples. Remaining plant samples were separated into treated leaves, leaves and stems above lowest labeled leaf, leaves below labeled area, stems below labeled area, flower buds/flowers/fruits, parent root, large new roots (>2 mm in diameter), and fine roots. Samples were lyophilized for 12-24 hours, weighed, ground until samples were homogenous, oxidized, and counted for ^{14}C. Total recovery of ^{14}C averaged 70.9% and was not statistically different among treatments (data not shown). Data are presented as percent of recovered ^{14}C-glyphosate. Although some plants have been shown to metabolize glyphosate (for a discussion of this see Eberbach and Bowmer 1995), it was assumed that glyphosate was not metabolized by this plant within the time period of this experiment. Exudation of ^{14}C-glyphosate from the roots was analyzed by counting aliquots from irrigation water for each treated plant, but none was detected (data not shown).

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[2] Glyphosate-phosphonomethyl-2-^{14}C, Sigma Chemical co., St. Louis, MO 63178

[3] Biosafe II Biodegradable counting cocktail, Research Products International, Mount Prospect, IL 60056.

[4] 1900TR liquid scintillation counter analyzer, Packard inc., Downers Grove, IL. 60515

All data were analyzed utilizing analyses of variance and if overall significant differences were detected, Fisher's protected LSD ($p < 0.05$) was utilized to determine differences between means. Normality and homogeneous variance were both checked prior to analysis and appropriate transformations were made as necessary. Data are presented untransformed.

Root TNC over time

Field photosynthate accumulation patterns were estimated over a one year period at a floodplain and riparian location (Yolo Bypass in 1998 and Putah Creek in 1999). Experiments were established in a randomized complete block design with 5 replicates at each site. Roots were removed from 625 cm^2 areas to a 40 cm depth. Plots were either not mowed or mowed at the flower bud stage. Mowing was performed with a sickle bar mower to a maximum height of 2 to 5 cm and shoots were removed from plots after mowing was completed. Collected samples were dried, ground and analyzed (U.C. Davis ANR Analytical Laboratory) for total nonstructural carbohydrates (TNC). Samples were collected every 2 to 4 weeks at each site throughout the year. Samples were not collected at the Woodland site in late winter through early spring due to flooding at that site. All samples were collected within 3 hours of sunrise to limit the daily fluxes of TNC within roots. Data are presented as TNC pools (g TNC/m^2). Curves were smoothed using a locally weighted regression function (LOWESS) for both mowed and unmowed curves at each site. Each curve utilized 40% of the total points to smooth data for each curve.

TNC pool values in mowed and unmowed treatments were compared to test if mowing reduced concentration in below ground roots. T-tests ($p \leq 0.05$) were conducted between unmowed values and mowed values 7 and 19 days after mowing at the Yolo Bypass and Putah Creek sites, respectively.

To compare translocation rates between mowed and unmowed areas these curves were separated into three phases: the phase before mowing (94 – 147 and 72 – 135 Julian days at the Yolo Bypass and Putah Creek site, respectively), the accumulation phase (166 – 243 and 167 – 266 Julian days at the Yolo Bypass and Putah Creek site, respectively), and the senescence phase (272 – 363 and 291 – 418 Julian days at the Yolo Bypass and Putah Creek site, respectively). Analysis of covariance was performed on data within the accumulation phase, with mowing as the treatment factor and date as the covariate for each site. Normality and homogeneous variance were checked prior to analysis and appropriate transformations were made as necessary. The interaction between mowing and dates was tested with ANCOVA to evaluate if slopes of mowed and unmowed lines were significantly different.

RESULTS AND DISCUSSION

Dye deposition and leaf area

In unmowed plants, total leaf area/m^2 was significantly reduced by 55 and 82% at the Colusa site and 31 and 36% at the Woodland site from the flower bud stage to the full flower and fruiting stages, respectively (Table 1). This resulted in a 43 and 48% reduction in the dye recovered at the Colusa site from the flower bud stage to the full flower and fruiting stages (Table 2). In contrast, the Woodland site showed an increase in deposition on plant tissue (48 and 65% increase in dye recovery) although only the fruiting stage was significantly greater than the flower bud stage. This may be due to differences in the canopy development of perennial pepperweed at each site. Perennial pepperweed above ground biomass was much greater at the Woodland site compared to the Colusa site (22, 26 and 55% greater at the flower bud, full flower and fruiting stages, respectively) (data not shown). This resulted in a more closed canopy compared to the Colusa site, especially as plants reached the fruiting stage. Increased biomass likely resulted in greater surface areas of stems, flower buds, flowers, and fruit, which could explain the increase in dye deposition. Absorption rates of herbicides by stems, flower buds, flowers, and fruit is likely less than leaf tissue (Ashton and Monaco 1991) and could in part account for the reduced effectiveness of herbicides when applied at the full flower and fruiting stages.

Total leaf area/m^2 was significantly reduced in all mowing treatments at various sampling stages at both sites compared to unmowed plants at the flower bud stage (Table 1). This resulted in either no difference or a reduction in the dye recovered in all of the mowed treatments compared to all of the unmowed treatments (Table 2). At the Colusa site, 34 – 44% of the dye was recovered from plants resprouting from mowing at the flower bud stage, while at the Woodland site, 57 – 65% of the dye was recovered. The greater recovery of dye at the Woodland site likely is due to the greater leaf area/m^2 present. Rosette plants recovered less dye when mowed at the full flower stage compared to the flower bud stage, although values were significantly different only at the Woodland site. This suggests that reduced deposition onto foliage will occur if ample time is not allowed for plants to resprout and leaf area to expand after mowing. This can also occur when mowing is conducted too late in the season, resulting in limited resprouting. Regardless of the site or mowing regime, mowing did not lead to significantly more dye deposited onto plant tissue compared to unmowed treatments, indicating this is not the mechanism responsible for enhanced control.

Total dye deposited was not increased due to mowing, but alterations in canopy architecture changed the location of dye deposition. In unmowed treatments, 78 – 95% and 71 – 80% of the total leaf area/m^2 was found within the middle and top third of the canopy at the Colusa and Woodland sites, respectively (Table 1). Mowing dramatically altered this pattern resulting in 67 – 100% of the leaf area in the basal third of the canopy at both sites. Much of the resprouting tissue remained rosettes throughout the remainder of the season. Inflorescences produced from resprouted shoots after mowing were reduced in height and had few flower buds, flowers, and fruit (personal observation). Basal leaf area in treatments mowed at the flower bud stage was highest at the rosette stage at the Colusa site and at the rosette and flower bud stage at the Woodland site. However, treatments that were mowed at the full flower stage did not reach maximum leaf area/m^2 until the flower bud to fruiting stages at both sites.

This change in canopy architecture altered the deposition of dye within the canopy. The majority of the dye in unmowed treatments was deposited within the top two-thirds of the canopy. In the top third of the canopy, 49 – 98% and 42 – 83% of the dye was recovered at the Colusa and Woodland sites, respectively, while very little dye was deposited onto the basal third of the canopy (2 – 6% at either site) (Table 2). In contrast, mowed treatments had 18 – 34% and 26 – 70% of the applied dye deposited on the basal third of the canopy at the Colusa and Woodland site, respectively. Reduced recovery in mowed treatments were, in part, due to the inability of resprouting perennial pepperweed plants to completely cover the soil surface, resulting in increased bare ground (personal observation). Greater resprouting and more leaf area/m^2 likely accounted for the more dye recovered in the mowed treatments at the Woodland site.

Previous research indicated that mowing perennial pepperweed at the flower bud stage and applying glyphosate to resprouting shoots increased control of perennial pepperweed compared to applications to unmowed plants at the flower bud stage (Chapter 1). To determine the mechanisms responsible, we tested the affect of mowing on leaf area and dye recovered throughout perennial pepperweed's canopy. We compared plants mowed at the flower bud or full flower stages and allowed to resprout to the flower bud stage with unmowed plants at the flower bud stage. The distribution pattern of leaf area and percent dye recovered in the unmowed plants at the flower bud stage was significantly different ($p < 0.01$) from that of the mowed plants at both sites (Figures 1 and 2). Comparing leaf area and dye deposition patterns for corresponding treatments at each site suggest that leaf area is a good predictor of the deposition pattern on perennial pepperweed for all treatments. Analyzing these treatments utilizing MRPP confirms that mowing alters both leaf area and percent dye recovered throughout the canopy, and is likely involved in the enhanced effectiveness of glyphosate used in combination with mowing.

Location of spray deposition can alter herbicide efficacy. Katovich et al. (1996) documented limited accumulation of triclopyr in roots of purple loosestrife *(Lythrum salicaria* L.) when herbicide deposition was mainly in the upper portion of the canopy. They suggested that basal applications would enhance the accumulation of triclopyr in perennial roots. Improved control has been reported when herbicide applications were directed toward the basal portion of monocotyledonous weeds (Knoche 1994).

McWhorter and Hanks (1993) also found improved control of johnsongrass (*Sorghum halepense* L.) with several herbicides applied at higher spray volumes and increased spray pressure. They suggested this was due to improved herbicide deposition within the lower portion of the canopy. Improved control from increased basal deposition has been shown to increase herbicide absorption rates and translocation into below ground organs from basal tissue (Coupland et al. 1978, Tardif et al. 1991). Stoltenberg and Wyse (1986) demonstrated that herbicide accumulation into below ground tissue can differ with location of herbicide deposition. They found more sethoxydim and haloxyfop accumulation in below ground perennial tissues when applications were placed on lower leaves of quackgrass (*Elytrigia repens* L.) compared to leaves higher in the canopy. O'Sullivan and Kossatz (1984) also found increased herbicide accumulation in roots when applications were made to lower leaves of flowering canada thistle (*Cirsium arvense* (L.) Scop.) compared to treatments in the upper canopy, although this difference was not significant. We found that mowing treatments allowed more glyphosate to be deposited onto the basal leaves of perennial pepperweed and hypothesize that this tissue may absorb glyphosate more readily and lead to faster translocation to below ground tissue. Furthermore, resprouting tissues have limited above ground sinks (flower buds, flowers, fruits) compared to unmowed plants, which would theoretically facilitate greater accumulation of glyphosate into stronger below ground sinks present. As a result, enhanced control of perennial pepperweed would be expected the following season.

^{14}C-Glyphosate absorption and translocation

The absorption of ^{14}C-glyphosate into perennial pepperweed leaves differed significantly. Mowed plants had 4.1 and 5.2% more ^{14}C-glyphosate absorbed into the plant tissue compared to unmowed plants at the flower bud or fruiting stages, respectively, although the difference between mowed and not mowed flower bud treatments was statistically insignificant (Table 3). Leaves from mowed plants resprouted after mowing and likely had a less-developed cuticle compared to leaves of unmowed treatments, which could account for the greater absorption of glyphosate (Skoss 1955, Hess 1985).

Treated leaves retained 3.2, 6.9 and 7.9% of the ^{14}C-glyphosate in the flower bud, mowed and fruiting stages, respectively, 48 hours after treatment (Table 3). Significantly more ^{14}C-glyphosate remained in the treated leaves of the fruiting treatment compared to the flower bud and mowed treatments. Of the ^{14}C-glyphosate that was translocated out of the treated leaf, the majority remained within the above ground tissues in not mowed plants treated at the flower bud stage. In these plants, 7.0% ^{14}C-glyphosate was in the above ground shoots [4.23, 2.00 and 0.79% accumulating in the flower buds/flowers/fruit, stems and leaves above the lowest labeled leaf, and stems and leaves below the label, respectively] (Table 3). In contrast, the mowing treatment accumulated significantly less ^{14}C-glyphosate (0.8%) in the shoots (excluding treated leaves). A limited amount (0.6%) of ^{14}C-glyphosate was also found within plants treated at the fruiting stage.

Significantly more ^{14}C-glyphosate accumulated in roots of mowed plants compared to unmowed treatments. Mowed plants accumulated 6.7% ^{14}C-glyphosate in roots, whereas little ^{14}C-glyphosate (< 1%) was translocated to roots of unmowed plants treated at the flower bud and fruiting stages. The proportion of ^{14}C-glyphosate recovered in the mowed plants was fairly evenly distributed between the parent root, large new roots and the fine roots with 1.9, 2.2 and 3.4% recovered in each component, respectively (Table 3). [Very little ^{14}C-glyphosate was recovered within any of the roots of plants not mowed (0.0 – 0.7%) indicating the inability of ^{14}C-glyphosate to accumulate in below ground tissue when applied to the upper canopy at either of these stages.]

Decapitation experiments conducted by others on canada thistle and leafy spurge support our findings. Removal of two-thirds of the shoots of Canada thistle resulted in a 20 – 30% increase in ^{14}C-2,4-D within the roots (McIntyre et al. 1978). In another experiment, removal of one-third of the shoot resulted in a three to six fold increase in ^{14}C-2,4-D accumulation in roots of leafy spurge four and eight days after decapitation, respectively (Hunter and McIntyre 1974). In both of these studies, the authors suggest that sink strength of above and below ground tissues was altered with the removal of above ground tissue, and when most of the above ground sinks were removed enhanced accumulation occurred in the roots. Mowing perennial pepperweed plants modified the above ground shoot and leaf architecture, resulting in few above ground sinks compared to unmowed plants. Although some plants resprout and bolt under field conditions, the number of bolted and flowering stems is greatly reduced, compared to unmowed plants, again causing reduced sink strength of above ground tissue.

Timing of applications can also affect the accumulation of glyphosate into below ground tissues (Stamm-Katovich et al. 1998, Lym and Messersmith 1987). However, applications made at the same phonological stage to mowed plants and unmowed plants (fruiting) still showed large differences in absorption and translocation of glyphosate (Table 3). Limited absorption and translocation in unmowed fruiting plants may be due to several factors, including a more developed leaf cuticle, greater proportion of senesced leaves, or reduced sink strength. Regardless of the mechanism responsible, these results suggest that a change in canopy architecture and the location of herbicide deposition dramatically affect herbicide accumulation patterns. The canopy architecture of perennial pepperweed needs to be considered when applying glyphosate, especially to dense infestations where uneven deposition can occur.

Seasonal TNC accumulation

Accumulation of TNC pools in roots within the top 40 cm varied throughout the season at both sites. Minimum TNC pools were present when plants were bolting, and maximum accumulation rates of TNC pools occurred when plants were between flowering and seed set at both sites. As plants senesced, TNC pools decreased below maximum values (Figures 3 and 4). At the Putah Creek site, TNC pools were monitored throughout the winter and continued to decrease, but values were higher when spring growth began in 2000 compared to 1999 (Figure 4). This suggests that this population may be annually increasing its storage of TNC in below ground tissues.

This seasonal pattern of below ground stored energy depletion early in the growing season, followed by increased accumulation during the summer and a decrease as plants senesce has been observed within other herbaceous perennials including hemp dogbane (Becker and Fawcett 1998), leafy spurge (Lym and Messersmith 1987, Cyr and Bewley 1989), purple loosestrife (Stamm Katovich et al. 1998), and heart-podded hoary cress (Miller et al 1994). Understanding the accumulation patterns of stored energy in below ground tissues can improve management of these perennial weeds. Timing of manual defoliation or other disturbances of above ground tissues during periods when minimum pools of stored energy are present can deplete stores of energy for future growth. In addition, timing systemic herbicide applications with phenological stages that have maximal accumulation rates into below ground tissue should increase the accumulation of systemic herbicides to belowground reproductive structures and enhance long-term control. Based on our data, glyphosate applications should be applied between the full flower and fruiting stages to maximize control. However, Young et al. (1998) reported that optimal control of perennial pepperweed with systemic herbicides occurred at the flower bud to early flowering stages. We postulate that this discrepancy is due to deposition patterns of herbicides within the canopy and absorption and translocation rates within the tissues involved. Perennial pepperweed leaf area/m^2 is significantly less at the full flower and fruiting stages compared to the flower bud stage at both sites (Table 1). In addition, the dense canopy prevents the deposition of glyphosate into lower parts of the canopy (Table 2). All of these factors likely contribute to the reduced control of perennial pepperweed with herbicides applied after the flower bud stage. Although herbicide applications applied at the initial rosette would be ideal for maximal deposition to basal plant parts, limited efficacy at this stage has been reported (Young et al. 1998;

personal observation), perhaps because acropetal translocation patterns predominate at that time(Figures 3 and 4).

Accumulation patterns of perennial pepperweed mowed at the flower bud stage were very similar to unmowed plants. TNC pools of mowed plants were not different than unmowed plants 7 and 19 days after mowing at the Yolo Bypass and Putah Creek sites, respectively (Table 4). TNC from roots deeper than 40 cm could have been mobilized to prevent reductions from being observed. Alternatively, plants quickly resprouted after mowing, resulting in new leaves which rapidly expanded and began to photosynthesize. If this new tissue can quickly begin exporting photosynthates, the loss of TNC to growth and respiration would be limited. While TNC pools did not initially differ between mowed and unmowed treatments, over time there was a reduction in TNC pools in the mowed plots at the Putah Creek site, but not the Yolo Bypass site. It is not clear as to why this pattern was only seen at the Putah Creek site, but it is possible that the Yolo Bypass site had higher TNC pools available deeper within the soil profile and these were reallocated to roots within the top 40 cm. Alternatively, extended flooding in the Yolo Bypass site from February through March (1998) may have reduced TNC pool levels to such low levels that no differences could be observed. These data suggest that perennial pepperweed could be managed by repeated mowings when TNC pools are at a minimum, however, changes in the canopy architecture from mowing will likely prevent this from being very effective. Most shoot tissue remains as basal leaves that are difficult to effectively remove by mowing, thus limiting the effectiveness of this method.

Reductions in stored reserves from mowing or defoliation have been reported in other plant species. Lacey et al. (1994) found spotted knapweed (*Centaurea maculosa*

Lam.) root and crown TNC pools were significantly less 4 months after one or several defoliations. Severe defoliation reduced carbohydrate concentrations 40 – 50% and 55 – 65% in crested wheatgrass (*Agropyron desertorum)* and bluebunch wheatgrass (*Pseudoroegneria spicatum*), respectively, by the end of the growing season (Richards and Caldwell 1985). This reduction in stored energy, however, may not alter the effectiveness of the roots to compete for photosynthates. Olson and Wallander (1999) also found no effect in apparent sink strength in leafy spurge roots 4 – 6 days after defoliation, indicating that although mowing reduces stored energy in below ground tissue, photosynthate accumulation in the root system was not reduced. These researchers suggested that this, in combination with the extensive root system and large amounts of stored energy, allowed leafy spurge to tolerate mowing or grazing. Perennial pepperweed responds to mowing in a similar fashion as leafy spurge and may utilize similar mechanisms to tolerate mowing or grazing.

Our previous studies indicate that glyphosate applications to resprouting tissue from mowing enhanced control of perennial pepperweed (Chapter 1). One hypothesis to explain this enhanced control of perennial pepperweed is that mowing increased translocation into below ground roots, enhancing accumulation of glyphosate, thus increasing long-term control. Based on the assumption that glyphosate translocates in a similar fashion as photosynthates (Crafts 1961, Robertson and Kirkwood 1970), we were able to indirectly estimate glyphosate basipetal translocation rates in the field. We compared slopes of TNC pools between mowed and unmowed areas at both sites throughout the season. By performing ANCOVA during the accumulation phase of growth and assuming that the relationship between time and TNC pool is linear during the accumulation phase, we tested whether the slopes differed between mowed and unmowed treatments. For both sites, the treatment * date interaction was not significant, thus slopes were not different and translocation rates were not increased due to mowing (Table 5). These data show that seasonal translocation patterns were not affected by mowing. Therefore, increased translocation rates into roots do not appear to be a mechanism for enhanced control.

TNC accumulation rates were much lower when unmowed plants were at the flower bud stage compared to plants that had been previously mowed. Glyphosate applications to mowed plants were not made until plants resprout and this delay (48-59 days in deposition experiments) allows synchronization of optimal basal foliage deposition of glyphosate and maximal below ground translocation rates. This synchronization did not occur in treatments to unmowed plants at the flower bud stage. As is evident in the ^{14}C-glyphosate treatment to fruiting plants, little herbicide accumulated in roots even when applications were made to plants with maximal below ground translocation rates (fruiting stage). The limited deposition of herbicide throughout the canopy and strong above ground sinks most likely account for poor translocation to roots.

Based on our findings, mowing enhances the effectiveness of glyphosate for control of perennial pepperweed due to several factors. First, mowing changes the canopy architecture of perennial pepperweed, removing nearly all of the above ground sinks and allowing the majority of glyphosate to be deposited onto resprouted basal leaves. Second, these basal leaves absorb more glyphosate and translocate more glyphosate to the roots compared to leaves in the top third of the canopy of unmowed plants. Finally, applications to plants in mowed areas are synchronized for both maximal seasonal translocation into roots and optimum deposition. It appears that all of these factors contribute to the enhanced effectiveness with glyphosate, and would likely improve control with other systemic herbicides in dense, tall, closed-canopy infestations. Our results demonstrate that location and timing of glyphosate applications can dramatically affect the accumulation of glyphosate in roots and enhance control when applied at the proper timing.

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Table 1. Leaf area (cm^2/m^2) data for both sites under various mowing regimes.

Site	Mowing	Stage when sampled	Days after mowing	**Leaf area (cm^2/m^2)**[a] Basal 1/3rd	Middle 1/3rd	Top 1/3rd	Total
Colusa	Not mowed	flower bud	-	83 de	334 a	1096 a	1512 a
		full flower	-	117 cde	242 a	324 bc	682 b
		fruiting	-	59 e	53 b	157 b	268 de
	Flower-bud	rosette	31	410 a	-	-	410 bc
		flower bud	58	263 b	79 b	51 bc	393 bc
		fruiting	99	158 cd	25 bc	31 c	214 e
	Full flower	rosette	32	208 bc	-	-	208 e
		flower bud	54	394 a	-	-	394 bc
		fruiting	88	374 a	4 c	2 d	381 cd
Woodland	Not mowed	flower bud	-	331 b	367 a	961 a	1658 a
		full flower	-	244 b	426 a	469 a	1140 b
		fruiting	-	304 b	229 ab	525 a	1058 bc
	Flower-bud	rosette	29	721 a	-	-	721 cd
		flower bud	48	845 a	93 cd	41 bc	978 bcd
		fruiting	83	442 b	130 bc	80 b	652 d
	Full flower	rosette	24	335 b	-	-	335 e
		flower bud	59	936 a	31 e	13 d	980 bcd
		fruiting	87	960 a	38 de	18 cd	1016 bc

[a] Data from within each column at each site were statistically analyzed and different letters indicate significant differences ($p<0.05$).

Table 2. Percent dye recovered for both sites under various mowing regimes.

				% of dye recovered[a]			
Site	Mowing	Stage when sampled	Days after mowing	Basal 1/3rd	Middle 1/3rd	Top 1/3rd	Total
Colusa	Not mowed	flower bud	-	4 d	14 a	98 a	116 a
		full flower	-	2 d	6 b	58 b	66 b
		fruiting	-	3 d	8 b	49 b	60 bc
	Flower bud	rosette	31	34 a	-	-	34 de
		flower bud	58	21 bc	5 bc	11 cd	38 d
		fruiting	99	18 c	5 bc	21 c	44 cd
	Full flower	rosette	32	21 c	-	-	21 e
		flower bud	54	33 a	-	-	33 de
		fruiting	88	30 ab	1 c	1 d	31 de
Woodland	Not mowed	flower bud	-	6 c	13 a	42 b	60 b
		full flower	-	5 c	12 ab	54 ab	71 ab
		fruiting	-	6 c	10 abc	83 a	99 a
	Flower bud	rosette	29	57 a	-	-	57 b
		flower bud	48	55 a	4 cd	6 c	65 ab
		fruiting	83	26 b	14 a	25 bc	65 ab
	Full flower	rosette	24	27 b	-	-	27 c
		flower bud	59	65 a	2 d	0 c	66 ab
		fruiting	87	70 a	6 bcd	4 c	80 ab

[a] Data from within each column at each site were statistically analyzed and different letters indicate significant differences ($p<0.05$).

Table 3: Percent ^{14}C-glyphosate recovered in various tissue of perennial pepperweed 48 hours after labeling.[a]

Tissue	% ^{14}C-glyphosate[b] Not mowed flower bud	Mowed rosette	Not mowed fruit
TOTAL ABSORPTION	**10.2 AB**	**14.4 B**	**9.1 A**
TREATED LEAVES	**3.2 B**	**6.9 AB**	**7.9 A**
TOTAL ABOVE GROUND[c][d]	**7.0 A**	**0.8 B**	**0.6 B**
Flower buds/ flowers/ fruits[e]	4.23 ± 1.88	-	0.12 ± 0.11
Leaves and stems above lowest labeled leaf[e]	2.00 ± 0.35	-	0.12 ± 0.04
Leaves below labeled area[e]	0.01 ± 0.01	-	0.08 ± 0.03
Stems below labeled area[e]	0.78 ± 0.43	-	0.24 ± 0.04
TOTAL BELOW GROUND[d]	**0.04 B**	**6.7 A**	**0.7 B**
Parent root[e]	0.01 ± 0.00	1.89 ± 0.50	0.22 ± 0.04
Large new roots[e]	0.01 ± 0.01	2.15 ± 1.38	0.19 ± 0.07
Fine roots[e]	0.03 ± 0.03	3.37 ± 1.01	0.38 ± 0.11

[a] Percent recovery of ^{14}C-glyphosate was 70.9%. Percentages were not statistically different ($p<0.05$) among treatments.
[b] Average values ± standard errors.
[c] Excluding treated leaves.
[d] Calculated by summing components for each replication then averaging all replications.
[e] Calculated by averaging each value for all replications.

Table 4. Comparison of below ground TNC pools just prior to mowing 7 and 19 days after mowing.

		TNC pools (g TNC/m^2)[a]		
Site	Days after mowing	Not mowed	Mowed	T-test[b]
Yolo bypass	7	86.7	97.3	NS
Putah creek	19	255	254	NS

[a] Values are averaged between 4 blocks and not smoothed as in Figures 3 and 4.

[b] Values were considered significantly different utilizing $p \leq 0.05$.

Table 5. ANCOVA table testing if significant differences between slopes of mowed and unmowed TNC pool curves during the accumulation phase from Figures 3 and 4.

Site	Factor	DF	MS	F	P
Yolo Bypass[a]	Block	1	244181	2.5	0.0559
	TNC pool	1	162747	1.72	0.194
	Time	1	8581350	90.71	<0.0001
	TNC pool x time	**1**	**146653**	**1.55**	**NS (0.2221)**
	Error	32	94602	-	-
Putah Creek[b]	Block	1	936345	6.05	0.0013
	TNC pool	1	18141	0.07	0.7907
	Time	1	2775040	10.96	0.0024
	TNC pool x time	**1**	**332804**	**0.01**	**NS (0.9409)**
	Error	27	154827	-	-

[a] dates were 166 – 243 Julian days for the accumulation phase at the Yolo Bypass.

[b] dates were 167 – 266 Julian days for the accumulation phase at Putah Creek.

Figure 1. Leaf area and percent dye recovered on foliage of perennial pepperweed at the Colusa site. All treatments were applied when plants were at or resprouted to the flower bud stage. Different letters indicate significant differences between curves ($p < 0.01$)

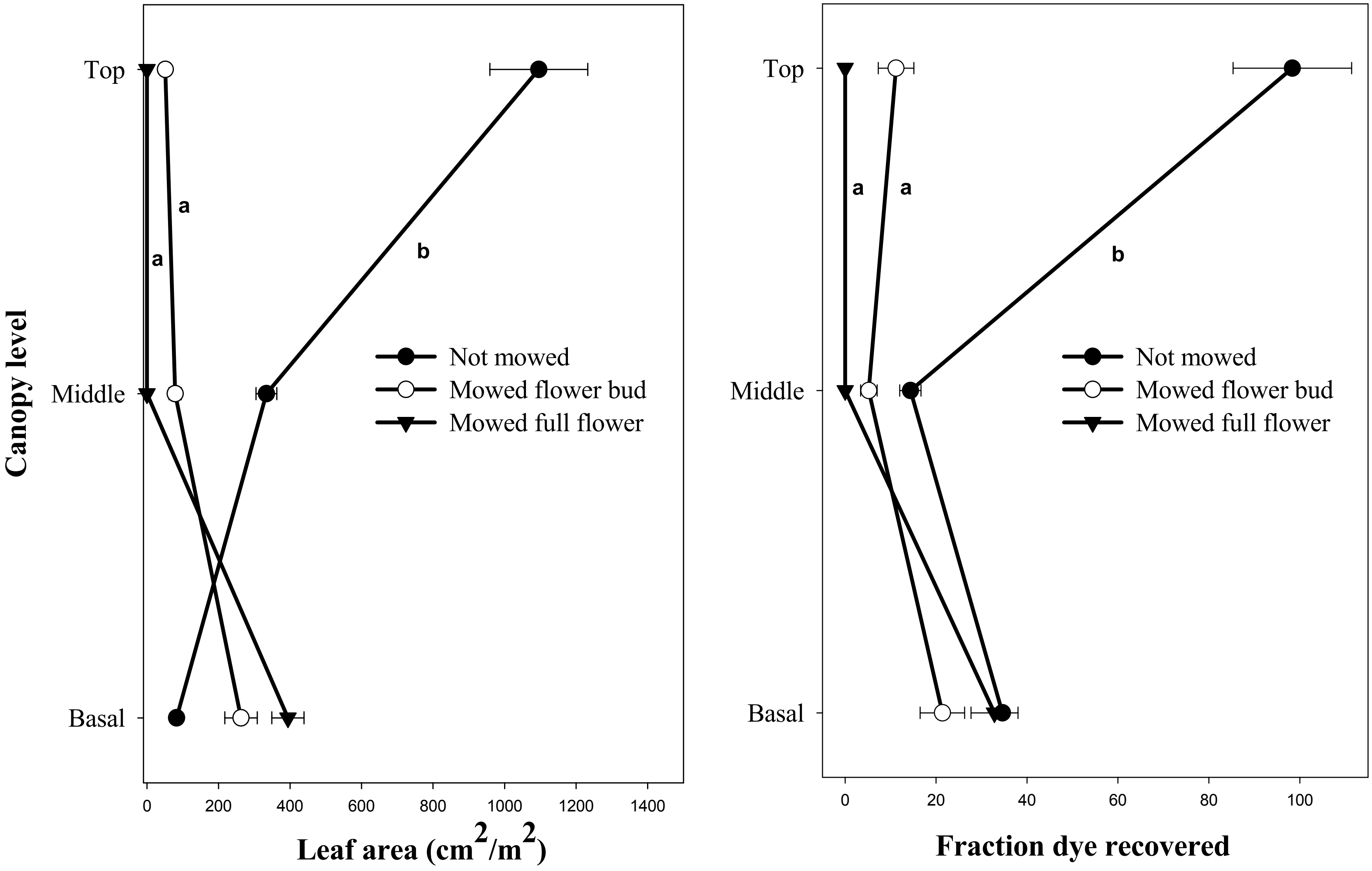


Figure 2. Leaf area and percent dye recovered on foliage of perennial pepperweed at the Woodland site. All treatments were applied when plants were at or resprouted to the flower bud stage. Different letters indicate significant differences between curves ($p < 0.01$)

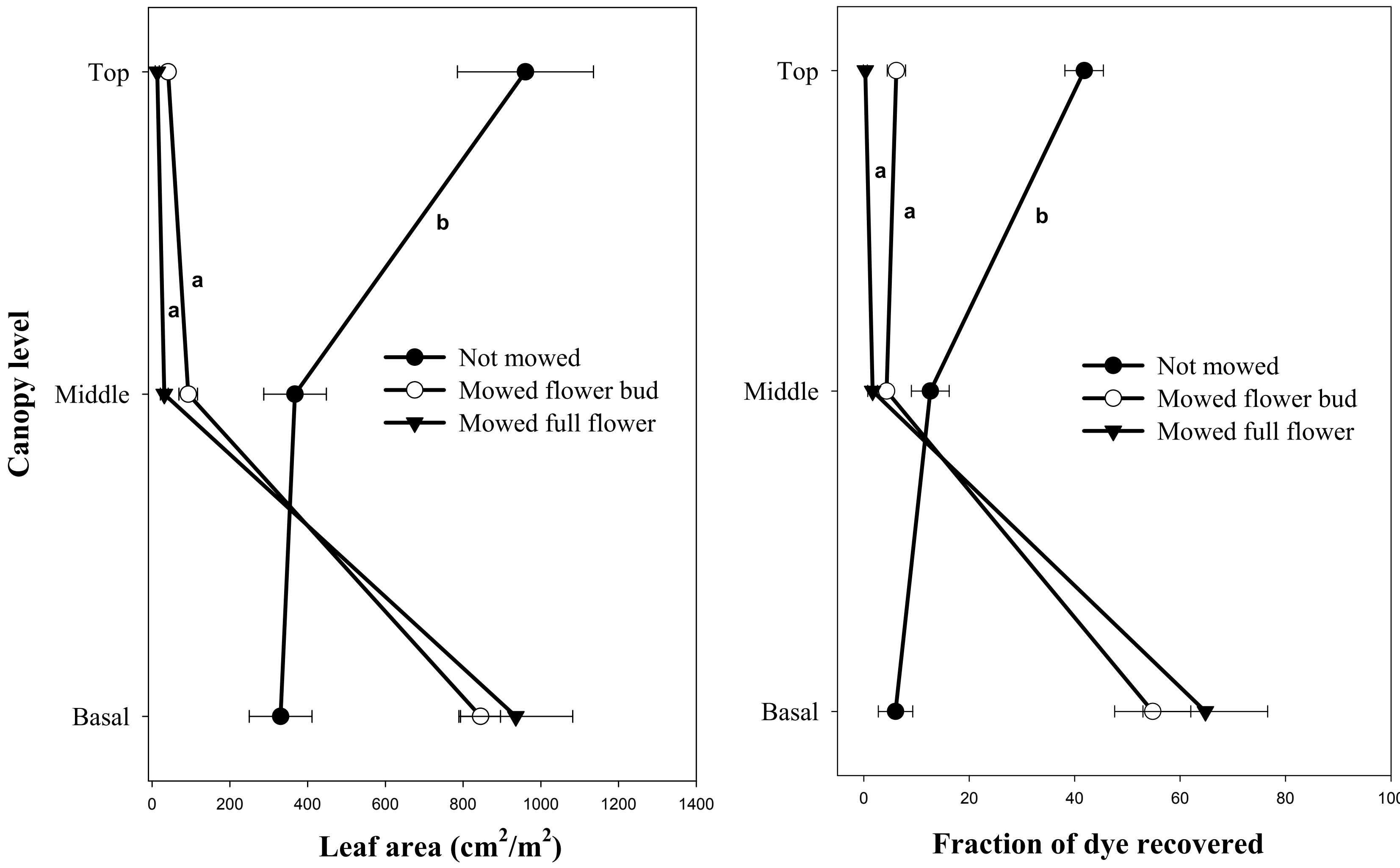
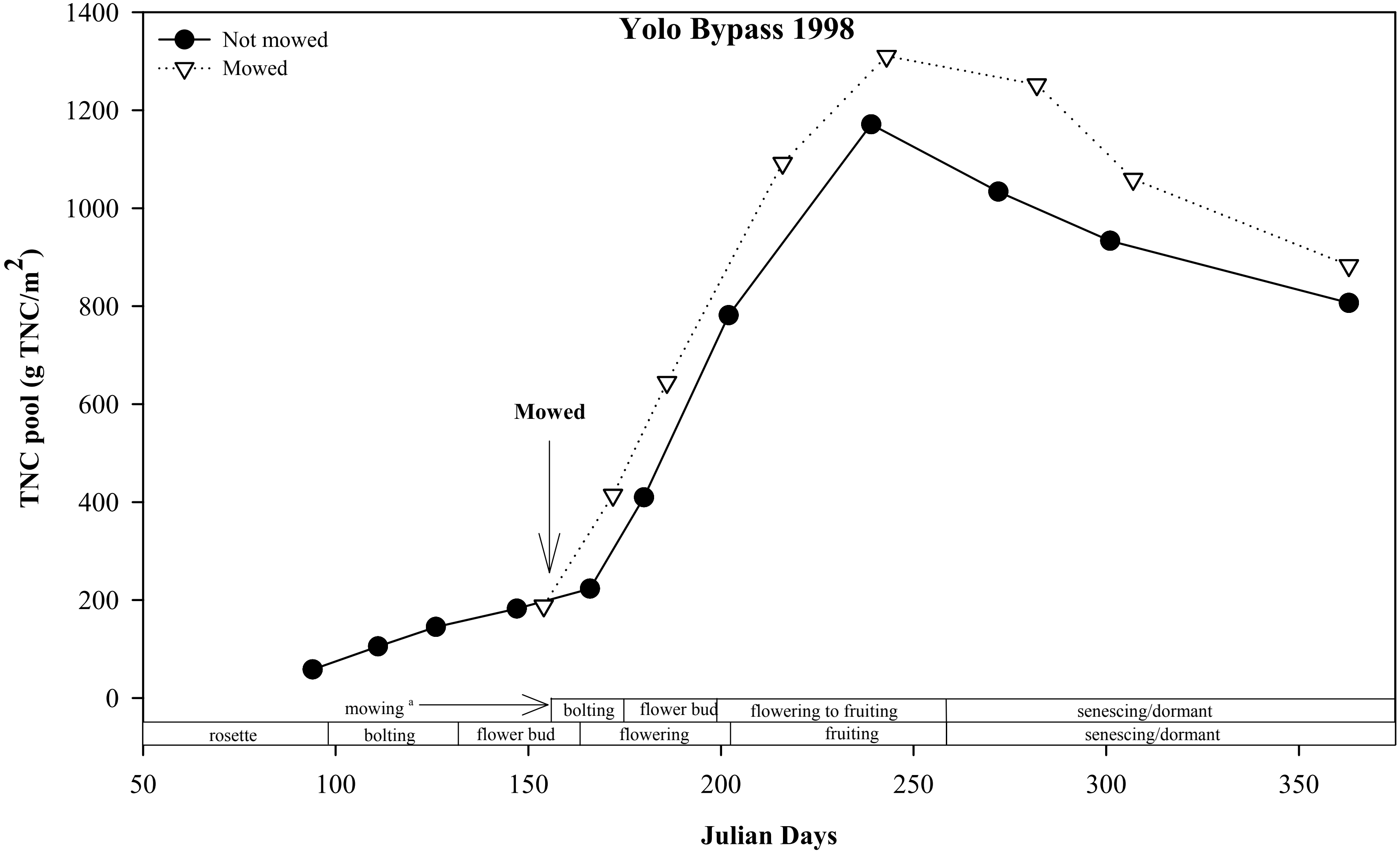
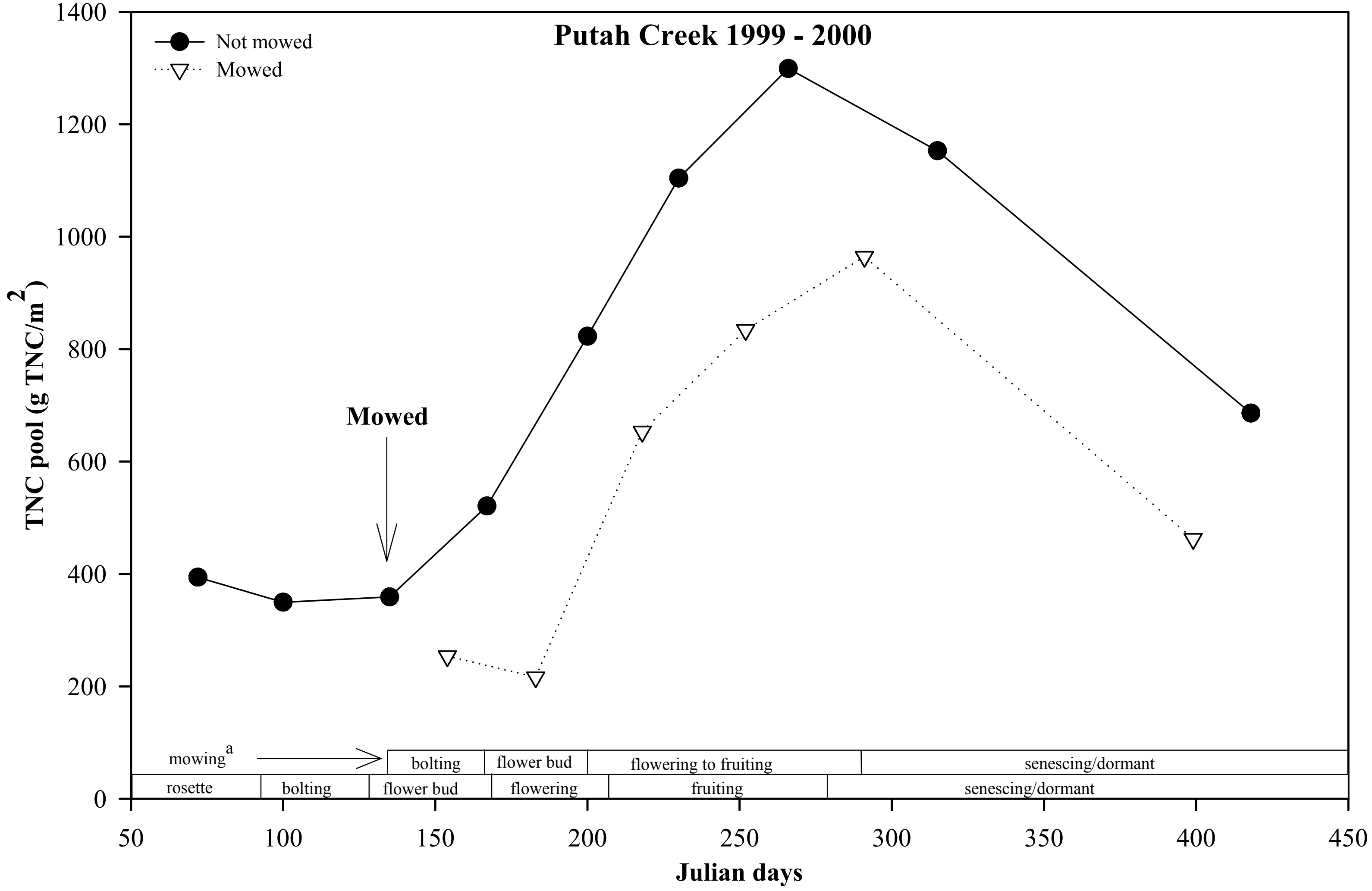


Figure 3. The effect of mowing on the accumulation of TNC in roots within the top 40 cm of the soil at the Yolo Bypass in 1998. Each curve was smoothed utilizing a locally weighted regression function (LOWESS) which utilized 40 % of the total points to smooth curve.



[a] As a result of mowing, all plots had at least 50% of resprouted shoots remain rosettes until senescence in the fall.

Figure 4. The effect of mowing on the accumulation of TNC in roots within the top 40 cm of the soil at Putah Creek in 1999 - 2000. Each curve was smoothed utilizing a locally weighted regression function (LOWESS) which utilized 40% of the total points to smooth curve.



[a] As a result of mowing, all plots had at least 50% of resprouted shoots remain rosettes until senescence in the fall.

CHAPTER 3

Management of perennial pepperweed (*Lepidium latifolium* L.) and a comparison of the effects of control methods on resident plant populations within dense and establishing infestations

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ABSTRACT

This study examined an integrated approach for managing perennial pepperweed in sensitive habitats near water by combining mowing with subsequent systemic herbicide treatment to resprouted plants. The experiment was conducted within the Sacramento flood plain in Yolo County, California. Two perennial pepperweed infested sites were studied, one a dense monospecific stand, and the other a sporadic, establishing population. Mowing enhanced the effectiveness of herbicides in reducing perennial pepperweed biomass one year after treatments in the dense infestation, but not in the establishing infestation. In the dense infestation, chlorsulfuron at 0.052 or 0.104 kg ai/ha with or without mowing and glyphosate at 3.33 kg ae/ha in combination with a previous mowing treatment were the only methods that provided > 80% reduction in perennial pepperweed biomass. In contrast, perennial pepperweed biomass in the establishing infestation was significantly reduced by 93, 78 and 76 % with applications of glyphosate at 3.33 kg ae/ha, 2,4-D at 2.11 kg ae/ha, and chlorsulfuron at 0.104 kg ai/ha, respectively. Integrating mowing at this site provided no additional advantage. Following control, reestablishment of resident plant species was limited in the dense infestation, but extensive in the establishing perennial pepperweed site. Response of annual dicot, annual grass and perennial plant cover varied considerably between sites and herbicide treatments. In general, annual dicot and perennial species cover increased to a greater degree in the low density perennial pepperweed site compared to the high density site, whereas non-native annual grass cover increased significantly at both sites. These results indicate successful control of dense stands of perennial pepperweed in a seasonal

floodplain may require an integrated approach using both mechanical and chemical methods, but chemical control options may be sufficient in less dense or establishing infestations. In addition, recovery of resident plant populations is increased when management programs are initiated before perennial pepperweed infestations become dense monospecific stands.

INTRODUCTION

Perennial pepperweed has been spreading rapidly throughout a wide range of habitats in the west (Young et al. 1995). Effective control of perennial pepperweed has been demonstrated in dense infestations (perennial pepperweed cover > 85%) with chlorsulfuron at 0.104 kg ai/ha (Young et al. 1998) and mowing in combination with glyphosate at 3.33 kg ae/ha (Chapter 1). No research has been conducted on the effectiveness of these methods on lower density infestations.

Density of infestations can influence the effectiveness of weed management techniques. Dieleman et al. (1999) found that the number of surviving individuals with various management methods was dependent upon initial plant density. While this research was conducted on two annual dicot species (*Abutilon theophrasti* and *Helianthus annuus* L.), the same premise may apply to perennial plants, the greater the initial plant density, the less herbicide will accumulate within individual plants. If sublethal amounts of herbicide accumulate in individual plants, poor control will result (Hoffman and Lavy 1981, Winkle et al. 1981).

Unlike dense stands of perennial pepperweed, establishing infestations have less developed roots, a more open canopy architecture, and lack a thick thatch layer from previous years' stems. These differences between dense and establishing infestations may eliminate the need to incorporate mowing with herbicides to attain adequate control of perennial pepperweed. When stem densities are low, the canopy is more open, with leaves present throughout the canopy. In contrast, when stem densities are high, the canopy is closed, resulting in significantly less leaf area in the lower two-thirds of the canopy (Chapter 2). Previous research has demonstrated that the location of herbicide deposition is an important factor in the enhanced effect of mowing combined with glyphosate or chlorsulfuron (Chapter 2). Mowing dramatically altered canopy architecture and increased herbicide deposition on basal leaves of shoots resprouting after mowing, whereas herbicide applied to dense unmowed infestations was primarily deposited in the top third of the canopy (Chapter 2). Furthermore, the number of above ground sinks was dramatically reduced in resprouting stems. This reduction in sink strength of above ground tissue can increase herbicide accumulation in perennial roots (Chapter 2). Although establishing infestations have many above ground sinks, the canopy architecture is more open with many basal leaves present. We hypothesized that herbicide deposition will be much greater in open, establishing infestations compared to dense infestations. Since location of herbicide deposition can dramatically affect accumulation, translocation and efficacy of systemic herbicides (Chapter 2), we tested whether incorporating mowing with various herbicide treatments was necessary to attain adequate control in establishing infestations of perennial pepperweed.

Few weed management experiments provide information that link weed control to restoration. A better understanding of the reestablishment of resident plant populations from specific treatments can assist in the selection of the most appropriate management techniques for a particular area. Consequently, an additional objective of this study was to compare the recovery of resident plant populations following several management methods, including those that incorporate mowing and herbicides, in dense and establishing infestations of perennial pepperweed.

MATERIALS AND METHODS

Experiments were conducted at two sites in Yolo County, California (Davis and Woodland) approximately 17 km apart within the seasonal floodplain of the Sacramento River. Sites were very similar except for perennial pepperweed infestations (Table 1).

Experiments were established as a split plot design with four blocks. Mowing was the main plot factor and herbicide treatment the sub-plot factor. Applications were made in 1998 and 1999 at the Davis and Woodland sites, respectively (Table 2), as previously described (Chapter 1). In brief, plots were 3 meters wide and 9 meters long and were either mowed or treated with the appropriate herbicide when plants reached the flowerbud stage. In mowed areas, perennial pepperweed was allowed to resprout and herbicide treatments were made when bolted shoots resprouted to the flowerbud stage. Herbicide treatments (see Tables 3-6 for herbicide rates) were applied in a three meter wide swath with a $C0_2$ propelled backpack sprayer, at 310 kPa of pressure, set to deliver 382 L/ha through 8004 nozzles.

Perennial pepperweed biomass was determined at both sites one year following treatments. At the Woodland site, perennial pepperweed biomass was measured within one 0.25 m^2 quadrat per plot. Due to the heterogeneity of perennial pepperweed at the Davis site, three 0.25 m^2 quadrats were utilized to estimate perennial pepperweed biomass per plot. The quadrats were randomly placed within plots and perennial pepperweed shoots were cut at the soil surface within the quadrats, dried, and weighed.

Relative plant cover was visually estimated for two summers following treatments (Table 2). Three randomly located sub-samples were taken within each plot with a 0.25 m^2 quadrat to estimate relative resident plant cover. For ease of interpretation, cover was grouped into the following three life history classes: annual dicots, annual grasses and herbaceous perennials (excluding perennial pepperweed). Plant cover was also divided into native and non-native cover classes, and number of species/m^2 (species richness/m^2) was calculated from these data.

Biomass data from the Woodland site has been previously reported (Chapter 1). The close proximity of the two sites allowed comparisons of the effectiveness of mowing in combination with herbicides in controlling dense and establishing infestations of perennial pepperweed and the resulting affects on resident plant recovery.

Statistics

Due to highly significant differences between sites ($p < 0.01$), each site was analyzed separately. At each site, individual analyses of variance (ANOVA) were performed on biomass, total plant species cover and species richness (Appendices A, B and I respectively). Normality and homogeneity of variance was checked prior to all analyses and appropriate transformations were made as necessary. All data are presented untransformed. If significant differences were found, a Fisher's protected LSD ($p < 0.05$) was performed to test differences among means.

Life history and native/non-native cover classes were also analyzed separately for each site. Due to the correlation between dependant variables, classes were initially analyzed utilizing a multivariate analysis of variance (MANOVA) (Scheiner 1993)(Appendices C, F). If significant differences were found, a protected ANOVA was performed on each cover class followed by a Fisher's protected LSD ($p < 0.05$) to test the difference among means. While many interactions were significant from ANOVAs performed (Appendices D, E, G, H), we present only significant interactions of importance to management and restoration of perennial pepperweed infested areas.

RESULTS AND DISCUSSION

Perennial pepperweed control

Perennial pepperweed infestations varied dramatically between the two sites (Table 1). The Woodland site infestation had a very high shoot density with a closed canopy, whereas the Davis infestation had a low shoot density and an open canopy. While biomass of perennial pepperweed was not significantly altered one year after the mowing only treatment at the Woodland site, there was nearly a three-fold increase in biomass following mowing at the Davis site (Table 3). Previous research at other sites with dense infestations indicate that mowing alone either reduces or has no significant impact on biomass of perennial pepperweed one year after treatment (Chapter 1). Thus, mowing in an establishing infestation may give a competitive advantage to perennial pepperweed in a floodplain system and lead to increased biomass and expansion rates the following year.

When pooling all herbicide treatments at the Woodland site, mowing in combination with herbicides reduced perennial pepperweed biomass compared to herbicide treatments alone (Figure 1). While specific herbicides had varying levels of success, chlorsulfuron at 0.052 or 0.104 kg ai/ha was most successful in reducing perennial pepperweed biomass ($\geq$ 99% reduction) with or without an initial mowing treatment (Table 3). However, incorporating mowing dramatically improved the effectiveness of glyphosate at 3.33 kg ae/ha on perennial pepperweed control. Without mowing, 3.33 kg ae/ha of glyphosate increased the biomass of perennial pepperweed by 20% the following year. By comparison, incorporating mowing reduced perennial pepperweed biomass 73% compared to untreated mowed plots, and 81% compared to untreated unmowed plots. Triclopyr at 2.52 kg ae/ha, 2,4-D at 2.11 kg ae/ha, or glyphosate at 1.67 kg ae/ha did not significantly reduce perennial pepperweed biomass at the Woodland site.

When pooling all herbicides at the Davis site, mowing did not improve the effectiveness of herbicides in controlling perennial pepperweed (Figure 1). Perennial pepperweed biomass was significantly reduced 93, 78 and 76 % with applications of glyphosate at 3.33 kg ae/ha, 2,4-D at 2.11 kg ae/ha, or chlorsulfuron at 0.104 kg ai/ha, respectively, in unmowed treatments (Table 3). While the overall effect of mowing was not significant, control of perennial pepperweed biomass with chlorsulfuron at 0.052 kg ai/ha significantly improved from 7 to 97% when mowing was incorporated. Glyphosate at 1.67 kg ae/ha also reduced biomass by 40% without mowing and 81% with mowing, although the latter was not statistically significant. Only glyphosate at 3.33 kg ae/ha, 2,4-D at 2.11 kg ae/ha and chlorsulfuron at 0.104 kg ai/ha provided satisfactory control of perennial pepperweed in establishing infestations without the need for incorporating mowing.

Our previous research showed that the location of herbicide deposition may account for the enhanced effectiveness of herbicides following mowing (Chapter 2). Canopy cover can dramatically influence the location of herbicide deposition and may explain the different response between the high and low density site. Previous research showed that in dense unmowed infestations the majority of herbicide is deposited in the top third of the canopy (Chapter 2). In contrast, the canopy architecture at the low density Davis site was more open with many basal leaves present. Thus, we believe that much greater herbicide deposition occurred in the lower canopy of the establishing infestation compared to the dense infestation. The location of herbicide deposition in combination with a less developed perennial root system may have accounted for the enhanced effectiveness of herbicides, in the absence of mowing, in the establishing infestation.

Resident plant population response

Response of resident plant populations to perennial pepperweed management techniques was highly variable at both sites. Total plant cover increased from one to two years after treatments at the Woodland site, but decreased at the Davis site (Figure 2). Yearly environmental fluctuations such as timing of and total precipitation can dramatically affect plant cover within this system and may account for this difference. Many other factors could also be involved. Total plant cover had significant year*mowing and year*herbicide interactions at both sites and herbicide and year*mowing*herbicide interactions at the Davis site (Appendix B). Total plant cover response to mowing and herbicide treatments averaged over both years (Table 3) explains some of the relationship between vegetative cover and the effectiveness of control methods on perennial pepperweed.

At the Woodland site, the combination of mowing and herbicide applications that significantly reduced perennial pepperweed biomass (chlorsulfuron at 0.052 and 0.104 kg ai/ha with and without mowing and glyphosate at 3.33 kg ae/ha with mowing) also resulted in significant reductions in total plant cover (Table 3). In comparison, total plant cover in unsuccessful treatments was not different compared to untreated controls. In contrast, there were no differences in vegetative cover among all treatments at the Davis site (Table 3). This suggests that resident plant species in the establishing, but not dense infestation, were able to recover and reoccupy areas previously infested with perennial pepperweed. There are several hypotheses as to why resident vegetation did not effectively reestablish in the dense infestations. Resident plant seedbanks in the dense stands may have become depleted from a lack of replenishment over many years of perennial pepperweed infestation. Dense infestations also accumulate a thick thatch layer on the soil surface consisting of stems from the previous year's growth. This thatch layer can remain intact even after control techniques are conducted, preventing the reestablishment of resident plants. Allelochemicals or salts may also be released and accumulate in the upper soil profile. This could prevent germination and growth of resident plants.

Life history classes had a significant year interaction at both sites (Appendix C). Annual grass cover increased approximately three to four-fold from one to two years after treatments at both sites, while annual dicot cover was reduced by 50% at the Davis site (Tables 4, 5; Figure 3). Reduction in annual dicot cover may be due to yearly environmental fluctuations, as the predominant annual dicot, *Plagiobothrys stipitatus* (popcorn flower), appears to have a high degree of variability in its relative cover from year to year within this floodplain system (personal observation).

Although year*mowing and mowing*herbicide interactions were significant for the life history classes at both sites (Appendix C), only the herbicide effects on cover, averaged over mowing treatments, are presented. At each site, herbicide treatments significantly affected cover of one or more life history classes one and two years after treatment (Figure 3). At the Woodland site, even after two years, very few resident plants other than perennial pepperweed were present in the untreated plots one and two years after treatments (< 2 % cover for each class) (Table 3). Annual dicot cover was significantly increased with 2,4-D at 2.11 kg ae/ha and glyphosate at 3.33 kg ae/ha one year after treatment, but after two years little to no annual dicots were present in all treated plots. Thus, annual dicots were unable to reestablish in the dense infestation even after successful control of perennial pepperweed. Annual grass recruitment also was limited in the first year after treatment. After two years, however, annual grass cover was significantly higher when treated with 0.052 kg ai/ha of chlorsulfuron compared to untreated controls. Although not significant, chlorsulfuron at 0.104 kg ai/ha also increased annual grass cover. Similar results on perennial plant cover were obtained with chlorsulfuron at 0.052 kg and 0.104 kg ai/ha one and two years after treatments. The increase in perennial species cover was primarily due to the expansion of *Cynodon dactylon* L. (bermudagrass) and *Rumex crispus* L. (curly dock).

At the lower density Davis site, resident plants occupied a much higher percentage of the area compared to the Woodland site (8 – 35 % cover for each class one and two years after treatments) (Table 5). Annual dicot cover significantly increased with all herbicide treatments except chlorsulfuron at 0.104 kg ai/ha one year after application. After two years, annual dicot cover remained significantly higher in chlorsulfuron at 0.052 kg ai/ha and glyphosate at 3.33 kg ae/ha treated plots. Annual grass cover was significantly higher one year after chlorsulfuron (0.104 kg ai/ha) treatment. After two years, however, 2,4-D at 2.11 kg ae/ha and triclopyr at 2.52 kg ae/ha had greater annual grass cover compared to untreated controls. Members of the Asteraceae (predominately *Grindelia camporum* and *Hemizonia parryi*) were the predominant perennial species at the Davis site. These species were sensitive to all herbicide treatments and were significantly reduced compared to untreated controls in all treatments except chlorsulfuron at 0.104 kg ai/ha both one and two years after treatment and chlorsulfuron at 0.052 kg ai/ha two years after treatment (data not shown).

Although the response of life history classes to specific herbicide treatments was dependant upon the susceptibility of individual species present at each site and year, overall results indicate that dense infestations had a limited degree of resident plant reestablishment. Both sites were in a seasonal floodplain that flooded both years, so ample seeds were likely deposited onto the soil surface. Furthermore, a dense perennial pepperweed infestation adjacent to the Woodland study site was disked the fall before treatments were initiated then mowed and treated with a systemic herbicide. Recovery of resident vegetation one and two years after treatment was similar (90 and 91% relative cover, respectively) to the low density infestation at the Davis site (unpublished results), providing further evidence that the resident seedbank was not limiting at the Woodland site. Mowing has the additional benefit of removing or fragmenting thatch from previous years' growth. This may facilitate a much faster breakdown of the thatch layer. Although all mowed tissues including thatch, were removed after the mowing treatments, limited reestablishment occurred in these plots. This indicates other mechanisms were likely responsible for the limited reestablishment of the resident vegetation.

Poor resident plant reestablishment after control methods have been performed has also been reported in soils infested with *Acroptilon repens* L. (Russian knapweed) (Bottoms and Whitson 1998, Benz et al. 1999). Researchers hypothesized that Russian knapweed released an allelochemical that suppressed resident plant growth. Several potential allelochemicals have been isolated from Russian knapweed tissue (Fletcher and Renny 1963). Other researchers have also found three to four-fold increases in zinc in the top 2 cm of the soil compared to uninfested areas (Bottoms et al. 2002). It is unknown whether soil zinc alone or in combination with other chemicals are responsible for the allelopathic response of Russian knapweed. However, if soils were disturbed in or after control of Russian knapweed, resident plants readily reestablished (Bottoms and Whitson 1998, Benz et al. 1999). Disturbing the soil surface in these infested areas is believed to dilute the concentration of these potentially phytotoxic compounds at the soil surface, facilitating recovery of the resident vegetation. Perennial pepperweed lifecycle and growth characteristics are similar to Russian knapweed. Blank and Young (1997) showed that perennial pepperweed acts as a salt pump and redistributes a large amount of mono and divalent cations from deep within the soil profile to the soil surface. A buildup of these cations at the soil surface may be involved in the possible inhibitory allelopathic response in resident plant species associated with perennial pepperweed infestations.

Response of native plants, non-native plants and species richness

At the Davis site, native plant cover was significantly reduced and the cover of non-native plants increased from one to two years after treatments (Figure 4). Although a similar trend occurred at the Woodland site, it was not statistically significant. At both sites, resident plant reestablishment was primarily due to increased cover of non-native species.

Native cover demonstrated significant year*mowing interactions at the Davis site, while non-native plant cover had significant year*mowing interactions at both sites (Appendix F). Cover of non-native plants also had a significant year*herbicide and mowing*herbicide interaction at the Woodland site (Appendix F). Data were pooled across years and mowing treatments to compare the affect of various herbicide treatments on native and non-native plant reestablishment within this floodplain.

Herbicide treatments significantly affected native plant cover at the Davis site, but no differences were detected at the Woodland site (Table 6). Only chlorsulfuron at 0.104 kg ai/ha increased native plant cover compared to untreated controls at the Davis site. In contrast, several herbicide treatments increased non-native plant cover at both sites, including chlorsulfuron at 0.052 and 0.104 kg ai/ha at the Woodland site and 2,4-D at 2.11 kg ae/ha and triclopyr at 2.52 kg ae/ha at the Davis site. Thus, under some situations, native plant cover can increase after control of perennial pepperweed. Native plant recovery depends upon the herbicide used and resident plant species present. In most cases, increased cover was due to non-native plants, particularly annual grasses. Treatments including 2,4-D, chlorsulfuron, and triclopyr, which typically do not injure grasses and were probably responsible for increased recovery of annual grasses.

Species richness was reduced from one year to two years after treatments at both sites (Figure 2). Competition between established plant species one year after treatments may have caused this reduction. Incorporating mowing into the management of perennial pepperweed also reduced species richness at the Davis site, but not at the Woodland site

(Figure 1), suggesting that some resident plant species at the Davis site were negatively affected by mowing, and had reduced coverage as a result.

Herbicide treatments caused significant differences in species richness at both sites (Appendix I). At the Woodland site, species richness was low overall. Treatment with chlorsulfuron at 0.052 kg ai/ha and 2,4-D at 2.11 kg ae/ha significantly increased species richness at this site, due to an increase in the number of annual grass species. At the Davis site, all treatments except chlorsulfuron at 0.052 kg ai/ha increased species richness compared to the untreated control.

These data provide evidence that site-specific factors, such as environmental variability and the specific species present can greatly influence species richness response as well as native and non-native plant recovery following chemical control of perennial pepperweed. Our results also emphasize the difficulty in establishing resident plants in a dense infestation, even when successful control of perennial pepperweed is obtained.

Conclusions

Mowing in combination with glyphosate and chlorsulfuron provided more effective control of perennial pepperweed in dense infestations, but did not improve the effectiveness of herbicides in enhancing control of establishing infestations. Resident plant species had limited reestablishment in the dense infestation, but recovered rapidly in the establishing infestations. Species richness was increased by most herbicide treatments, mainly of non-native taxa at both sites. If perennial pepperweed infestations can be managed before they become well established, more cost-effective control can be achieved, avoiding the need for an expensive revegetation program. This is particularly true if desirable plant species are present at the infested site.

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Table 1. Site and treatment information.

	Woodland	**Davis**
Coordinates	38° 40.63 N 121° 40.35 W	38° 31.85 N 121° 37.24 W
Soil type	Maria silty clay loam, flooded	Sacramento soils, flooded
Previous management	Seasonal flooding and biannual disking	Seasonal flooding
Perennial pepperweed biomass of untreated controls (g/m^2)	1192	45
Perennial pepperweed density of untreated controls (shoots/m^2)	170	26
Dominant vegetation present	*Lepidium latifolium*	*Lepidium latifolium,* *Grindelia camporum,* *Lolium multiflorum*
Precip. the year of applications (mm)	805.8	327.6
Precip. one year after applications (mm)	377.6	424.8
Precip. two year after applications (mm)	495.1	366.7
30 year average annual precip. (mm)	535.4	482.6

Annual precipitation was calculated starting July 1st of the previous year to June 30th of the current year.

Table 2: Dates of applications and measurements.

	Woodland	**Davis**
Mowing & herbicide treatments in unmowed plots	5/22/1998	5/26/99
Herbicide treatments in mowed plots	7/24/1998	7/22/99
Biomass measurement	7/30/1999	8/1/2000
Plant cover measurement one year after treatment	6/14/99	7/7/2000
Plant cover measurement two years after treatment	7/4/00	8/07/01

Table 3: Perennial pepperweed biomass one year after treatments and total plant cover averaged over two years.

			Perennial pepperweed[a]			
			Biomass (g/m^2)		**Total % plant cover**	
Mowing regime	**Herbicide**	**Rate**[b]	**Woodland**[c]	**Davis**	**Woodland**	**Davis**
Not mowed	2,4-D	2.11	677 cde	10 d	95 ab	88
	Glyphosate	1.67	1987 a	27 cd	91 ab	87
	Glyphosate	3.33	1426 ab	3 d	94 ab	81
	Chlorsulfuron	0.052	11 fg	42 bc	70 c	85
	Chlorsulfuron	0.104	0 g	11 d	39 d	82
	Triclopyr	2.52	781 cde	25 cd	95 ab	85
	Untreated	---	1192 bc	45 bc	100 a	88
Mowed FB	2,4-D	2.11	450 defg	44 bc	85 abc	85
	Glyphosate	1.67	721 cde	22 cd	77 bc	86
	Glyphosate	3.33	231 efg	14 d	68 c	86
	Chlorsulfuron	0.052	2 g	4 d	34 d	86
	Chlorsulfuron	0.104	0 g	3 d	41 d	88
	Triclopyr	2.52	570 def	67 b	92 ab	78
	Untreated	---	860 cd	118 a	97 ab	78
LSD			564	28	20	ns

[a] Letter indicates significant differences ($p<0.05$) of values within column only.

[b] kg ai or ae/ha.

[c] Data taken from Chapter 1.

Table 4: Effects of treatments on relative resident plant cover one and two years after treatments at the Woodland site.

			Percent cover[a]		
Years after treatment	**Herbicide**	**Rate[b]**	**Annual dicots**	**Annual Grasses**	**Perennials[c]**
One	2,4-D	2.11	8.6 ab	5.8 b	7.9 d
	Glyphosate	1.67	3.6 bcd	0.3 b	7.3 d
	Glyphosate	3.33	11.3 a	6.0 b	5.9 d
	Chlorsulfuron	0.052	0.1 cd	2.5 b	23.8 abc
	Chlorsulfuron	0.104	0.4 cd	6.0 b	11.9 bcd
	Triclopyr	2.52	5.5 bc	0.4 b	9.3 cd
	Untreated	---	1.9 cd	0.4 b	0.6 d
Two	2,4-D	2.11	0.0 d	3.8 b	4.2 d
	Glyphosate	1.67	0.0 d	0.6 b	0.2 d
	Glyphosate	3.33	0.0 d	3.8 b	0.5 d
	Chlorsulfuron	0.052	1.1 cd	31.9 a	25.4 ab
	Chlorsulfuron	0.104	0.0 d	12.6 b	32.1 a
	Triclopyr	2.52	0.0 d	0.8 b	1.0 d
	Untreated	---	0.0 d	0.0 b	0.0 d
LSD			5.4	13.8	15.2

[a] Because differences between mowed and unmowed plots were not significant, data were pooled.
[b] kg ai or ae/ha.
[c] Excluding perennial pepperweed.

Table 5: Effects of treatments on relative resident plant cover one and two years after treatments at the Davis site.

			Percent cover[a]					
Years after treatment	**Herbicide**	**Rate[b]**	**Annual dicots**		**Annual grasses**		**Perennials[c]**	
One	2,4-D	2.11	54.6	bc	13.5	e	9.2	cd
	Glyphosate	1.67	59.8	ab	8.5	e	10.0	cd
	Glyphosate	3.33	72.9	a	6.5	e	4.2	d
	Chlorsulfuron	0.052	41.3	cd	12.9	e	18.8	bc
	Chlorsulfuron	0.104	27.3	def	31.5	abc	21.9	abc
	Triclopyr	2.52	38.5	cde	15.6	de	12.5	cd
	Untreated	---	17.8	fg	11.9	e	34.7	a
Two	2,4-D	2.11	25.6	defg	38.3	ab	9.6	cd
	Glyphosate	1.67	21.4	efg	35.7	abc	14.0	cd
	Glyphosate	3.33	35.6	de	25.8	cd	10.8	cd
	Chlorsulfuron	0.052	21.5	efg	37.7	abc	15.4	bcd
	Chlorsulfuron	0.104	26.7	def	26.7	bcd	19.6	bc
	Triclopyr	2.52	16.9	fg	40.6	a	11.9	cd
	Untreated	---	8.1	g	26.3	cd	28.1	ab
LSD			17.7		11.9		12.9	

[a] Because differences between mowed and unmowed plots were not significant data were pooled.

[b] kg ai or ae/ha.

[c] Excluding perennial pepperweed

Table 6: Species richness and native and nonnative plant cover combined for one and two years after treatments at both sites.

		Native plant cover[a]		**Non-native plant cover**[a]		**# species/m^2** [a]	
Herbicide	**Rate**[b]	Woodland	Davis	Woodland	Davis	Woodland	Davis
2,4-D	2.11	4.3	41.2 bc	10.8 b	34.3 a	1.5 ab	10.0 ab
Glyphosate	1.67	1.8	44.5 abc	4.2 b	30.8 ab	0.8 bc	10.8 a
Glyphosate	3.33	5.7	52.0 ab	8.1 b	25.9 ab	1.1 abc	9.7 ab
Chlorsulfuron	0.052	1.7	45.9 ab	40.8 a	27.8 ab	2.0 a	8.1 cd
Chlorsulfuron	0.104	0.4	53.5 a	32.3 a	23.2 b	1.3 abc	8.6 bc
Triclopyr	2.52	2.8	33.2 c	5.8 b	34.5 a	1.1 abc	9.8 ab
Untreated	---	1.0	41.0 bc	0.6 b	22.4 b	0.5 c	7.1 d
LSD		ns	12.2	11.1	8.9	0.9	1.4

[a] Different letters indicates significant differences ($p<0.05$) of values within column only
[b] kg ai or ae

Figure 1. Effects of herbicide treatments with or without mowing on the biomass of perennial pepperweed one year after treatments and species richness averaged over both years.
(*** indicates significant differences ($p<0.05$) between bars)

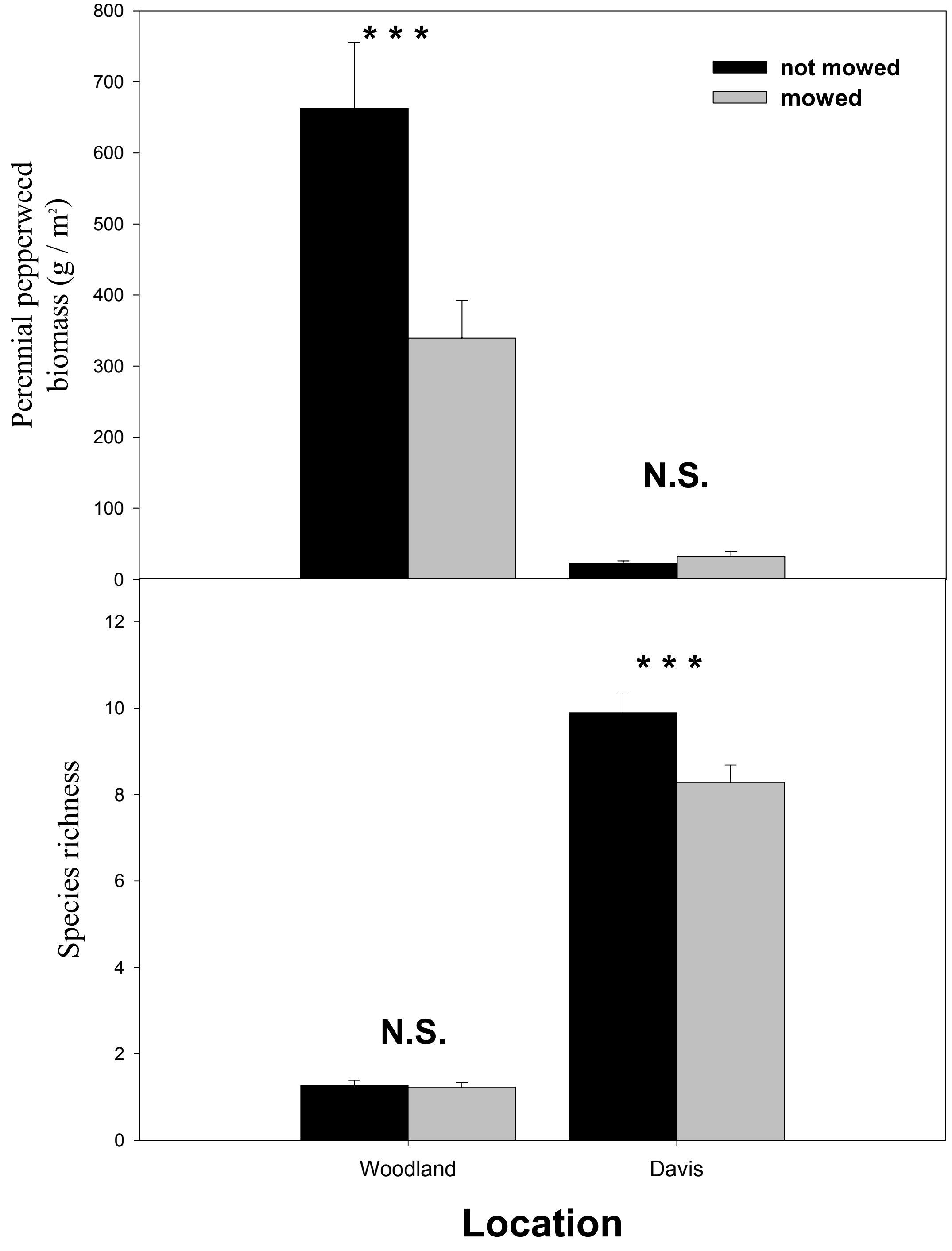


Figure 2. Effect of time after treatment on plant cover and species richness.
(*** indicates significant differences (p<0.05) between bars)

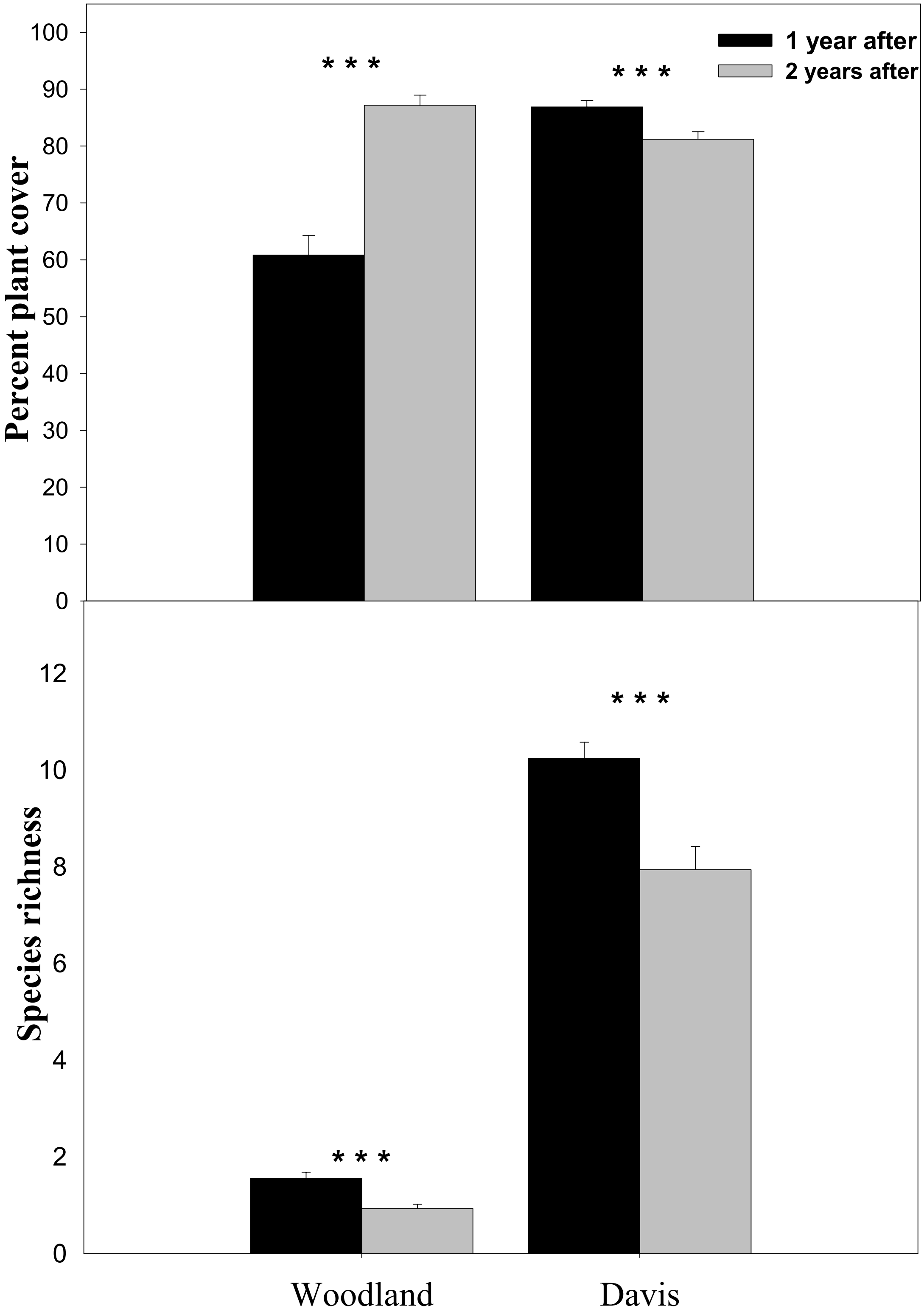


Figure 3. Response of life history classes 1 and 2 years after treatments. Data pooled across all treatments within each year.
(*** indicates significant differences (p<0.05) between bars)

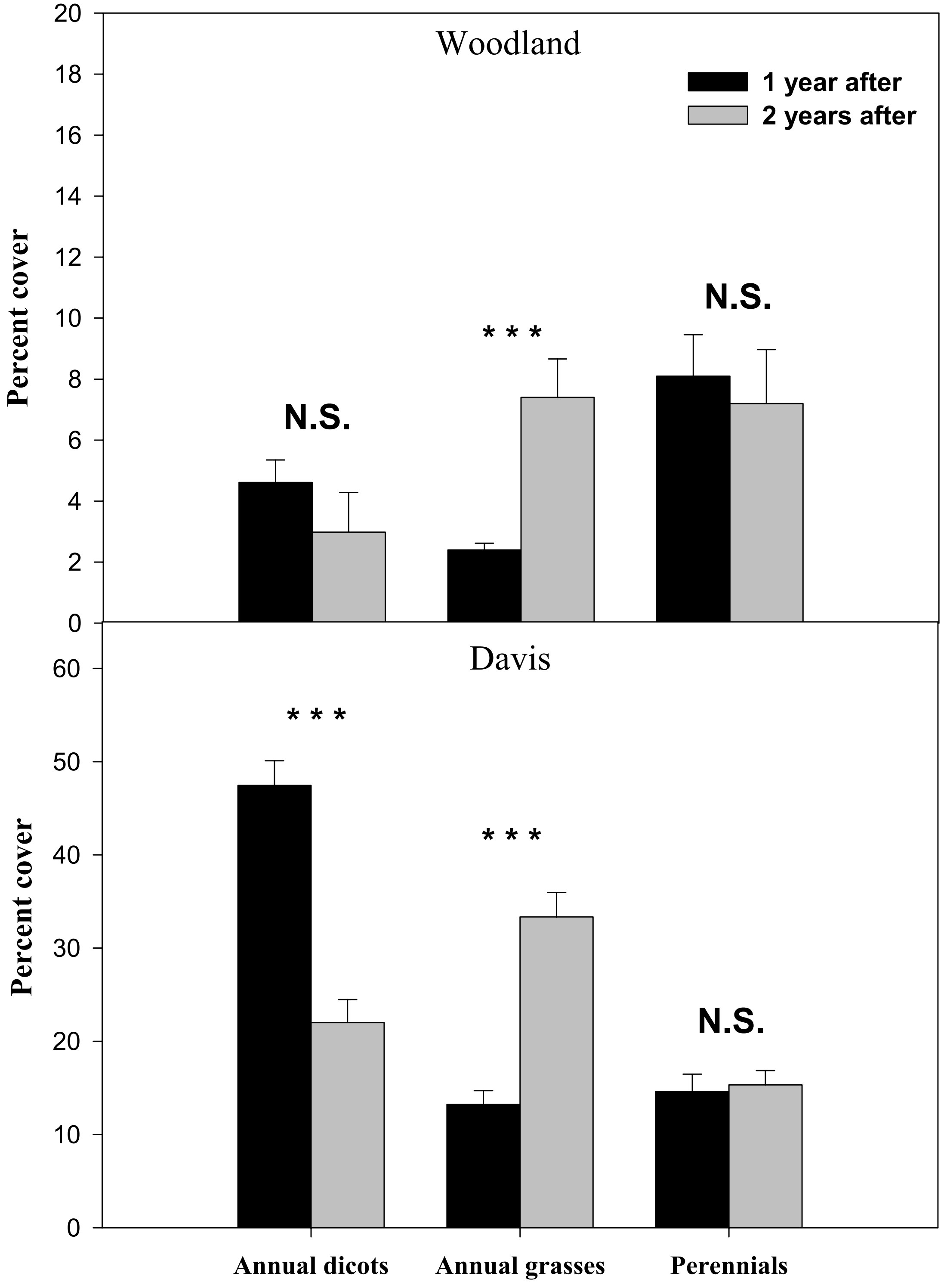
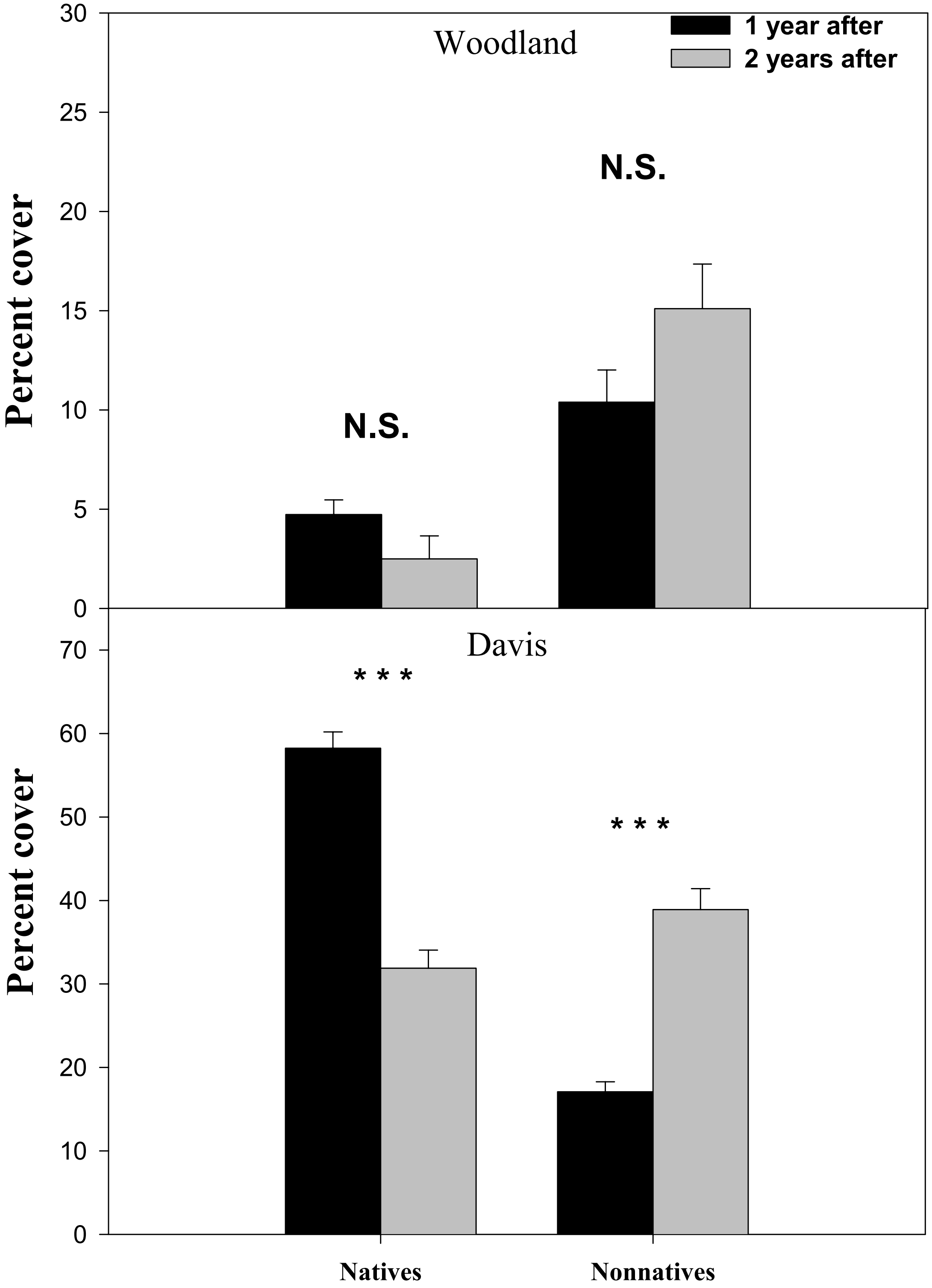


Figure 4. Response of native and non-native plants 1 and 2 years after treatments. Data pooled across all treatments within each year. (*** indicates significant differences (p<0.05) between bars)



CHAPTER 4

Spread of perennial pepperweed within seasonal wetlands in three bioregions in California

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ABSTRACT

Perennial pepperweed is an invasive weed expanding rapidly throughout the western United States. In California it has become extremely aggressive in seasonal wetlands degrading habitat quality and productivity. The objectives of this study were to determine the rate of spread of perennial pepperweed at three locations in California. Research was conducted at the Colusa National Wildlife Refuge, Grizzly Island Wildlife Area, and the Lower Klamath National Wildlife Refuge each representing different bioregions of California. Undisturbed infestations spread clonally 1-2 meters per year along the leading edge. Initial size and area of infestations were found to influence the rate of spread, with infestations with a small area and large perimeter expanding at the greatest rate. Rosette and stem density was also found to vary, with the center of infestations having higher densities compared to the leading edge. Similar rates of expansion were observed in all undisturbed plots at Colusa and Grizzly Island with populations expanding from 44 to 129% from 1999 to 2001. Select infestations were disturbed by various methods. Prescribed burning in the winter at Colusa caused reductions in one of two plots the following spring. However, two years after burning both infestations expanded 7 and 128% respectively. Disking at Grizzly Island also increased perennial pepperweed spread, with populations expanding more than 100% both one and two years after disking. In contrast to the Colusa and Grizzly Island sites, perennial pepperweed infestations at Lower Klamath decreased in area in plots from 23 to 100% from 1999 to 2001. The majority of these reductions occurred within the 2000 to 2001 season following a prescribed burn the previous fall. Although temporary suppression of perennial pepperweed growth can occur after burning, over the long-term

disking and burning were not effective in limiting the spread of perennial pepperweed infestations. More effective techniques should be used to manage perennial pepperweed in these areas.

INTRODUCTION

Perennial pepperweed (*Lepidium latifolium* L) is an herbaceous perennial that forms dense colonies that exclude nearly all other herbaceous vegetation. It is native to temperate portions of Europe, central and southwestern Asia and the Mediterranean region (Lyeik 1989). Perennial pepperweed was accidentally introduced into the United States in the 1930s as a sugar beet seed contaminant. It is now widely distributed in North America, particularly in riparian habitats from mountain meadows to alkaline sinks in both desert valleys and coastal marshes (Weber 1989). Within these areas perennial pepperweed is an aggressive colonizer and has displaced many native riparian and wetland species (Young et al. 1995). Perennial pepperweed is currently found in all California counties except these associated with coastal rainforest (Humboldt and Del Norte counties) and desert habitats (Imperial and San Bernadino counties) (Young et al. 1997).

Perennial pepperweed shoots emerge early in the season from either semi-woody crowns, perennial roots, or seeds. Shoots can reach 1.5 m in height and produce dense stands, resulting in near monotypic populations. As stand densities increase, roots quickly establish throughout the soil profile. Our previous results showed that perennial pepperweed allocates 85% of its below ground biomass within the top 60 cm of the soil (Renz et al. 1997). Other researchers however have observed roots present many meters deep along the capillary fringe of water tables (USDA 1997, pers. comm. Leigh Fredickson). Such plastic growth may allow plants to avoid water stress during dry periods and may contribute to their high level of competitiveness in seasonally dry habitats.

Plant communities displaced by perennial pepperweed are often dominated by native species that provide important habitat for wildlife. Dense stands may discourage nesting waterfowl and in one example, have been reported to displace *Salicornia subterminalus* (pickleweed) habitat vital to the endangered salt marsh harvest mouse (Trumbo 1994). The increased spread of perennial pepperweed has created concern by federal and state resource managers in California, and other western states (USDA 1997). Within California, perennial pepperweed has become established within seasonal wetlands in many state and federal refuges. The primary function of these areas is to provide suitable habitat for waterfowl and other wildlife. Perennial pepperweed infestations appear to reduce habitat quality and natural diversity within these sensitive areas (Trumbo 1994). Furthermore, these refuges appear to be extremely vulnerable to invasion by perennial pepperweed (personal observation). Although, perennial pepperweed can produce over 16 billion seeds/ha annually (Young et al. 1997), few seedlings are found in the field (Young et al. 1997, personal observation) and the invasion process is poorly understood. Blank and Young (1997) found expansion occurring clonally along the edge of an invasion within an alkali flat in California. It is not known how typical this pattern of spread is throughout California, or how management techniques can impact the spread of perennial pepperweed. Understanding the mechanism of spread of this plant and the effects various management techniques have on that spread is critical to the development of appropriate management plans and prioritizing control efforts. The objectives of this study were to determine the rate of spread of establishing infestations of perennial pepperweed, and assess the impact of management techniques on this spread within three distinct seasonal wetlands in California.

MATERIALS AND METHODS:

Site description

Research was conducted at two National Wildlife Refuges and one State Wildlife Area representing three California bioregions. These included the Colusa National Wildlife Refuge (Central Valley bioregion), Grizzly Island Wildlife Area (San Francisco Bay Area bioregion), and the Lower Klamath National Wildlife Refuge (Cascade/Modoc bioregion) (Table 1). Average maximum and minimum temperature patterns are similar at Colusa and Grizzly Island, except for slightly cooler summers and warmer winters at Grizzly Island (Figure 1). The Lower Klamath site is the coolest, with lower maximum and minimum temperatures throughout the year resulting in a greatly reduced growing season for perennial pepperweed. Average minimum temperatures drop below 0 °C in October and remain there through April at Klamath, whereas minimum temperatures rarely drop below 0 °C at the Colusa and Grizzly Island sites.

Plant communities were unique at each site. Non-native annual grasses dominated the Colusa and Grizzly Island sites. Although species richness ranged from two to five species per square meter at Colusa and Grizzly Island, few native plants were dominant within these sites (we considered a native plant dominant if its average cover was > 10%) at Colusa or Grizzly Island (*Grindelia camporum* and *Malvella leprosa* at Colusa, and *Salicornia subterminalis* at Grizzly Island). Three species dominated all plots at Klamath, the natives *Eleocharis macrostachya* and *Juncus balticus* and the one introduced *Erysimum cheiranthoides* (Table 2).

Site selection

Isolated nascent foci (satellite populations) (Moody and Mack 1988) of varying sizes and densities were selected throughout each site. Selected infestations were located at the center of 50 by 50 meter plots (Colusa and Lower Klamath sites with 5 replicates, Grizzly Island with 3 replicates) so the expansion rate of each infestation could be measured over a three-year period without interference from other perennial pepperweed populations. Infestations were composed of a mix of perennial pepperweed and other resident plant species.

Management of sites

All three sites were managed primarily as nesting sites for waterfowl and other ground nesting birds. Management practices at Colusa and Grizzly Island were minimal. At Colusa, a prescribed burn was conducted on plots 1 and 2 in December of 1999, and Grizzly Island plot 3 was disked in the fall of 1999. All other plots were not manipulated. In contrast, all plots in Lower Klamath were annually flooded to a maximum level of 42, 58 and 69 cm in the winter of 1999, 2000 and 2001, respectively. Flood levels varied throughout the winter, but areas were inundated in October of the previous year and water was maintained on plots until early May. In addition, all plots at Lower Klamath were completely burned in October 2000.

Density measurements

Plots were established and divided into a 2500 m^2 grid utilizing a temporary grid system allowing densities to be measured within each specific square meter of the grid throughout the experiment. In 1998 to 1999, plots were established and initial perennial pepperweed shoot density within each square meter was measured. In 2000 and 2001, perennial pepperweed shoots were counted when the majority of the bolted shoots were at the flower bud stage at each site (Table 3). Perennial pepperweed rosettes and stems were counted each year within every square meter of each plot. Perennial pepperweed presence/absence was determined within each square meter to evaluate the change in area of infestations over the course of the experiment. Initial perimeter and area of individual infestations within undisturbed plots (Colusa 3,4 and 5, Grizzly Island 1 and 2) were also determined and compared to the spread in area from 1999 to 2001.

In order to evaluate the changes in density within an infestation, individual square meter areas were classified as either on the edge or within the center of the infestation. In order for a square meter to be classified as within the center its perimeter must have been directly surrounded by square meter areas containing perennial pepperweed. Number of rosettes and stems were averaged for each class and compared between the center and edges of infestations utilizing t-tests for each year and over the course of the experiment.

To test if populations increased in density over time, the density of rosettes and stems were compared between years within the center and edge of an infestation. Comparisons were made between specific square meter areas based on 1999 classifications as within the center or edge of the infestation. This was utilized because a square meter can change its classification from the edge to a center of the infestation or vice versa over the course of the experiment. By utilizing 1999 classification data we avoid this influence on our dataset allowing us to follow the changes in density of specific square meters that were either classified as within the center or edge of the infestation in 1999. Stem and rosette densities were compared between 1999 and 2000 as well as 2000 and 2001. Frequencies of individual square meters increasing or decreasing in density from the previous year were determined for each class within each plot. Probabilities that the frequencies observed were non-random was tested using a χ^2 test (if densities were identical they were classified as increasing). Sites were not compared between years if density data were not taken within 14 days of the previous year's count.

RESULTS AND DISCUSSION

Expansion of infestations

Similar rates of expansion were observed in all undisturbed plots at Colusa (3, 4 and 5) and Grizzly Island (1 and 2) with expansions from 44 to 129% from 1999 to 2001 (Table 4). While rates of expansion within each plot varied, all plots increased in area invaded. Several parameters were measured to determine if any of these factors limited spread including soil moisture in the top 30 cm, soil salinity in the top 30 cm, and plant species present. However, there was no relationship detected between spread of perennial pepperweed and any of these factors (data not shown). Thus, with no management within Colusa and Grizzly Island, perennial pepperweed infestations will continue to expand and invade new areas.

Colusa plots that were burned in the winter of 1999 had varying results. After one year, burning reduced the infested area at Colusa 1 by 6%, but at Colusa 2 a 55% increase in area infested occurred (Table 4). This variability suggests results may be dependant upon other factors such as the intensity of the fire, which was strong at Colusa 1, compared to Colusa 2 (data not shown). Two years after the burn, both areas increased in the area invaded with a 7 and 128% increase in area infested over a two year period within Colusa 1 and 2, respectively (Table 4). While burning may provide temporary reductions in infestation size, unless repeated annually, burning alone is ineffective in long-term management of perennial pepperweed.

Grizzly Island 3 was disked in the fall of 1999, resulting in increases in area invaded greater than 100% from both 1999 to 2000 and 2000 to 2001, and a 400% increase in two years. Disking can fragment perennial roots and transports these fragments to new areas within the plot where they can establish new infestations (Figure 10). Thus, disking as a sole management strategy is not an effective control option.

Initial perennial pepperweed infestations at Lower Klamath were the smallest of the three sites and declined in all plots but one (Lower Klamath 3 had a 6 % increase) over the course of the experiment. The level of reduction ranged from 23% to complete elimination from 1999 to 2001 (Table 4). The majority of the reductions in area infested occurred within the 2000 to 2001 season, with 17 to 100% reductions in all plots (Table 4). Management of these areas differed dramatically from 1999 to 2000 and 2000 to 2001. A late-season prescribed burn occurred within all plots in October of 2000 and was likely responsible for the reduction measured from 2000 to 2001. This reduction may be due to the reduced amounts of stored energy in the roots due to the prescribed burn. While it is not known how population size affects recovery after prescribed burns, data from burned Colusa sites indicate rapid recovery and expansion the following year.

Differences in expansion among individual plots at Lower Klamath appear to be affected by the location of individual plots. Lower Klamath 3 and 5 plots were located at high points within the field and therefore were the last areas to be flooded and the first to drain. These areas with the shortest inundation period had the greatest perennial pepperweed expansion increasing 28 and 19% in area, respectively during the 1999 to 2000 season. In contrast, Lower Klamath 1, 2 and 4 were in low-lying areas which did not expand. In fact, Lower Klamath 1 infestation area declined by 29% from 1999 to 2000.

During the 2000 to 2001 season all infestations within each plot were reduced in size. Unfortunately all plots were burned and flooded, so the two treatments cannot be separated and analyzed. Fredrickson and Murray (1999) also documented that perennial pepperweed infestations are sensitive to long-term flooding. They eliminated perennial pepperweed from areas of Colorado that were flooded 15 cm deep for the entire growing season for two consecutive years (Fredrickson and Murray 1999). Success of seasonal flooding has only been demonstrated in areas with a short growing season and long durations of inundation. It is not clear how effective flooding would be in areas with a longer growing season and in areas with short flood durations. It is possible that plants could recover from damage incurred by flooding when in longer growing seasons.

Relationship between size and spread

Undisturbed plots at Colusa and Grizzly Island expanded from 44 to 129% from 1999 to 2001 (Table 4). We hypothesized that the initial size or perimeter of the infestations could explain the variability in expansion. To test this, 15 individual infestations were identified within Colusa and Grizzly Island plots. A nonlinear quadratic relationship existed between initial area and the rate of spread. Small infestations expanded at a linear rate, but as initial area exceeds 30 m^2, the rate of spread decreased (Figure 2B), suggesting a high priority should be given to controlling infestations that are small in area, as their rate of expansion is greatest. The reduction in the expansion rate of infestations with larger areas may be due to reinvasion back into the center of the infestation. Such reinvasion would lead to higher densities in the middle of the infestation, a pattern seen at all sites (see Tables 5, 6 and 7).

At the same time a positive linear relationship between initial perimeter of the infestation and area spread was observed (Figure 2A). Thus infestations with the largest perimeter should be initially targeted for management, as they will expand more within one year than infestations with a smaller perimeter.

The differing relationship between initial area and initial perimeter to area spread can be explained mathematically. Assuming infestations are circular, both the area and perimeter of a circle are a function of the radius of the infestation. The perimeter is a related to the radius ($2\pi r$) in such a way that an increase in the radius would lead to a linear increase in the perimeter. Area, however, is related to the square of the radius (πr^2).

Utilizing both the initial area and perimeter may also be valuable in predicting expansion rates of noncircular infestations. For instance, many perennial pepperweed infestations occur along roadsides or riverbanks. These areas are typically narrow and follow the river or road. Assuming there is no physical or environmental constraint to expansion of the infestation, our data suggests this kind of infestation would be expected to expand at a very high rate given its high perimeter to area ratio. Previous researchers have suggested that these infestations should receive the highest management priority, primarily due to their ability to introduce propagules for long distance dispersal (Dewey et al. 1995). Our data also suggest that these infestations have the highest potential to spread.

Pattern of Spread

All infestations consisted of discrete patches of various sizes, with no apparent expansion in a particular direction. New areas invaded in 2000 and 2001 were found only along the edge of the infestation (leading edge), with only five satellite populations greater than two meters away from locations infested in the previous year across all sites (4 at Colusa, 2 at Grizzly Island) (Figures 3-14). Satellite populations were small in area (1 to 2 m^2) and density, suggesting they were recently established. Although seedlings were not found in any of these satellite populations, these populations may have been initiated from seedlings undetected the previous year. Distance of spread varied between and within sites, but was typically 1 meter per year, and never exceeded 3 meters per year (Figures 3-14). Nearly all shoots emerged from clonal structures within all sites, with only 6 seedlings observed over the course of the experiment throughout all sites. Although local expansion is almost exclusively clonal, seedlings may contribute to long-distance dispersal. This same pattern of invasion, with expansion only occurring along the leading edge, was also seen by Blank and Young (1997), although expansion appeared to be greater than 1-2 meters/year. It is still unclear how perennial pepperweed spreads along dispersal corridors (e.g. rivers and roadways), but isolated populations spread in a very predictable form along the front of the infestation (Phalanx growth strategy; see Lovett-Doust and Lovett-Doust, 1982).

Changes in density

As discussed, the leading edge is where expansion of perennial pepperweed infestations occur. Rosette and stem density along this leading edge were less than or equal to densities at the center of the infestation at all sites over all three years (Table 5, 6, 7). While data between sites and years were highly variable, this pattern was consistent throughout the experiment. Previous research (Chapter 3) has shown varying success in the control of perennial pepperweed infestations with varying densities. Therefore, in order to optimize control, the edge and center of an infestation may require different management techniques.

We also examined the frequency of square meter areas increasing or decreasing in rosette and stem density from 1999 to 2000 and 2000 to 2001. The probability of rosette and stem density increasing or remaining the same in the center and edge of infestations was significantly greater ($p<0.05$) than chance from 1999 to 2000 and 2000 to 2001. From 2000 to 2001 this pattern was seen with rosettes in three plots within the center and six plots along the edge of the infestation (Table 8 and 9), and with stems in five plots within the center and eight along the edge (Table 8 and 9). Remaining sites showed no significant differences, but no sites saw statistically significant decreases in the frequency of rosettes or stems. Due to different dates of counts, comparisons made from 1999 to 2000 had fewer plots that could be compared (only Colusa 2, Colusa 5, and Lower Klamath 3), but similar results were seen (Table 10, 11). Although many factors can affect densities from year to year, these data indicate that infestations across all three bioregions were not decreasing in perennial pepperweed density, even if burned or disked, and presence of various plant species.

Conclusions/Management implications

Results of this study can be incorporated into management programs for perennial pepperweed. Undisturbed infestations spread clonally in a predictable pattern along the leading edge. Initial size and area of infestations may influence the rate of spread, with a large perimeter to area ratio infestation expanding at the greatest rate. Infestations that are not managed will likely continue to expand and increase in density over time. Furthermore, densities will likely be greater within the center compared to the edge of the infestation, potentially warranting different management techniques for each area.

Management of perennial pepperweed will likely be more intensive and costly as infestations age (Chapter 3). Without management, infestations are expected to increase in density, store energy in below ground tissues, and close the canopy structure. Previous research has implicated all of these factors as important in increasing the difficulty of managing perennial pepperweed (Chapter 2). Furthermore, even if perennial pepperweed is eliminated, we have shown that resident plants reestablished poorly in areas that had dense infestations. However, controlling establishing infestations that are not dominated by perennial pepperweed results in rapid reestablishment of resident plants (Chapter 3). The reasons for this are not known, but may involve the release of an allelochemical and/or deposition of salts on the soil surface (Blank and Young 1997), reducing seed germination (Chapter 3). Regardless of the mechanism, revegetation may not be necessary if infestations are young and establishing, but may be required after control of dense perennial pepperweed stands. Thus early detection and eradication is highly desirable and will likely reduce costs of long-term management of perennial pepperweed.

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Table 1. Site information.

	Colusa NWR	**Grizzly Island Wildlife Area**	**Lower Klamath NWR**
Elevation (meters)	50	5	1200
Soil type	Willow silty clay	Valdez silty clay loam (Valdez series)	Capjae silty loam (Forbar series)
Observed perennial pepperweed growing season	February - October	Year round	April – September
30 year average annual precip. (mm)	435	337	289
1999 annual precip. (mm)	278	253	294
2000 annual precip. (mm)	406	337	280
2001 annual precip. (mm)	317	275	177

Table 2. Species composition, number of plants and dominant plants within each plot at each site, measure in August of 2001.

Site	Plot #	Percent cover[1]				Average # plants m^2	Dominant plants[2]
		Annual dicots	Annual grasses	Perennial monocots	Perennial dicots		
Colusa NWR	1	10	48	0	15	5	*Lolium multiflorum, Hordeum marinum, Grindelia camporum*
	2	3	72	0	5	4	*Lolium multiflorum, Hordeum marinum*
	3	6	63	7	5	4	*Lolium multiflorum*
	4	13	43	1	2	4	*Lolium multiflorum, Malvella leprosa*
	5	6	73	0	0	4	*Lolium multiflorum, Hordeum marinum*
Grizzly Island Wildlife Area	1	2	60	2	14	4	*Hordeum marinum, Salicornia subterminalus*
	2	5	76	0	0	2	*Lolium multiflorum*
	3	5	71	0	0	3	*Lolium multiflorum, Hordeum marinum*
Lower Klamath NWR	1	18	1	62	8	4	*Eleocharis macrostachya*
	2	18	0	72	2	5	*Eleocharis macrostachya, Erysimum cheiranthoides*
	3	9	1	71	1	4	*Eleocharis macrostachya, Juncus balticus*
	4	11	0	79	3	3	*Juncus balticus*
	5	10	0	67	8	4	*Eleocharis macrostachya, Erysimum cheiranthoides*

[1] Measurements were taken of species cover surrounding each nascent foci within each plot. Perennial pepperweed cover was excluded from all categories, and bareground cover is not reported.

[2] Dominant plants averaged 10% or more cover within the site.

Table 3. Dates perennial pepperweed counts taken at all sites.

	Dates counts taken				
Colusa	Fall 1998	Spring 1999	Summer 1999	Spring 2000	Spring 2001
1	10/13	3/5	7/26	4/24	4/16
2	11/18	4/10	7/27	4/11	4/19
3	12/15	-	7/27	4/13	4/26
4	12/15	-	7/28	4/14	4/23
5	-	-	7/19	4/20	4/23
Grizzly Island		Spring 1999	Summer 1999	Spring 2000	Spring 2001
1		6/2	8/2	5/4	5/10
2		6/18	8/3	5/3	5/14
3		6/11	8/3	5/11	5/8
Klamath	Fall 1998	Summer 1999	Fall 1999	Summer 2000	Summer 2001
1	10/22	8/12	9/16	6/27	6/12
2	10/22	8/10	9/16	6/27	6/12
3	10/22	7/13	-	6/27	6/13
4	10/22	8/12	9/16	6/27	6/12
5	10/22	6/29	-	6/26	6/13

Table 4. Area and percent increase in area infested by perennial pepperweed from 1999-2001.

	Area infested (m^2)					Percent increase between years		
Colusa	Fall 1998	Spring 1999	Summer 1999	Spring 2000	Spring 2001	Spring[1] 1999-2000	Spring 2000-2001	Spring[1] 1999-2001
1	154	208	166	195	223	-6	14	7
2	20	38	25	59	87	55	47	128
3	22	-	32	56	73	75	30	128
4	137	-	247	293	356	19	22	44
5	-	-	38	52	87	37	67	129
Grizzly Island		Spring 1999	Summer 1999	Spring 2000	Spring 2001	Spring 1999-2000	Spring 2000-2001	Spring 1999-2001
1		41	42	57	78	39	37	90
2		52	58	86	113	65	31	117
3		62	60	125	331	102	165	434
Klamath	Fall 1998	Summer 1999	Fall 1999	Summer 2000	Summer 2001	Summer 1999-2000	Summer 2000-2001	Summer 1999-2001
1	3	7	6	5	1	-29	-80	-86
2	6	8	6	8	2	0	-75	-75
3	40	80	-	102	85	28	-17	6
4	7	7	8	7	0	0	-100	-100
5	9	26	-	31	20	19	-35	-23

[1] If plots were not counted in the spring, summer counts were utilized

Table 5. Comparison of the rosette and stem density between the center and edge of perennial pepperweed infestations at Colusa.

Site		1999			2000			2001			1999 -2001		
		Center	T-test	edge	center	T-test	edge	center	T-test	edge	center	T-test	edge
Colusa 1	Rosette	5.9	NS	6.1	12.1	<.0001	5.7	11.2	<.0001	5.7	10.6	<.0001	5.8
	Stem	6.4	NS	5.6	7.9	0.0002	3.6	2.4	0.0009	1.1	5.3	0.0006	3.4
	n =	41		125	89		106	95		128	225		359
Colusa 2	Rosette	-		4.4	7.0	0.0855	2.3	7.0	NS	4.6	7.0	0.0093	3.8
	Stem	-		1.5	18.6	0.0321	2.2	9.3	0.0071	1.7	11.6	0.0009	1.8
	n =	0		38	5		54	15		72	20		164
Colusa 3	Rosette	1.3	NS	2.6	15.9	0.0241	4.8	13.0	0.0023	4.6	13.6	<.0001	4.2
	Stem	12.7	NS	3.4	8.9	0.0097	2.0	9.0	0.0001	2.0	9.3	<.0001	2.3
	n =	3		29	10		46	20		53	33		128
Colusa 4	Rosette	27.8	<.0001	8.8	25.6	<.0001	11.5	24.1	<.0001	11.4	25.5	<.0001	10.7
	Stem	7.1	0.0002	3.5	5.8	0.0037	3.5	10.2	0.0046	7.2	8.1	<.0001	4.9
	n =	65		182	73		219	108		248	246		649
Colusa 5	Rosette	7.6	NS	3.2	10.4	0.0310	3.7	8.4	0.0031	2.7	8.7	<.0001	3.1
	Stem	6.6	0.0535	1.4	11.0	0.0064	3.1	12.7	<.0001	2.8	11.2	<.0001	2.6
	n =	7		31	9		43	23		64	39		138

Table 6. Comparison of the rosette and stem density between the center and edge of perennial pepperweed infestations at Grizzly Island.

		1999			2000			2001			1999 - 2001		
Site		center	T-test	edge	center	T-test	edge	center	T-test	edge	center	T-test	edge
Grizzly Island 1	Rosette	23.6	.0004	6.5	14.7	<.0001	3.0	7.1	NS	5.1	12.2	<.0001	4.8
	Stem	14.7	.0002	4.1	16.6	<.0001	3.4	19.1	.0008	6.6	16.4	<.0001	4.9
	n =	14		27	25		32	37		41	76		100
Grizzly Island 2	Rosette	1.7	NS	2.2	3.1	0.0002	1.1	1.1	NS	1.0	1.9	0.0514	1.3
	Stem	2.5	NS	2.7	10.3	0.0017	3.8	16.7	<.0001	6.7	12.9	<.0001	4.8
	n =	6		46	23		63	32		81	61		190
Grizzly Island 3	Rosette	0.0	-	0.8	1.1	NS	0.5	1.7	0.0001	0.7	1.6	<.0001	0.7
	Stem	5.0	-	2.9	20.4	0.0003	3.4	13.2	<.0001	4.5	14.1	<.0001	3.9
	n =	1		61	11		114	68		263	80		438

Table 7. Comparison of the stem and rosette density between the center and edge of perennial pepperweed infestations at Lower Klamath.

		1999			2000			2001			1999 – 2001		
Site		center	T-test	edge	center	T-test	edge	center	T-test	edge	center	T-test	edge
Klamath	Rosette	-		2	-		2.8	-		0	-		2.1
1	Stem	-		1.8	-		1.6	-		2	-		1.6
	n =	0		7	0		5	-		1	0		13
Klamath	Rosette	-		0.6	-		1.6	-		0.5	-		1.1
2	Stem	-		1.4	-		0.4	-		2	-		1.0
	n =	-		8	-		8	-		2	0		18
Klamath	Rosette	8.8	0.0003	2.8	8.5	0.0011	3.2	7.6	0.0019	2.7	8.4	<.0001	2.9
3	Stem	18.4	0.0002	3.1	40.6	<.0001	5.0	7.9	0.0297	1.9	25.5	<.0001	3.4
	n =	18		62	27		75	16		69	61		206
Klamath	Rosette	-		1.4	-		0.9	-		-	-		1.1
4	Stem	-		3.6	-		0.4	-		-	-		20
	n =			7			7			0	0		14
Klamath	Rosette	6.7	NS	3.2	4.0	NS	3.4	-		3.1	5.1	0.0664	3.2
5	Stem	2	NS	2.3	1.3	NS	0.9	-		0.4	1.6	NS	1.2
	n =	3		23	4		27			20	7		70

Table 8. Probability of square meter areas within the edge of the infestation increasing in rosette or stem density from 2000-2001

	Rosette density				Stem density			
Site	n=	% Increased[1]	% Decreased	Probability (χ^2)	n=	% Increased[1]	% Decreased	Probability (χ^2)
Colusa 1	77	63	38	NS	77	49	51	NS
Colusa 2	40	85	15	0.0008	40	83	18	0.0021
Colusa 3	36	72	28	0.0531	36	94	6	<.0001
Colusa 4	180	68	32	0.0006	180	95	5	<.0001
Colusa 5	28	72	29	0.1007	28	96	4	<.0001
Grizzly Island 1	17	88	12	0.0169	17	94	6	0.0045
Grizzly Island 2	50	76	24	0.0071	50	96	4	<.0001
Grizzly Island 3	66	85	15	<.0001	66	88	12	<.0001
Klamath 1	1	0	100	NS	1	0	100	NS
Klamath 2	1	0	100	NS	1	100	0	NS
Klamath 3	40	45	55	NS	40	45	55	NS
Klamath 5	8	63	38	NS	8	100	0	0.0209

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[1] If densities did not increase or decrease they were placed within this category

Table 9. Probability of square meter areas within the center of the infestation increasing in rosette or stem density from 2000-2001

	Rosette density				Stem density			
Site	n=	% Increased[1]	% Decreased	Probability (X^2)	n=	% Increased[1]	% Decreased	Probability (X^2)
Colusa 1	77	55	46	NS	77	42	58	NS
Colusa 2	-	-	-		-	-	-	
Colusa 3	10	90	10	0.051	10	80	20	NS
Colusa 4	73	66	34	0.0547	73	90	10	<.0001
Colusa 5	8	63	38	NS	8	100	0	0.0209
Grizzly Island 1	19	32	68	NS	19	95	5	0.0019
Grizzly Island 2	22	36	64	NS	22	91	9	0.0029
Grizzly Island 3	11	91	9	0.0332	11	73	27	NS
Klamath 3	10	30	70	NS	10	0	100	0.0098

[1] If densities did not increase or decrease they were placed within this category

Table 10: Probability of square meter areas within the edge of the infestation increasing in rosette and stem density from 1999-2000

	Rosette density				Stem density			
Site	n=	% Increased[1]	% Decreased	Probability (χ^2)	n=	% Increased[1]	% Decreased	Probability (χ^2)
Colusa 2	27	59	41	NS	27	85	15	0.0054
Colusa 5	25	72	28	NS	25	92	8	0.0011
Klamath 3	46	70	30	0.0557	46	100	0	0.0022

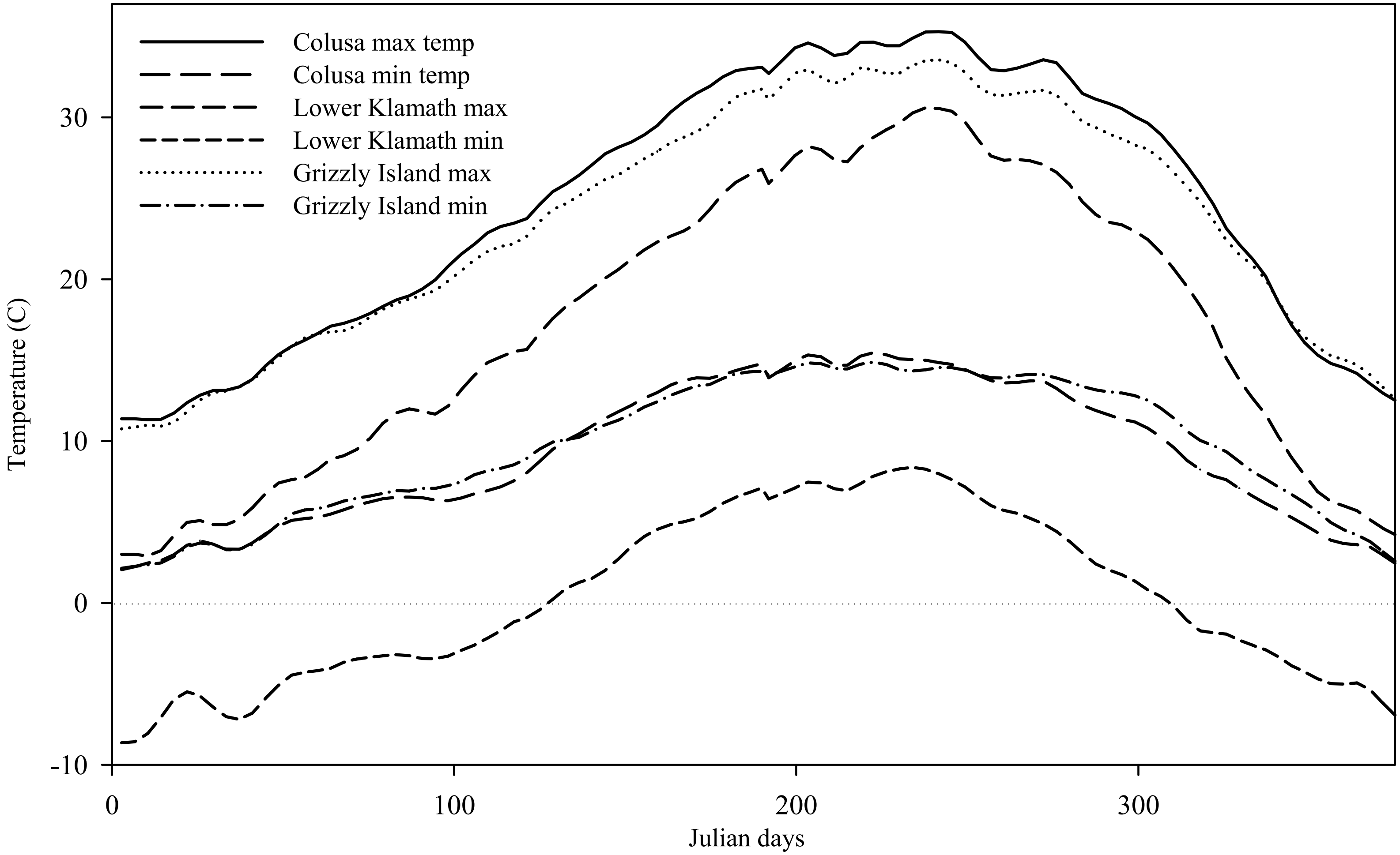
[1] If densities did not increase or decrease they were placed within this category

Table 11. Probability of square meter areas within the center of the infestation increasing in rosette and stem density from 1999-2000

	Rosette density				Stem density			
Site	n=	% Increased[1]	% Decreased	Probability (χ^2)	n=	% Increased[1]	% Decreased	Probability (χ^2)
Colusa 2	5	100	0	0.0730	5	20	80	NS
Colusa 5	6	50	50	NS	6	83	17	NS
Klamath 3	17	41	59	NS	17	100	0	0.0005

[1] If densities did not increase or decrease they were placed within this category

Figure 1: Long-term average high and low temperatures at all 3 sites[1]



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[1] Temperatures were smoothed using a locally weighted function utilizing 40% of the datapoints to smooth curves

Figure 2. Increase in the spread of individual patches compared to initial perimeter and area at Colusa and Grizzly Island.

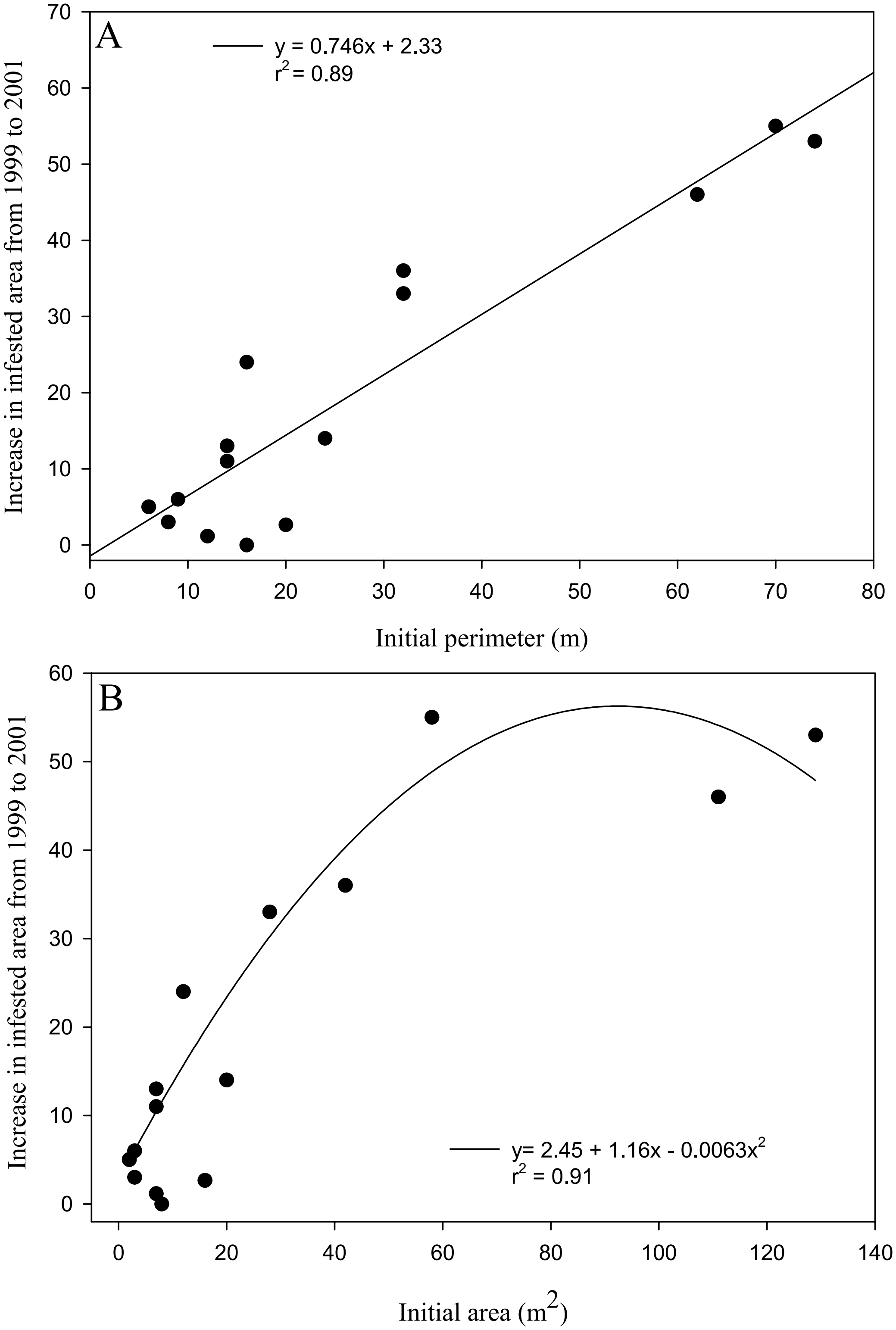


Figure 3. Presence and absence of perennial pepperweed at Colusa plot #1 1999 to 2001.

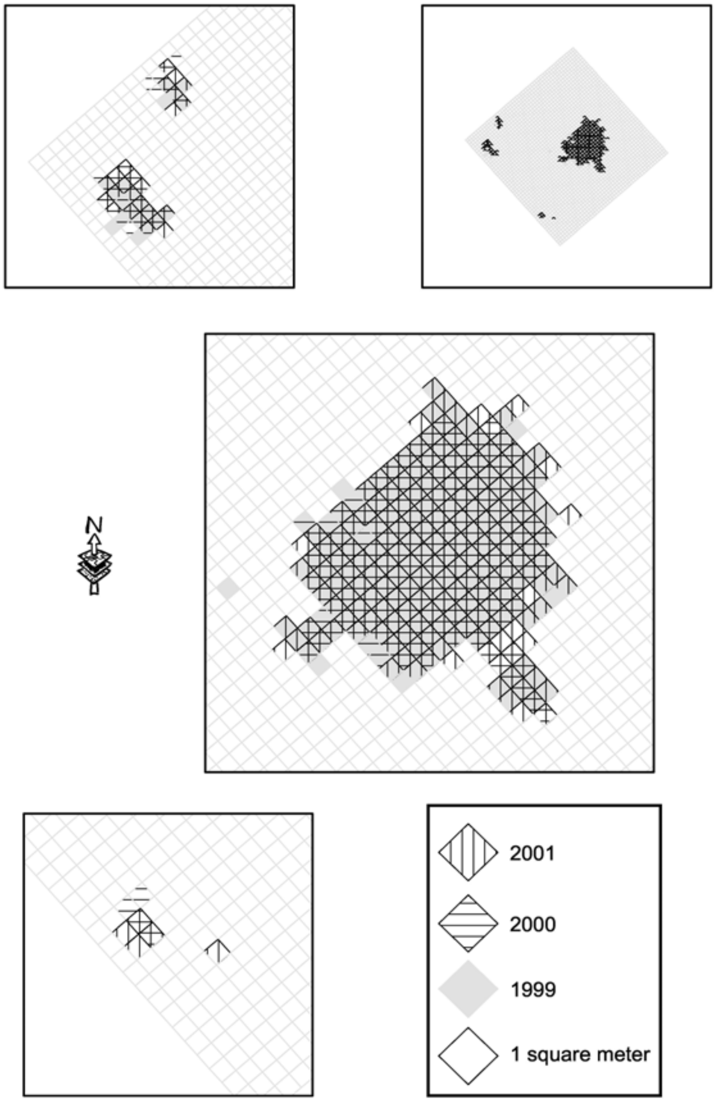


Figure 4. Presence and absence of perennial pepperweed at Colusa plot #2 1999 to 2001.

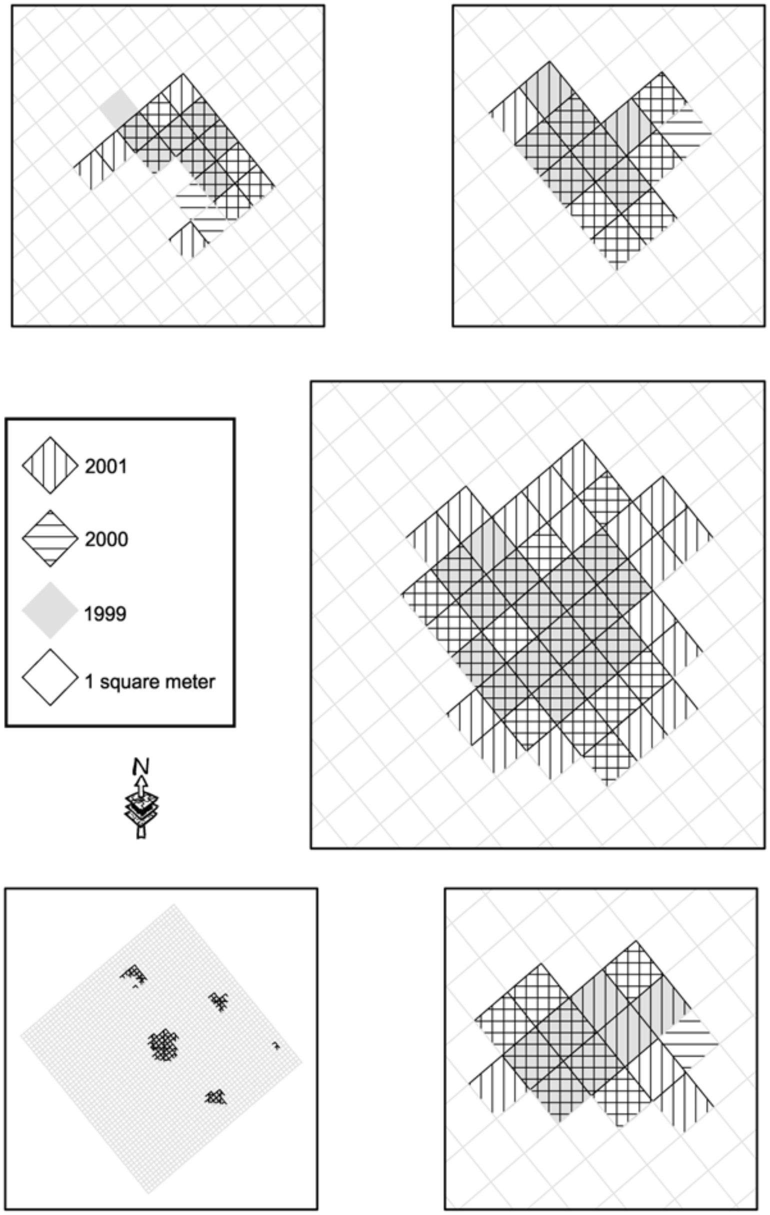


Figure 5. Presence and absence of perennial pepperweed at Colusa plot #3 1999 to 2001.

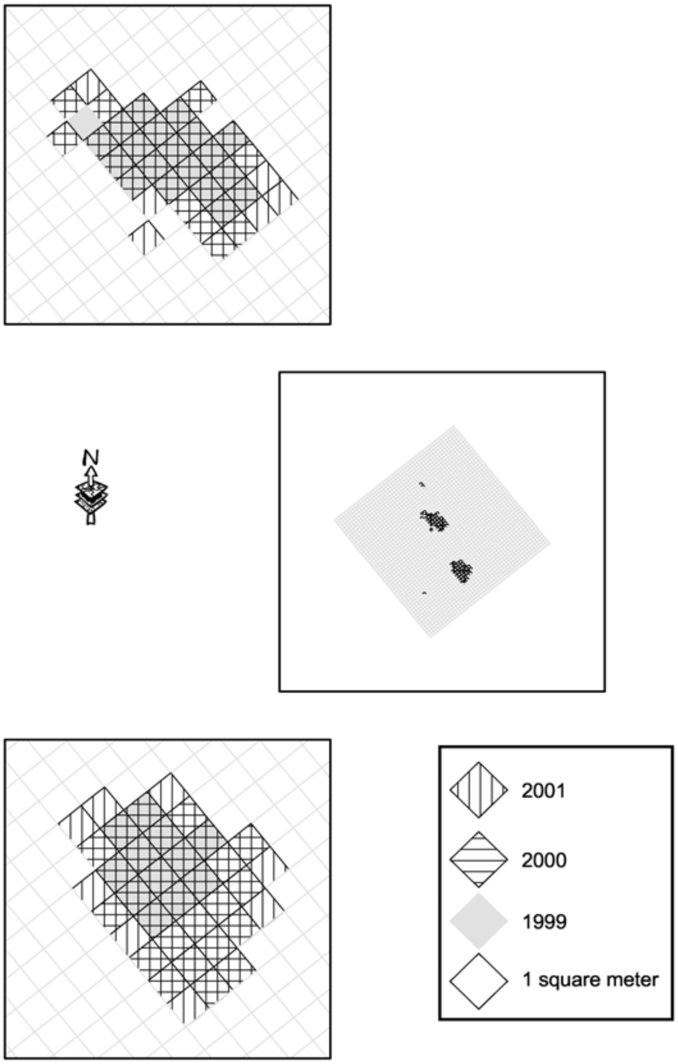


Figure 6. Presence and absence of perennial pepperweed at Colusa plot #4 1999 to 2001.

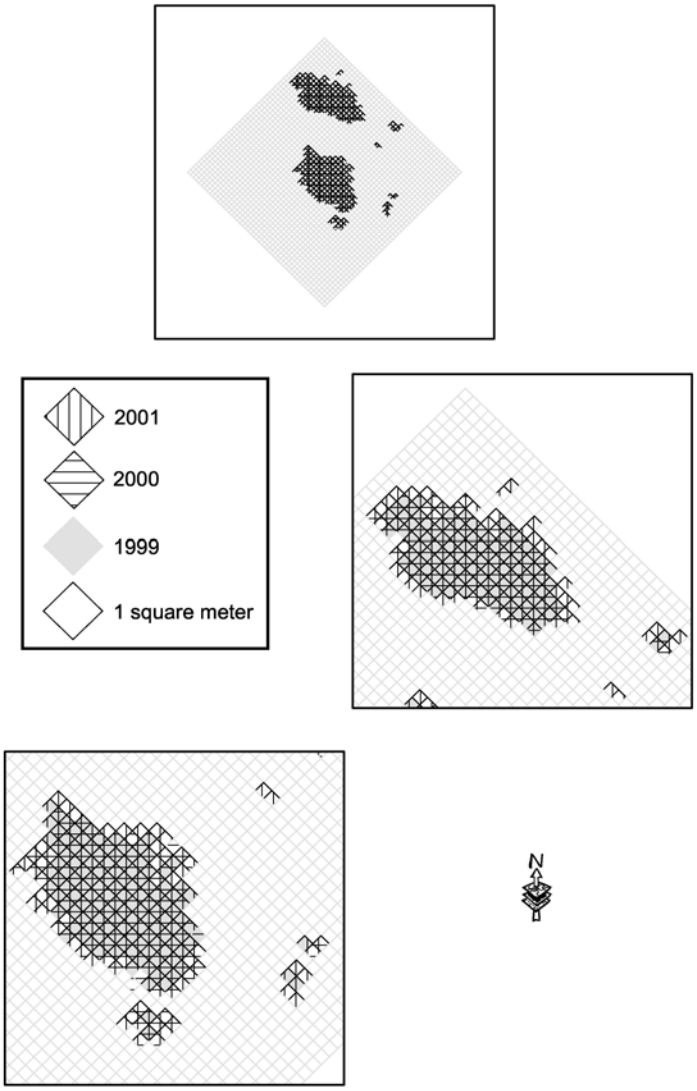


Figure 7. Presence and absence of perennial pepperweed at Colusa plot #5 1999 to 2001.

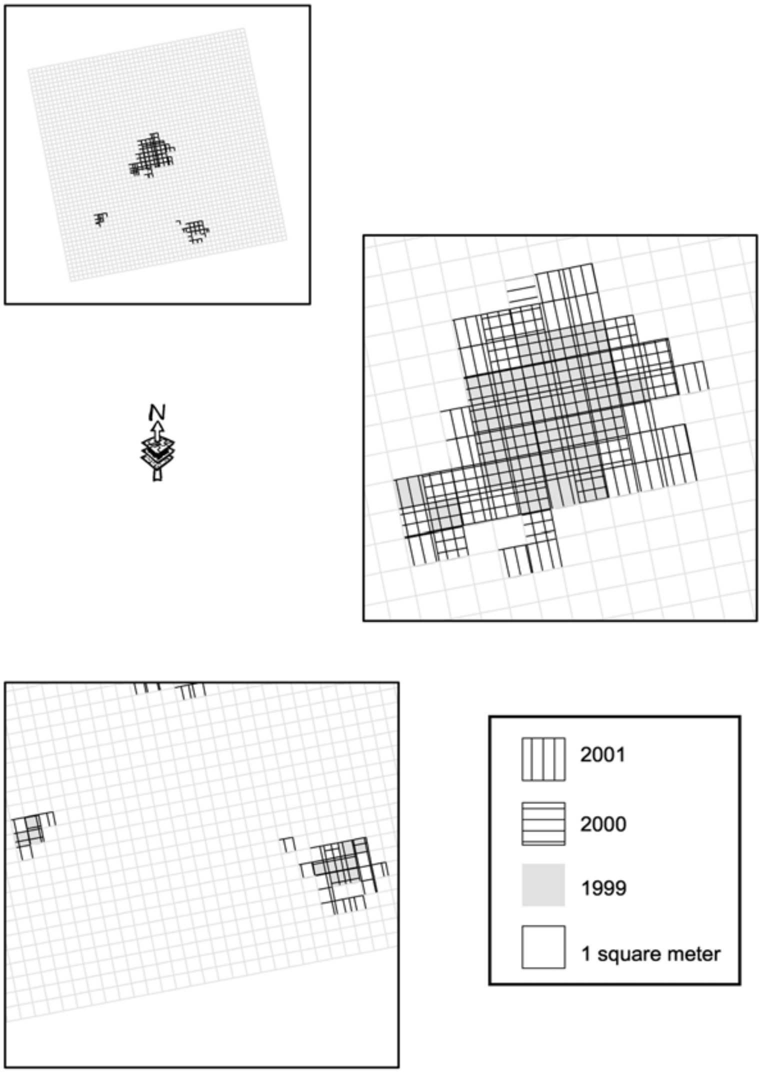


Figure 8. Presence and absence of perennial pepperweed at Grizzly Island plot #1 1999 to 2001.

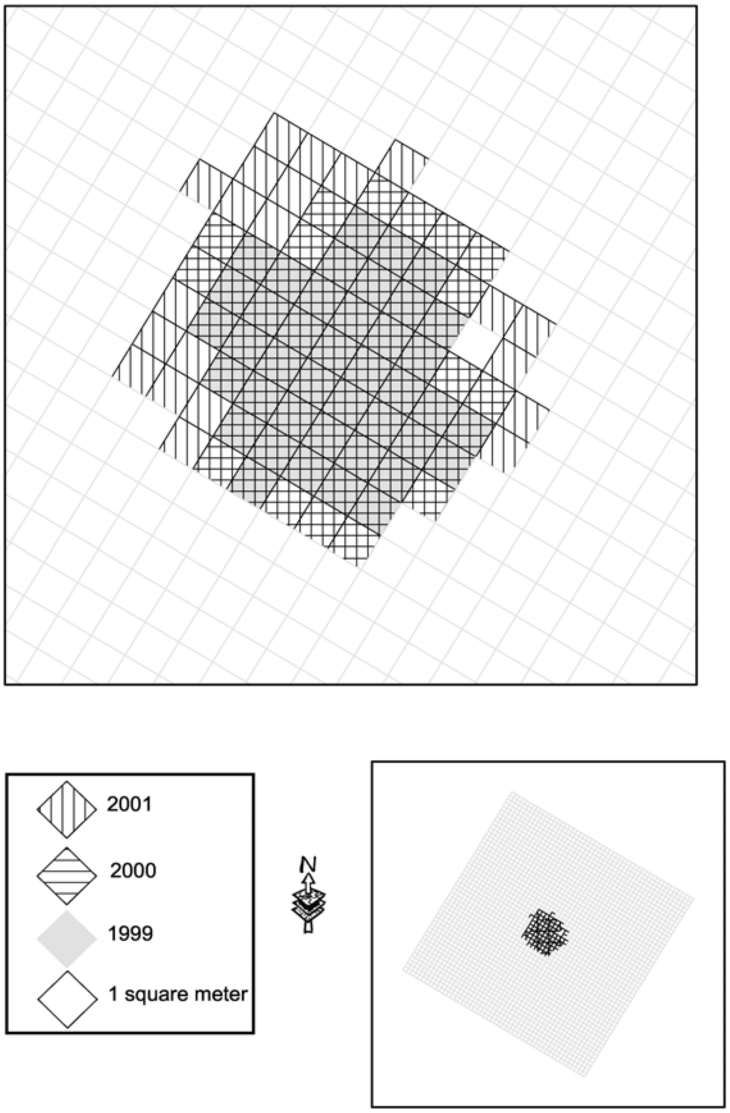


Figure 9. Presence and absence of perennial pepperweed at Grizzly Island plot #2 1999 to 2001.

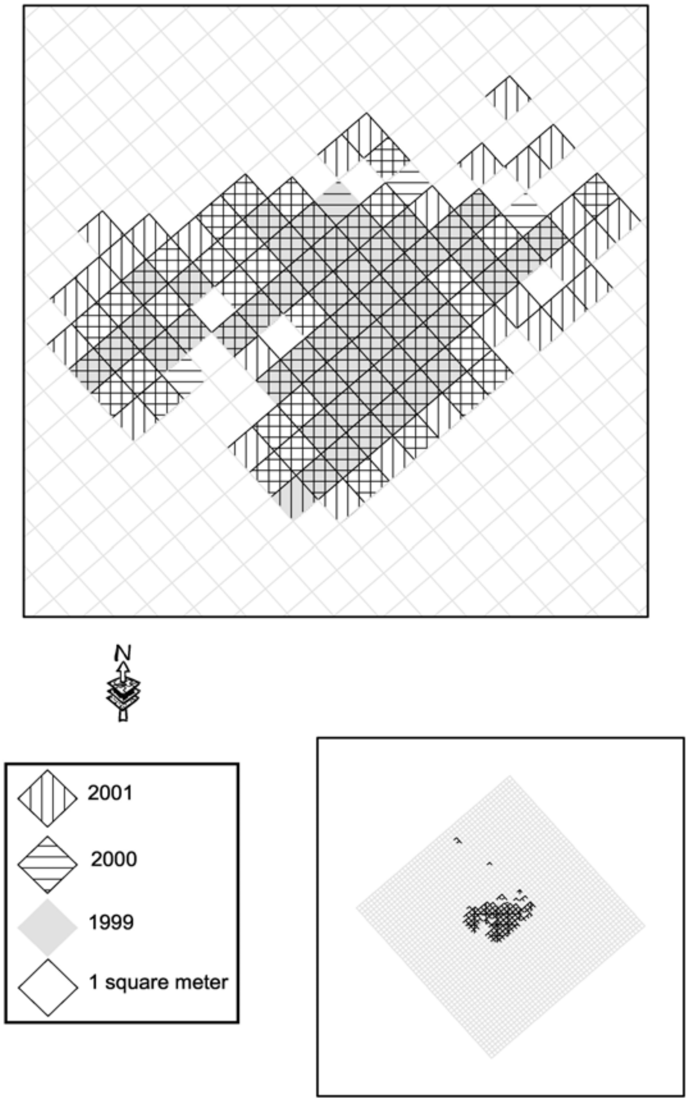


Figure 10. Presence and absence of perennial pepperweed at Grizzly Island plot #3 1999 to 2001.

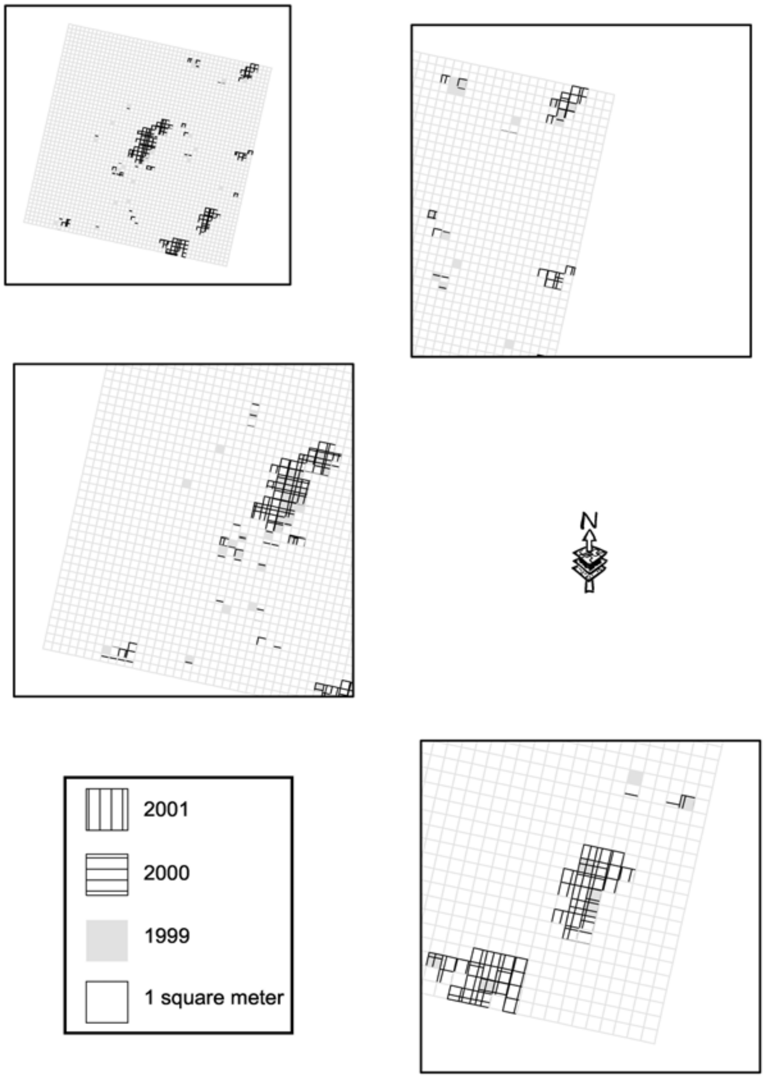


Figure 11. Presence and absence of perennial pepperweed at Klamath plot #1 1999 to 2001.

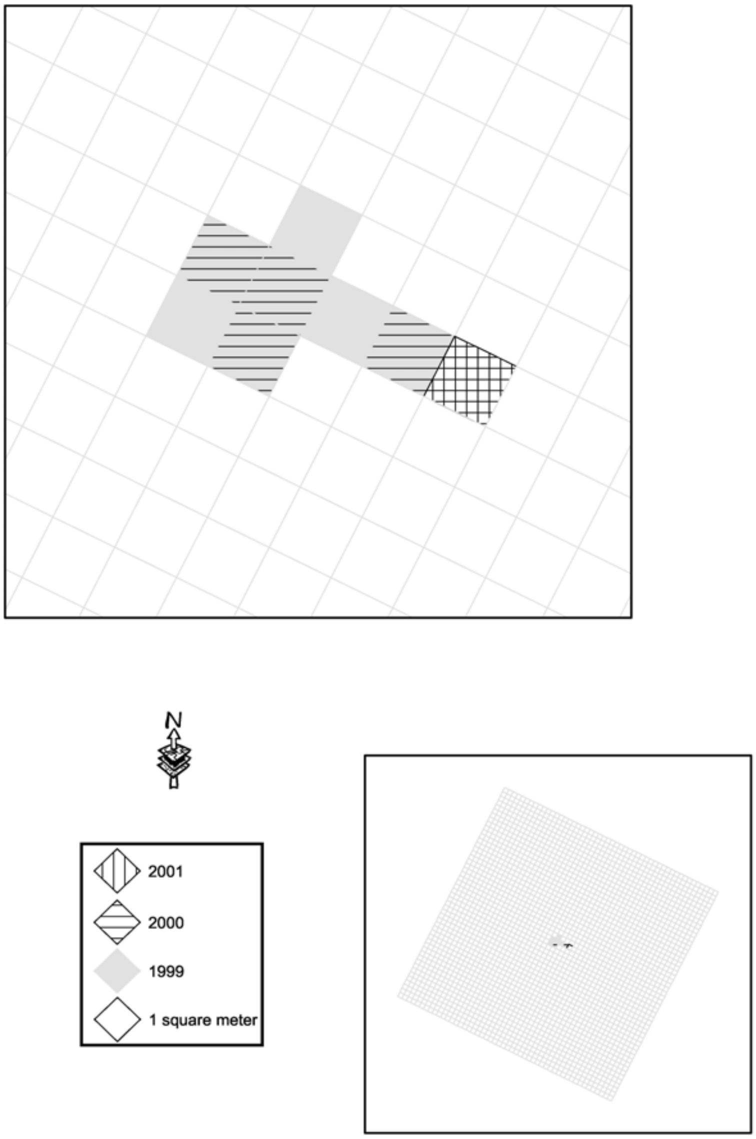


Figure 12. Presence and absence of perennial pepperweed at Klamath plot #2 1999 to 2001.

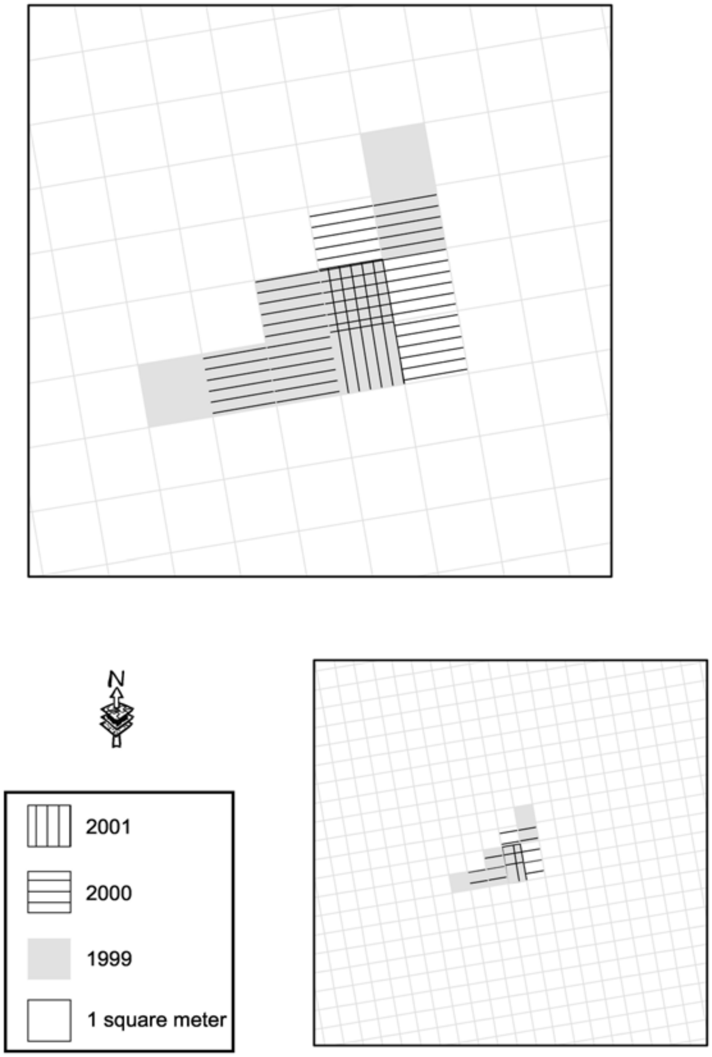
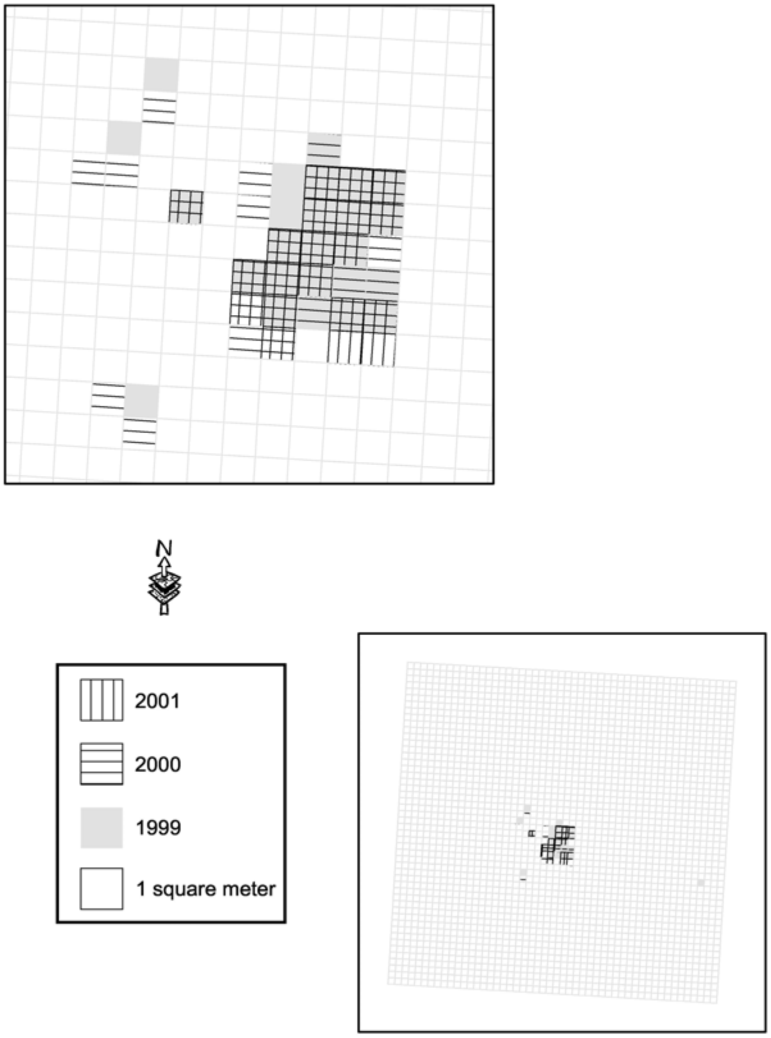


Figure 13. Presence and absence of perennial pepperweed at Klamath plot #3 1999 to 2001.

Figure 14. Presence and absence of perennial pepperweed at Klamath plot #5 1999 to 2001.



APPENDICES

Appendix A. ANOVA table for biomass of perennial pepperweed 1 year after treatments (Chapter 3).

	Woodland		**Davis**	
Source	DF	Pr > F	DF	Pr > F
Block	3	0.2562	3	0.2665
Mowing[1]	1	0.0215	1	0.5841
Herbicide	14	< 0.0001	8	< 0.0001
Block*mowing	3	0.2327	3	0.2059
Mowing*herbicide	14	0.0036	8	< 0.0001
Error	83		71	

[1] Since split-plot used block*mowing as error term

Appendix B. ANOVA table for total plant cover. (Chapter 3)

	Woodland		**Davis**	
Source	DF	Pr > F	DF	Pr > F
Block	3	0.4730	3	0.0020
Year	1	< 0.0001	1	< 0.0001
Mowing[1]	1	0.0032	1	0.8217
Herbicide	14	< 0.0001	8	0.6809
Year*mowing	1	0.0090	1	< 0.0001
Year*herbicide	14	< 0.0001	8	0.0008
Block*mowing	3	0.0406	3	0.7338
Mowing*herbicide	14	0.0338	8	0.0952
Year*Mowing*herbicide	14	0.1954	8	0.0006
Error	233		142	

[1] Since split-plot used block*mowing as error term

Appendix C. MANOVA table for life history classes. (Chapter 3)

	Woodland		**Davis**	
Source	DF	MANOVA Probability (Wilks' Lambda)	DF	MANOVA Probability (Wilks' Lambda)
Year	3	0.0012	3	<0.0001
Mowing[1]	3	NS	3	NS
Herbicide	42	<0.0001	24	<0.0001
Year*mowing	3	0.0258	3	<0.0001
Year*herbicide	42	<0.0001	24	0.0445
Mowing*herbicide	42	0.0357	24	NS
Year*mowing*herbicide	42	NS	24	NS

[1] Since split-plot used block*mowing as error term

Appendix D. Protected ANOVA table for life history classes (Woodland). (Chapter 3)

Woodland		Protected ANOVA Pr > F		
Source	DF	Annual dicots	Annual grasses	Perennials
Year	1	NS	<0.0001	NS
Mowing[1]	1	NS	NS	NS
Herbicide	14	0.0079	<0.0001	<0.0001
Year*mowing	1	NS	NS	0.0087
Year*herbicide	14	0.0070	<0.0001	NS
Mowing*herbicide	14	NS	NS	0.0005
Year*Mowing*herbicide	14	NS	NS	NS
Error	233			

[1] Since split-plot used block*mowing as error term

Appendix E. Protected ANOVA table for life history classes (Davis). (Chapter 3)

Davis		Protected ANOVA Pr > F		
Source	DF	Annual dicots	Annual grasses	Perennials
Year	1	<0.0001	<0.0001	NS
Mowing[1]	1	NS	NS	NS
Herbicide	8	<0.0001	0.0171	<0.0001
Year*mowing	1	0.0108	<0.0001	NS
Year*herbicide	8	0.0091	0.0039	NS
Mowing*herbicide	8	NS	NS	NS
Year*Mowing*herbicide	8	NS	NS	NS
Error	142			

[1] Since split-plot used block*mowing as error term

Appendix F: MANOVA table for native/nonnative classes. (Chapter 3)

	Woodland		**Davis**	
Source	DF	MANOVA Probability (Wilks' Lambda)	DF	MANOVA Probability (Wilks' Lambda)
Year	2	NS	2	<0.0001
Mowing[1]	2	0.0032	2	NS
Herbicide	28	<0.0001	16	<0.0001
Year*mowing	2	0.0010	2	0.0003
Year*herbicide	28	0.0001	16	NS
Mowing*herbicide	28	0.0003	16	NS
Year*mowing*herbicide	28	NS	16	NS

[1] Since split-plot used block*mowing as error term

Appendix G: Protected ANOVA table for native and non-native classes (Woodland). (Chapter 3)

Woodland		Protected ANOVA Pr > F	
Source	DF	Native	Nonnative
Year	1	NS	NS
Mowing[1]	1	NS	NS
Herbicide	14	0.0388	<0.0001
Year*mowing	1	0.0110	0.0084
Year*herbicide	14	NS	<0.0001
Mowing*herbicide	14	NS	0.0008
Year*mowing*herbicide	14	NS	NS
Error	233		

[1] Since split-plot used block*mowing as error term

Appendix H: Protected ANOVA table for native and non-native classes (Davis). (Chapter 3)

Davis		Protected ANOVA Pr > F	
Source	DF	Native	Nonnative
Year	1	<0.0001	<0.0001
Mowing[1]	1	NS	NS
Herbicide	8	0.0013	0.0183
Year*mowing	1	NS	0.0009
Year*herbicide	8	NS	NS
Mowing*herbicide	8	NS	NS
Year*mowing*herbicide	8	NS	NS
Error	142		

[1] Since split-plot used block*mowing as error term

Appendix I. ANOVA table for species richness. (Chapter 3)

	Woodland		**Davis**	
Source	DF	Pr > F	DF	Pr > F
Block	3	0.0930	3	< 0.0001
Year	1	< 0.0001	1	< 0.0001
Mowing[1]	1	0.8821	1	0.0011
Herbicide	14	< 0.0001	8	0.0113
Year*mowing	1	0.3621	1	< 0.0001
Year*herbicide	14	0.0760	8	0.0944
Block*mowing	3	0.1863	3	0.0011
Mowing*herbicide	14	0.2869	8	0.8171
Year*Mowing*herbicide	14	0.3337	8	0.8978
Error	233		142	

[1] Since split-plot used block*mowing as error term

Appendix J. Coordinates and specific management techniques of all plots within each site (Chapter 4).

Site	Plot #	Coordinates	Specific management
Colusa NWR	1	39° 10.820 N 122° 02.540 W	Managed as an upland area for waterfowl nesting cover; Burned December 30th 1999, low intensity burn
	2	39° 10.579 N 122° 02.635 W	Managed as an upland area for waterfowl nesting cover; Burned December 30th 1999, high intensity burn
	3	39° 10.130 N 122° 02.55 W	Managed as an upland area for waterfowl nesting cover;
	4	39° 10.268 N 122° 02.535 W	Managed as an upland area for waterfowl nesting cover;
	5	39° 10.312 N 122° 02.558 W	Managed as an upland area for waterfowl nesting cover;
Grizzly Island Wildlife Area	1	38° 08.327 N 121° 57.881 W	Managed as an upland area for waterfowl nesting cover
	2	38° 08.327 N 121° 58.085 W	Managed as an upland area for waterfowl nesting cover
	3	38° 08.497 N 121° 58.001 W	Managed as an upland area for waterfowl nesting cover; Disked fall/winter 1999
Lower Klamath NWR	1	41° 54.991 N 121° 43.364 W	Burned October 3rd, 2000; Average flood mark visible on post of plots =31.5 cm
	2	41° 54.991 N 121° 43.364 W	Burned October 3rd, 2000; Average flood mark visible on post of plots =39 cm
	3	41° 55.344 N 121° 43.690 W	Burned October 3rd, 2000; Average flood mark visible on post of plots = 6.4 cm
	4	41° 54.989 N 121° 43.742 W	Burned October 3rd, 2000; Average flood mark visible on post of plots = 1 cm
	5	41° 54.891 N 121° 43.781 W	Burned October 3rd, 2000; Average flood mark visible on post of plots = 17.4 cm