Challenges to Introducing and Managing Disturbance Regimes for *Holocarpha macradenia*, an Endangered Annual Grassland Forb

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Abstract: *Introducing rare plants to new sites for conservation to offset effects of habitat destruction requires detailed knowledge of habitat requirements, plant demography, and management needs. We conducted a factorial experiment replicated at three coastal prairie sites to test the effects of clipping frequency and litter accumulation on seed germination, seedling survival, reproduction, and seedling recruitment of introduced populations of the endangered, tall-stature, annual forb,* Holocarpha macradenia *(DC.) E. Greene. Clipping favored* H. macradenia*, primarily by enhancing seed germination and flower production. Litter accumulation had no effect on seed germination, even after 5 years of treatments. Seedling recruitment was highly site specific with large numbers of recruits recorded at only one of three sites. Although recruitment of seedlings was higher in clipped plots for 2–3 years, by 4–5 years after introduction very few seedlings survived to reproduction in any treatment. We attribute this result to a combination of poor habitat quality, small population size, and lack of a seed bank. We were unsuccessful in introducing this relatively well-studied species of concern to apparently suitable habitat at multiple sites in multiple years, which suggests that translocating rare plant populations to mitigate for habitat destruction is an expensive and highly uncertain endeavor.*

Keywords: California coastal prairie, grazing, litter, mitigation, rare plant, Santa Cruz tarplant, seed germination, seedling, translocation

Retos de la Introducción y Gestión de Regímenes de Perturbación para *Holocarpha macradenia,* una Hierba Anual en Peligro

Resumen: *La introducción de plantas raras en sitios nuevos para compensar los efectos de la destrucción del hábitat requiere de conocimiento detallado de requerimientos de hábitat, demografía de plantas y necesidades de gestión. Realizamos un experimento factorial replicado en tres sitios en la pradera costera para probar los efectos de la frecuencia de poda y acumulación de hojarasca sobre la germinación de semillas, supervivencia de plántulas, reproducción y reclutamiento de plántulas de poblaciones introducidas de la hierba anual, en peligro* Holocarpha macradenia *(DC.) E. Greene. La poda favoreció a* H. macradenia*, principalmente porque incrementó la germinación de semillas y la producción de flores. La acumulación de hojarasca no tuvo efecto en la germinación de semillas, aun después de 5 años de tratamientos. El reclutamiento de plántulas fue altamente sitio específico, con números altos de reclutas registrados solo en uno de los tres sitios. Aunque el reclutamiento de plántulas fue mayor en parcelas podadas por 2-3 años, a los 4-5 años después de la introducción muy pocas plántulas sobrevivían hasta reproducción en cualquier tratamiento. Atribuimos este resultado a la combinación de hábitat de pobre calidad, tamaño poblacional pequeño y ausencia de un banco de semillas. No tuvimos éxito en la introducción, en hábitat aparentemente adecuado en múltiples sitios en múltiples años, de esta especie relativamente bien estudiada; lo que sugiere que la translocación de poblaciones de plantas raras para mitigar la destrucción del hábitat es un propósito costoso y altamente incierto.*

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Palabras Clave: germinación de semillas, *Holocarpha macradenia*, hojarasca, mitigación, pastoreo, planta rara, plántula, pradera costera de California, Santa Cruz, translocación

Introduction

A recent review (Hoekstra et al. 2005) identifies temperate grasslands and Mediterranean ecosystems as the two most threatened biomes globally, where habitat area converted to human uses is more than eight times the area protected. As a result most remnant temperate grasslands remain as small fragments within a matrix of agricultural and urban land uses (Stromberg et al. 2001; Hodgson et al. 2005; Romermann et al. 2005). Temperate grasslands host a wide diversity of forbs that have evolved with a complex history of disturbance from fire, soil disturbance by small mammals, and grazing by domestic and native ungulates, which helps to maintain safe sites among dominant grasses (Grubb 1986; Hobbs & Huenneke 1992; Noy-Meir 1995; Collins et al. 1998). A large number of these species of rare forbs are declining dramatically, in part due to alteration of disturbance regimes (Collins et al. 1998; Lennartsson & Oostermeijer 2001; Hayes & Holl 2003*a*; Hodgson et al. 2005). Moreover, grasslands worldwide, and in California in particular, have been affected by introduction of species from other regions with similar climatic conditions and adaptations to disturbance (Huenneke & Mooney 1989; D'Antonio & Vitousek 1992). Together these impacts pose a challenge to managing existing populations in situ.

Therefore, translocation and establishment of new populations are used increasingly to reduce extinction risk of rare plant species. Although translocation is often proposed to "mitigate" for habitat destruction, the long-term success of such efforts is rarely evaluated (Falk et al. 1996; Guerrant & Pavlik 1998; Morgan 1999). In the few cases where the results of plant introduction efforts have been evaluated systematically, only a small percentage was successful (Fiedler 1991; Morgan 1999; Drayton & Primack 2000).

The common failure of plant translocation and introduction efforts most likely stems from several causes (Falk et al. 1996). First, such efforts are usually based on a poor understanding of plant demography and habitat needs (Fiedler 1991; Howald 1996; Guerrant & Pavlik 1998). Second, because of funding constraints plants are often introduced only once, when climatic conditions may not be appropriate. This is a particular challenge in Mediterranean climates, where highly variable interannual rainfall makes recruitment and survival episodic (Hobbs & Mooney 1991; Sternberg et al. 2000; Levine & Rees 2004). Third, the size of the introduced populations may be small and suffer from Allee effects (Krauss et al. 2002; Lennartsson 2002). Finally, maintaining both existing and introduced populations of rare plants frequently requires long-term habitat management to maintain disturbance regimes and to minimize competition with exotic species (e.g., Morgan 1999; Carlsen et al. 2000; Kaye et al. 2001), yet management funds often are not included in budgets of introduction projects (Fiedler 1991; Falk et al. 1996).

Our goal was to determine appropriate disturbance regimes to facilitate transitions through critical life-history stages of *Holocarpha macradenia* (DC.) E. Greene (Santa Cruz tarplant), a federally and state-protected, tall-stature, annual forb endemic to California coastal prairie. It is part of a large guild of late-season native annual forbs; more than 200 taxa in this guild are listed as rare and endangered, including species in the genera *Amsinckia*, *Clarkia*, *Madia*, and *Hemizonia* (Carlsen et al. 2000). Short-stature forbs respond positively to grazing (Noy-Meir et al. 1989; McIntyre et al. 1995; Hayes & Holl 2003*a*), but the effect of clipping or grazing is less clear for tall-stature species. Understanding the effect of the type, timing, and frequency of disturbance regimes on all life-history stages of endangered plant species is critical to developing management plans (Holmes & Richardson 1999; Pavlik & Enberg 2001).

We conducted factorial experiments at three coastal prairie sites to evaluate the effects of frequency and type of disturbance on germination, seedling survival, fecundity, and seedling recruitment of introduced populations of *H. macradenia*. We hypothesized that more frequent disturbance would increase population persistence (Hayes 1998). We also predicted that individual components of grazing—live biomass removal, litter removal, and soil disturbance—would act differentially to affect survivorship. For example, litter accumulation can affect plant species composition by altering nutrient cycling and microclimatic variation (Facelli & Pickett 1991; Reynolds et al. 2001), whereas soil disturbance may increase safe sites for germination (McIntyre & Lavorel 1994). Differentiating among these effects is important, particularly because some managers use mowing as a disturbance regime at sites where grazing and fire are not feasible.

Methods

Site Selection and Description

We worked in coastal prairie: species-rich grasslands on deep soils within a maritime fog belt that moderates the summer drought of the Mediterranean climate. We conducted research at three sites within 4 km of the coast at elevations of <150 m, in central California (U.S.A.), near Santa Cruz. The sites, Elkhorn (near Elkhorn Slough), Swanton (near the town of Swanton), and UCSC (on the University of California, Santa Cruz campus), are separated by 25 km. They are located within the historical range of *H. macradenia,* and the Elkhorn site is approximately 0.5 km from an existing population. All sites (1) had been grazed by cattle before the study, (2) contained coastal prairie plant species normally associated with *H. macradenia*, (3) had <10% slopes facing south to southeast, and (4) had sandy loam soils deeper than 1 m.

We chose sites that appeared to be suitable habitat for (based on criteria 1–4 above; Munz & Keck 1968) but did not have populations of *H. macradenia* for three reasons. First, we were interested in the effects of disturbance on the demographics of introduced populations, given increasing use of introduction of rare plants as mitigation for habitat destruction. Second, because we studied an endangered species we were constrained from both a legislative and conservation perspective from conducting experimental manipulations on natural populations at the multiple sites necessary to make scientific and management generalizations. Third, by introducing the plant we could better quantify demographic parameters because we were certain of the number of seeds and plants introduced. Final site selection depended on obtaining permission to establish experimental populations of an endangered species.

During the 6 years of our research annual rainfall ranged from 29 to 84 cm, with most falling between October and April (data from California Department of Water Resources stations located at similar elevations within 4 km of each site). Seasonal rainfall was close to or below average in all 6 years and well below the 20-year average in 2000–2001.

Soil chemistry and moisture are discussed in detail in Hayes and Holl (2003*b*). Soils at all sites are sandy loams with minor variations in pH, organic matter, and most major nutrients. Phosphorus is higher at Elkhorn, and UCSC has higher clay content. Soil began to dry in early May of each year and dried fastest in 2001. Vegetation clipping and removal treatments (discussed below) had no consistent effects on soil moisture (Hayes & Holl 2003*b*).

At the beginning of the study, the non-native annual grasses *Bromus* spp., *Lolium multiflorum*, and *Vulpia bromoides* dominated cover at all sites (Hayes & Holl 2003*b*; plant nomenclature follows Hickman 1993). Exotic forbs, primarily *Erodium* spp., *Hypochaeris radicata, Plantago lanceolata*, and *Trifolium* spp., were more abundant at Swanton (47%) than at UCSC (29%) and Elkhorn (15%). Native grasses (*Danthonia californica* and *Nassella pulchra*) and forbs (*Eschscholzia californica* and *Madia sativa*) constituted 2–11% cover at the three sites.

Species Description

Holocarpha macradenia (Asteraceae: Madiinae) flowers from July to October. Most seeds remain on the plant until the first significant rain (15–30 mm) in late autumn. The basal rosette increases in size until approximately June, when plants produce a stem, which reaches a height of 0.3–0.8 m. Plants produce 1 to 60 flower heads (inflorescences) that have two types of achenes (hereafter “seeds”) with different morphologies and germination requirements. Seeds from ray flowers have a thicker seed coat, long-term dormancy, and complex germination cues. Seeds from disk flowers are lighter and narrower and do not appear to maintain viability in the soil after 1 year (S. Bainbridge, personal communication). Neither type of seed has any evident structure for dispersal, and most fall within 45 cm of the plant (G. Hayes, unpublished data).

Historically the species was found from Monterey through Contra Costa counties at elevations <300 m (Hickman 1993). Now, however, the species is limited to nine natural populations in Santa Cruz and northern Monterey County and a few introduced populations in Alameda County. The species is listed as endangered by the State of California and as threatened under the U.S. Endangered Species Act.

Experimental Design

At each site we installed a 52 × 52 m cattle exclosure in autumn 1998 and initiated experiments in January 1999. Within each exclosure we randomly allocated 30, 7 × 7 m plots to three replicates of 10 treatments (described below). A 1-m mowed buffer separated the plots.

We used a motorized rotary trimmer to clip vegetation to approximately 5 cm height at three frequencies: (1) 2 clippings/year, spring (March) and autumn (September); (2) 3 clippings/year, every other month through the growing season (January, March, May); and (3) 6 clippings/year, monthly through the growing season (January–June). We chose these treatments to provide a gradient of disturbance frequencies and to mimic common management regimes. The 2/year treatment was designed to constitute a feasible clipping frequency if cattle grazing were replaced with mowing. The 3/year treatment provided an intermediate level of disturbance and mimicked rotational grazing, where cattle are grazed intensively in an area for 3 to 5 days and rotated through areas at 45- to 60-day intervals (Savory 1988). The 6/year treatment equaled a high level of disturbance, simulating historical cattle grazing in California.

Each of the clipping frequencies was subjected to a secondary set of treatments designed to test three disturbances related to cattle grazing that affect plant community composition: reduced live vegetation cover, litter removal, and soil disturbance (see Hayes and Holl [2003*b*] for experimental design details). The litter removal treatment reduced litter depth but did not affect vegetation composition during the first 4 years of the study (Hayes & Holl 2003*b*). The soil disturbance treatment did not increase bare soil significantly, most likely because of extensive soil disturbance from burrowing mammal activity.

In addition to the nine clipping frequency × secondary treatment combinations, we included a "no disturbance" treatment where plots were neither clipped nor grazed. We established three additional 7 × 7 m plots in areas adjacent to the exclosure that were grazed by cattle. The seedlings planted in grazed plots at the Swanton site were heavily affected by feral pigs; therefore seedling and recruitment data from these plots are not presented. At Elkhorn cattle grazed the plots at a stocking rate of 6 animals/ha for approximately 4 days at 45- to 60-day intervals December–June each year, which is roughly equivalent to our 3/year treatment. At UCSC, 3 cattle/ha grazed the site continuously during March and May.

Treatment effects on vegetation community composition are presented elsewhere (Hayes & Holl 2003*b*). The primary effect of clipping was to favor exotic annual forbs and reduce cover of exotic annual grasses, whereas clipping had no effect on native perennial grasses.

Seed Germination and Seedling Survival, Reproduction, and Recruitment

We introduced *H. macradenia* as both seeds and seedlings because low and variable germination would have resulted in sufficiently small sample sizes to preclude analysis of treatment effects on seedling survival and reproduction. We collected seeds in August and September from the natural population nearest each site. We used only disk seeds because ray seeds do not germinate until after at least 1 year in the seed bank.

In early October 1999 and 2000, just before the onset of the winter rains, we placed 36 disk seeds 10 cm apart in a 6 × 6 seed grid on the soil surface in each plot. In 2003 we placed 36 seeds in the litter accumulation, litter removal, and no disturbance treatments at Elkhorn only to test whether litter accumulation affects germination 5 years after beginning the treatments, a substantial time for litter to accumulate. We recorded individual seeds that germinated in December and January of each year and summed the values to calculate percent germination. We removed germinating seeds at the end of this experiment. In 2003 we placed 36 seeds in petri dishes on moistened filter paper in the laboratory and recorded germination over a 2-week period. We placed five dishes in ambient light and covered five dishes with aluminum foil immediately after moistening to provide dark conditions.

We planted 25 seedlings 10 cm apart in a 5 × 5 plant grid in January 1999 and 2000 (all sites) and January 2001 (Elkhorn only, because of a lack of seedlings with the correct genetics for the other sites). Seedlings were grown in potting soil in a greenhouse from seed sown in late October the prior year. Seedlings were moved outdoors and fertilizer was withheld in late December to prepare the seedlings for field conditions. When planted, the seedling roots had filled the 3.5 cm deep × 1.5 cm wide planting cell, and seedlings had approximately four secondary leaves, a similar phenological stage to the natural populations. We monitored seedling survival once monthly during the growing season but present only data on survival to reproduction here because this is most relevant to population viability. We refer to earlier survival data to explain patterns observed at the end of the growing season. In each year seedlings were planted in a different corner of the plot with plantings separated by 3 m, so it is unlikely that seed dispersed between plantings. In only one case did we observe plants in subsequent years beyond a 1-m radius of the initial plantings.

From July through September of each year we monitored the number of small, medium, and large (1–5, 6–10, and ≥11 mm diameter, respectively) flowers on each plant and summed these for each year. We tried to count the number of apparently viable (darker, thicker) ray and disk seeds in five flowers of each size in each plot, but because of differential survival the total number of flowers counted was substantially less and was highly skewed toward treatments with higher survival. We had sufficient data to calculate mean number of disk and ray seeds in each flower size by site in 1999 but not to make comparisons across treatments.

For seedlings planted in January 1999 we estimated the production of disk and ray seeds produced per plot by multiplying number of plants surviving × flower production in each size category × site average number of ray and disk seeds in each flower size category. For disk seeds we multiplied this value by germination rates measured during autumn 1999 to provide a rough estimate of the number of seedlings we anticipated would recruit in winter 2000.

In autumn 2003 we took 10, 2.5 (diameter) × 2 cm (deep) soil cores in six 1 × 1 m plots at Elkhorn with the highest seed set in previous years. We did not sample from all plots because our main goal was to determine whether seeds remained in the seed bank after 2 years of minimal seed inputs and we wanted to minimize impacts on our plots.

In January 2000, 2001, and 2002 we monitored the number of seedlings recruited within a 1 × 1 m grid centered on areas where we had planted seedlings in prior years. We monitored additional recruits monthly February through May, marking each new recruit with a colored toothpick and removing markers for dead recruits. We calculated both the number of seedlings recruiting and the number surviving to reproduction. In 2003 and 2004 we monitored the number of plants that reproduced at the end of the growing season.

Statistical Analysis

The experiment had 11 levels (no disturbance, grazed, nine frequency [3] × litter removal/soil disturbance [3] treatments). As mentioned previously, our soil disturbance treatments did not increase bare ground, and in preliminary analyses in no case did the litter removal treatment have a significant effect on any *H. macradenia* life-history stage, so we pooled the data from the secondary treatments. We first analyzed data with two-way analysis of variance (ANOVA), with site and clipping frequency as fixed factors and the following response variables: germination, seedling survival, seed and flower production, and number of recruits. When treatment × site interactions were significant (all variables except germination), we conducted separate analyses by site. For most analyses, plots were considered the unit of replication and measurements for individual plants were averaged within plots. But for flower production the plant was considered the unit of replication because some plots had zero or one plant surviving to reproduction and others had numerous plants surviving. Therefore, averaging by plot would substantially overweight values from plants in plots with few plants. Treating plant as the unit of replication resulted in higher and more variable sample numbers for this analysis. Seed germination and seedling survival data, both percentages, were arcsine transformed before analysis. Other values were log transformed when necessary to meet the assumption of homogeneity of variance. We used Tukey's least significant difference mean comparison procedure to separate specific treatment effects when they were significant in the ANOVA. Throughout we report means ± 1 SE and consider $p < 0.05$ significant.

Results

Germination

Seed germination was much higher in 2000 than in 1999 (29.4 ± 2.2 vs. 11.8 ± 1.5%), although precipitation patterns were fairly similar in the 2 years. Germination was highest at Elkhorn and lowest at Swanton in both years with no significant site × treatment interaction (1999, Elkhorn = 15.9 ± 2.2%, Swanton = 6.2 ± 1.6%, UCSC = 13.3 ± 3.2%, $F = 5.3$, $p = 0.007$; 2000, Elkhorn = 45.7 ± 2.7%, Swanton = 8.5 ± 1.6%, UCSC = 34.0 ± 3.8%, $F = 53.9$, $p < 0.0001$).

In 2003 germination (Elkhorn only) was 34.9 ± 4.2% in the field compared with 63.3 ± 4.8% in light conditions and 64.4 ± 2.2% in dark conditions in the laboratory. Clipping and grazing enhanced seed germination in all years (1999, $F = 2.8$, $p = 0.034$; 2000, $F = 2.6$, $p = 0.045$; 2003: $F = 3.2$, $p = 0.049$), although not all pairwise comparisons between no disturbance and clipped or grazed plots were significant given high within-treatment variation (Fig. 1).

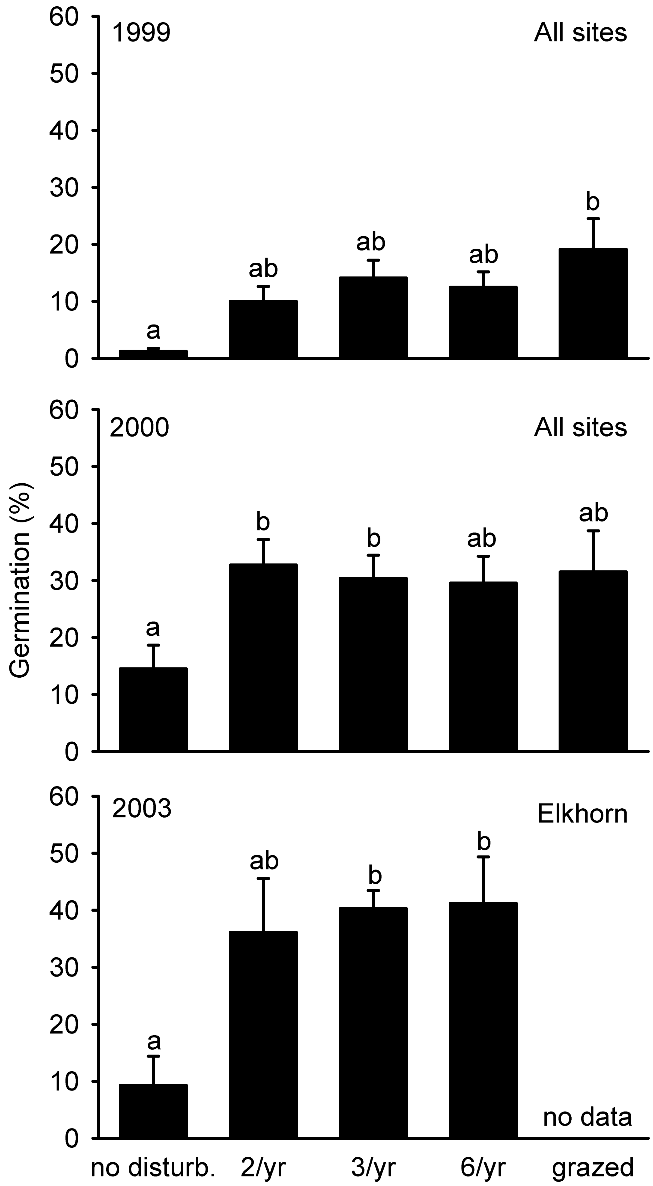

Figure 1. Seed germination (means ± SE by plot) of H. macradenia *in 3 years. Data for 1999 and 2000 are for all treatments (no disturbance, clipped twice per year, clipped three times per year, clipped six times per year, grazed) at all sites. Data for 2003 are for Elkhorn plots for all treatments except soil disturbance and grazing. Means with the same letter are not significantly different in Tukey's mean comparison procedure.*

Surprisingly, litter removal did not significantly affect seed germination in any year.

Seedling Survival

Survival of planted seedlings was much higher in 1999 (50.9 ± 3.0%) than in 2000 (10.2 ± 1.6%) or 2001 (11.1 ± 2.4% [Elkhorn only]) and was significantly higher at

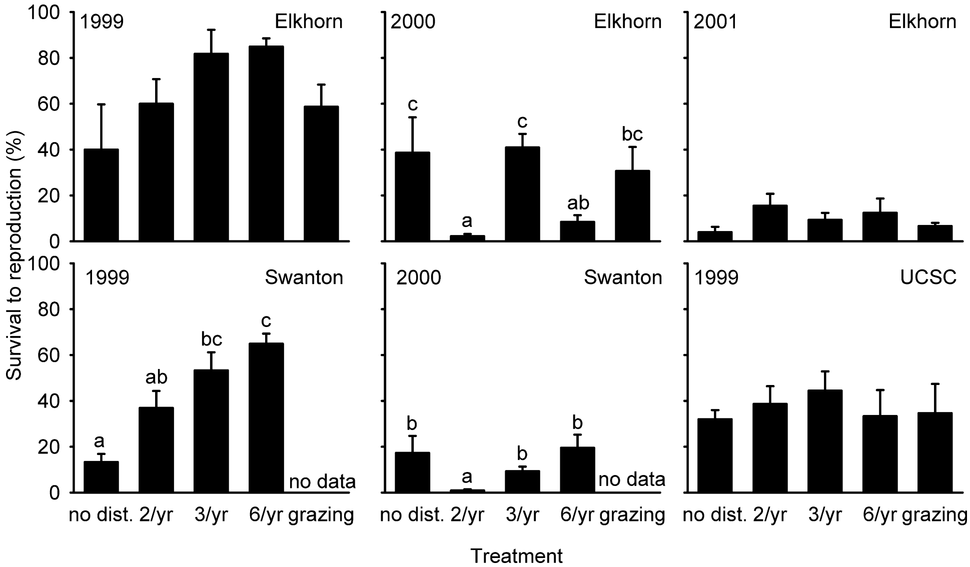

Figure 2. Survival to reproduction (means ± 1 SE by plot) of seedlings of H. macradenia *planted in 1999, 2000, and 2001 at Elkhorn, Swanton, and the University of California, Santa Cruz (UCSC), in all treatments (see Fig. 1 legend). Means with the same letter are not significantly different in Tukey's mean comparison procedure.*

Elkhorn (1999, $F = 4.4$, $p = 0.003$; 2000, $F = 14.8$, $p < 0.0001$; Fig. 2). At Elkhorn rainfall was lowest in 2001, and soil temperature from April through August was lowest in 1999 with temperatures 1–3° C higher in 2000 and 2–4° C higher in 2001. Litter-removal treatments did not affect seedling survival in any year.

Survival patterns differed across clipping treatments in the 3 years (Fig. 2). In 1999 survival at Swanton was highest in the 3/year and 6/year treatments and lowest in the no-disturbance treatment. Survival at Elkhorn showed a similar trend ($p = 0.063$), whereas survival was equal in all treatments at UCSC. In 2000 survival was lowest in 2/year clipped plots at Elkhorn and Swanton. A large portion of seedlings in 2/year plots died after the March clipping, in between the March and April censuses (data not shown). Only one plant survived to reproduction at UCSC in 2000. Survival at Elkhorn in 2001 was low in all treatments.

Flower and Seed Production

In 1999 total flower production and the proportion of small flowers was interactively affected by site and treatment (total flowers: site $F = 104.0$, treatment $F = 15.7$, site × treatment $F = 6.2$, $p < 0.0001$ in all cases; percent small flowers: site $F = 19.8$, treatment $F = 13.1$, site × treatment $F = 5.2$, $p < 0.0001$ in all cases). In general, total flower production was higher and proportion of small flowers was lower at Elkhorn and in clipped plots at all sites (Fig. 3). In 2000 and 2001, survival was sufficiently low in many plots to preclude comparisons.

Seed number per flower was slightly lower at UCSC, and the number of ray seeds was higher than disk seeds in all flower sizes (Table 1). Seed production per plot was much higher at Elkhorn than at UCSC or Swanton (disk $F = 28.2$, ray $F = 22.9$, $p < 0.0001$ in all cases; Fig. 4). Seed production was generally higher in more frequently clipped plots and intermediate in grazed plots (Fig. 4).

Four of the six seed bank samples collected in autumn 2003 contained 1019–1218 intact ray seeds/m^2. One had no seeds and the other had 406 ray seeds/m^2.

Recruitment and Survival of Recruits

Not surprisingly, the number of seedlings recruiting from 1999 plants was highest at Elkhorn in 2000–2002. At Elkhorn there were no treatment effects on recruitment in 2000, whereas in 2001 and 2002 recruitment was higher in more frequently clipped plots compared with no-disturbance and grazed plots (Fig. 5: 2000, $F = 2.1$, $p = 0.113$; 2001, $F = 5.1$, $p = 0.003$; 2002, $F = 3.7$, $p = 0.016$). At Swanton and UCSC the number of seedlings recruiting was low in all years. At Swanton recruitment was higher in more frequently clipped plots in 2000 only ($F = 5.4$, $p = 0.005$). At UCSC recruitment was higher in grazed plots in 2000 ($F = 3.6$, $p = 0.018$), primarily due to a large number of recruits in one grazed plot, with no significant treatment effects thereafter. The number of recruits per plot in 2000 was significantly correlated with the number of disk seeds set by plants in 1999 multiplied by germination measured in autumn 1999 ($r = 0.37$, $p = 0.032$). Recruit number in plots in 2000 and 2001 was strongly correlated with the number of ray seeds set in 1999 (2000, $r = 0.56$, $p < 0.0001$; 2001, $r = 0.77$, $p < 0.0001$).

Few recruiting seedlings survived to reproduction at Swanton or UCSC (<10 at each site in 2000 and 2001, 0 in 2002). At Elkhorn 2.2 ± 0.5 (2002) to 3.8 ± 1.1 (2001) seedlings per plot survived with no significant treatment effects. Survival of recruits from 1999 seedlings at Elkhorn (2000, 8.6 ± 1.9%; 2001, 11.6 ± 3.0%; 2002, 10.6 ± 2.8%) was much lower than for outplanted plants. In 2003 only three plants survived, one at Swanton and two at Elkhorn.

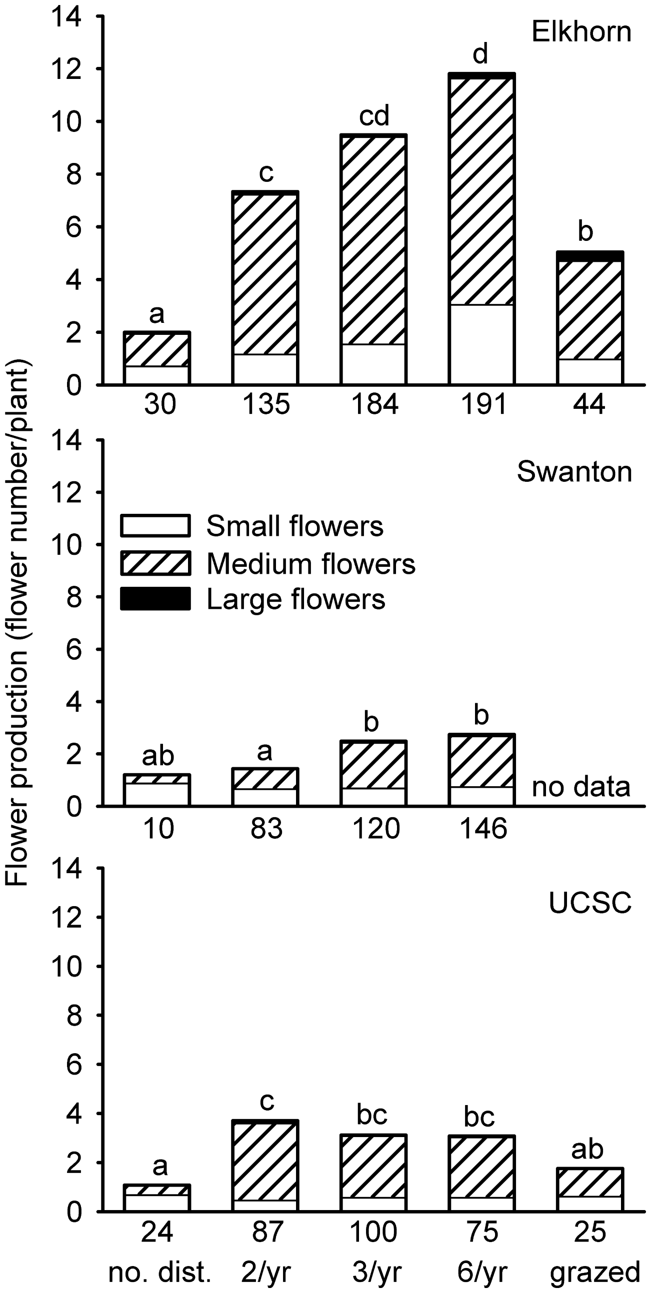

Figure 3. Flower production (means ± 1 SE by plant) on seedlings of H. macradenia *planted in 1999 at Elkhorn, Swanton, and the University of California, Santa Cruz (UCSC), in all treatments (see Fig. 1 legend). Sample sizes of plants are listed below each bar. Mean flower production values with the same letter are not significantly different in Tukey's mean comparison procedure.*

In 2004 plants were observed in multiple plots in late May, but none survived to reproduction.

No seedlings recruited in any year at UCSC from seedlings outplanted in 2000, and only one seedling recruited at Swanton. Recruitment from 2000 seedlings was low at Elkhorn, with an average of 2.0 ± 0.8 seedlings/plot in 2001 and 4.0 ± 1.2 seedlings/plot in 2002. In 2002 recruitment was higher in 3/year than 2/year clipped plots (Fig. 5). Survival to reproduction was higher (2001, 42.0 ± 18.2%; 2002, 26.1 ± 7.0%) than for recruits from 1999 plants; however, given the low number of recruits at the outset few seedlings survived to reproduction. In 2003 and 2004, no recruits from 2000 seedlings survived to reproduction.

Discussion

Disturbance

Our data clearly indicate that clipping increased *H. macradenia* population viability over time; this is consistent with anecdotal observations and related demographic modeling of *H. macradenia* (Hayes 1998; Barber 2002; Satterthwaite 2004) and a broad body of literature showing that grazing favors native annual forbs (e.g., Grubb 1986; Noy-Meir et al. 1989; McIntyre et al. 1995; Sternberg et al. 2000), although most species studied have been low-stature forbs. In our study, disturbance effects were most clear at the germination life-history stage. This result is most likely due to fluctuations in soil temperature, which may serve to stratify seeds and enhance seed germination (Fowler 1988; Gregory et al. 2001), because our greenhouse experiments indicated that *H. macradenia* germination is not light induced.

In grasslands, a shorter canopy may reduce light competition for seedlings (Grubb 1986; Tilman 1993) and enhance flower production of tall-stature annuals (Pavlik et al. 1993; Carlsen et al. 2000). Clipping increased flower and seed production in the 1 year for which sufficient data were available, whereas the effect of clipping on survival varied with year. More-frequent clipping resulted in higher survival of planted seedlings in 1999, and there was a similar nonsignificant trend in 2001. Elasticity analyses of demographic models of *H. macradenia* (Satterthwaite 2004) suggest that, aside from increasing the survival of the ray seed bank, increasing seedling survival to flowering and fecundity is most important for ensuring population viability.

Interestingly, seedling survival in 2000 was lowest in 2/year treatments, which may reflect morphological responses to light availability (Rincon & Grime 1989). Early rains resulted in a flush of exotic grasses, and by spring exotic grass cover was similar in no disturbance plots and 2/year plots. With high light competition, *H. macradenia* seedlings etiolated and did not create robust basal rosettes (G.F.H., personal observation), which most likely explains the high mortality of seedlings in 2/year treatments after the March clipping.

We were surprised that litter removal did not enhance seedling numbers, and, in particular, germination after 5

Table 1. Number of seeds per flower of *H. macradenia* in 1999.[a]

		Location		
Flower size	*Seed type*	*Elkhorn* (n)	*Swanton* (n)	*UCSC*[b]
Small	disk	0.9 ± 0.2 (87)	0.3 ± 0.1 (47)	0.5 ± 0.2 (36)
	ray	3.5 ± 0.3 (87)	4.7 ± 0.3 (47)	2.7 ± 0.3 (36)
Medium	disk	3.9 ± 0.4 (180)	3.6 ± 0.4 (113)	1.8 ± 0.3 (64)
	ray	7.5 ± 0.3 (180)	7.6 ± 0.4 (113)	5.8 ± 0.3 (64)
Large	disk	12.5 ± 1.5 (21)	8.1 ± 1.9 (7)	8.0 ± 2.1 (3)
	ray	14.4 ± 1.4 (21)	14.0 ± 0.8 (7)	12.1 ± 1.9 (3)

[a] *Values are mean ± SE (*n*).*
[b] *University of California, Santa Cruz.*

years of treatments. Litter-accumulation treatments had thicker litter (Hayes & Holl 2003*b*), which can inhibit seed germination (Facelli & Pickett 1991; Myster 1994; Reynolds et al. 2001; but see Pavlik et al. 1993). Light and temperature fluctuation may have been sufficient to cue germination in all clipped treatments because no disturbance plots were the only plots with phytomass >5 cm in height at the onset of the rainy season.

Anecdotal evidence (USFWS 2000) suggests that grazing benefits *H. macradenia*, which may be in part due to cows avoiding eating this species (A. Barber and G.F.H., personal observation). Clipping, in contrast, treats all plant species equally, and we often clipped *H. macradenia* later in the growing season. Yet seedling survival was generally equal in grazed and clipped plots and seed production was somewhat lower in grazed plots. We had few replicate plots in the grazed areas, grazing has much patchier effects than clipping, and grazing has additional effects, including trampling and nutrient redistribution. Regardless, our results suggest that properly timed mowing is a viable management alternative for *H. macradenia* in small areas where grazing is not feasible.

Translocation

Our results do not support translocation efforts. We introduced *H. macradenia* into three apparently suitable sites in multiple years with a range of management regimes, yet it appears that none of these populations was viable. Because seeds remain in the seedbank, population numbers may increase in the future, but we consider this prospect unlikely given 3 consecutive years of few individuals surviving to reproduction. Other *H. macradenia* introduction efforts show slightly better, but still low, success. By the mid-1980s all the Alameda and Contra Costa county populations were destroyed by development. Seeds from the last three populations were collected and introduced at multiple, apparently suitable sites between 1982 and 1986 (Howald 1996). Of the 16 introduced populations for which there are long-term data, 7 had > 2 individuals in any year between 1998 and 2004, and only 1 consistently had >200 individuals (East Bay Parks, unpublished data). We consider four possible explanations for the failure of our introduction efforts; all are common to many translocation efforts.

First, we may have chosen poor-quality habitat. We selected sites that had similar vegetation composition and soil to existing populations (Bainbridge 2003; A. Barber & T. Edell, unpublished data), typical criteria for categorizing suitable habitat. The more robust Elkhorn experimental population is only a few hundred meters from a natural population. Our demographic transition rates for plants from greenhouse grown seedlings in 1999 were similar to those from natural populations (Bainbridge 2003), but survival in subsequent years of both outplants and recruits was much lower, suggesting that our sites were not good habitat. For example, in two of the larger remnant populations in 2001 and 2002, Bainbridge (2003) recorded 171–435 seedlings/m^2 recruiting in grazed and mowed plots, whereas we recorded 32–84 seedlings/m^2 in clipped plots in the best year at the best site and < 20 seedlings/m^2 in most plots. In 2001 survival of naturally recruiting plants at our sites (11%) was much lower than that recorded by Bainbridge (39–77%). More detailed analysis of habitat parameters such as herbivory or pathogen pressure and soil microbial communities is needed to increase introduction success of this and other species (Parker et al. 1993; Falk et al. 1996; Morgan 1999).

Second, our introductions could have been poorly timed with respect to climatic conditions. Anecdotally, *H. macradenia* is reputed to need high rainfall particularly later in the rainy season, and Levine and Rees' results (2004) show that a high rainfall year after a low rainfall year benefits annual grassland forbs. But it is difficult to determine correlatively what makes a "good *H. macradenia* year" because long-term data (10–20 years) on existing populations show asynchronous fluctuations in population size (Satterthwaite 2004), which is partly because populations are subjected to different management regimes. Moreover, total rainfall is often a poor indicator of water stress in arid climates because frequency and intensity of precipitation events, and site-specific differences in soil texture profiles, strongly influence water availability (Loik et al. 2004). The particularly hot, dry year in 2001 most likely played a factor in the low survival and input into the seed bank. We emphasize, however, that

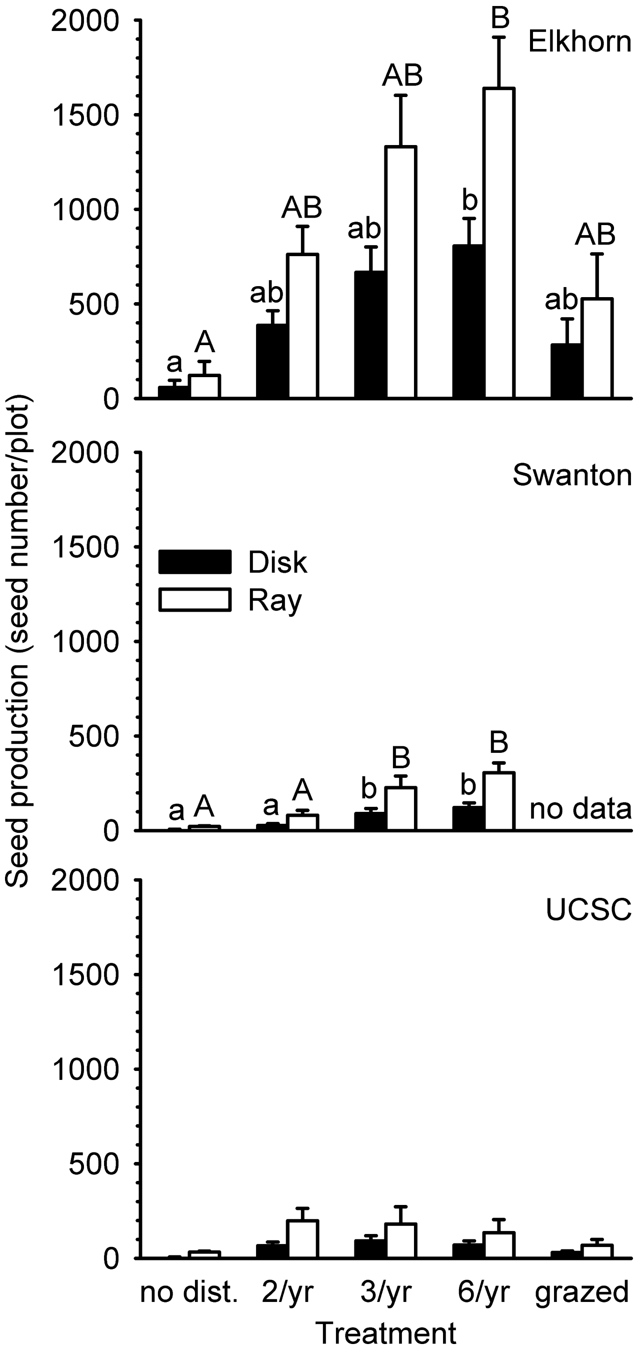

Figure 4. Seed production (means ± 1 SE) per plot of H. macradenia *from seedlings planted in 1999 at Elkhorn, Swanton, and the University of California, Santa Cruz (UCSC), in all treatments (see Fig. 1 legend). Means with the same letter are not significantly different in Tukey's mean comparison procedure (lower case letters, disk seeds; upper case letters, ray seeds).*

we introduced plants in 3 years, which is more than most reintroduction efforts.

Third, results of previous studies suggest that the number of plants introduced is often too small to establish viable populations (Krauss et al. 2002; Lennartsson 2002; but see Morgan 2000). We outplanted 750 plants per site, which is larger than some existing populations and not unusually low for experimental introductions. But it is a much smaller number than the large natural *H. macradenia* populations, and some of our plants were introduced into treatments with low survival. We collected seeds from large populations to minimize the risk of inbreeding, although we cannot rule out this possibility. Moreover, Barber (2002) found that smaller natural populations had similar seed production and viability to larger populations when grown in a common environment. Small population size may have had other size-related effects such as low pollination (Lennartsson 2002) or extensive herbivore pressure (Maze 2004).

Finally, lack of an established seed bank, a critical factor that is often overlooked in assessing population viability of annual plants (Pavlik & Espeland 1998; Menges 2000; Adams et al. 2005), was most likely important in the decline of our populations (Satterthwaite 2004). To distinguish recruits from plants introduced in different years, we separated plantings by a distance sufficient to ensure minimal movement of seeds. As a result, the input to the seed bank was for a single year by relatively few plants. The large natural populations have variable seed banks, ranging from approximately 500 seeds/m^2 to 30,000–35,000 seeds/m^2 (Bainbridge 2003). Demographic modeling by Satterthwaite (2004) demonstrates that *H. macradenia* population viability, even under an ideal disturbance regime, depends on germination from the ray seed bank to buffer against highly variable interannual climatic conditions typical of Mediterranean regions. Therefore, establishing a seed bank is an important consideration in the long-term introduction success of this species and, most likely, most annual plants with long-term dormancy in variable climates; however, this requires a large input of seeds, which can be problematic when working with rare plants (Pavlik & Espeland 1998).

Conclusions

First, maintaining populations of *H. macradenia*, and many native annual forbs in temperate grasslands, will require properly timed disturbances such as grazing or mowing (e.g., Noy-Meir et al. 1989; Lennartsson & Oostermeijer 2001; Hayes & Holl 2003*a*). Second, successful introduction of rare plants requires extremely detailed knowledge of habitat requirements, which is rarely available, even for well-studied species. Third, even with such information reintroductions will be successful only if plants are introduced at multiple sites in multiple years, given interannual climatic variation and subtle site-specific differences (Falk et al. 1996; Drayton & Primack 2000), which makes introduction an expensive measure

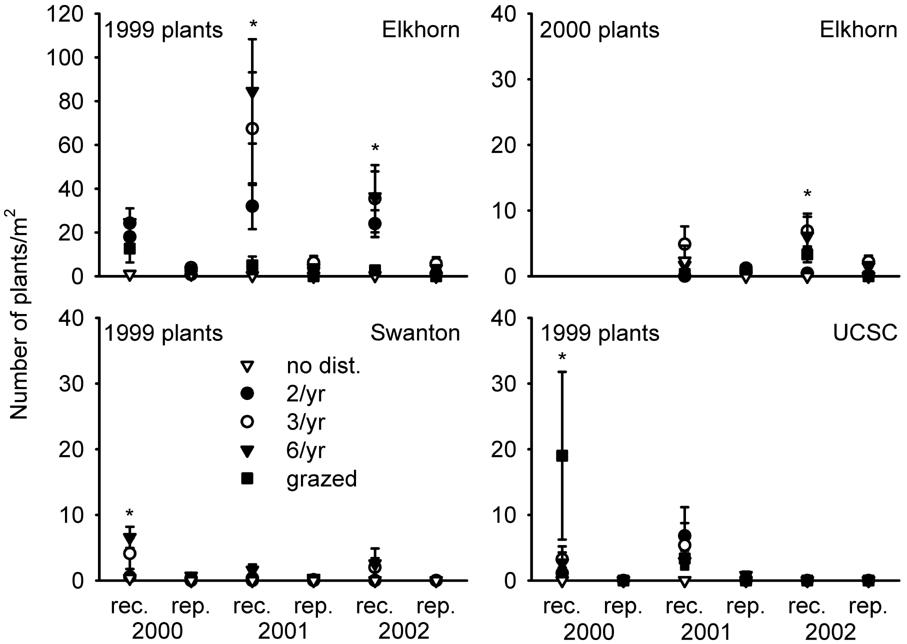

Figure 5. Number of plants (means ± 1 SE) recruiting from seeds of H. macradenia *produced by plants outplanted in 1999 at Elkhorn, Swanton, and the University of California, Santa Cruz (UCSC), in all treatments (see Fig. 1 legend) and 2000 (Elkhorn only). Recruits (rec.) is the total number of recruits counted in each year and reproduction (rep.) is the number of those plants that survived to reproduce. The y-axis scales are different (*indicates a significant [*p* < 0.05] treatment effect).*

to mitigate for habitat destruction. Finally, we repeat the oft-made call for long-term monitoring of introduction efforts (e.g., Falk et al. 1996; Guerrant & Pavlik 1998; Morgan 1999). If we had stopped monitoring after 3 years, a typical period for introduction efforts, we would have judged this project successful, despite the fact that the populations subsequently declined drastically.

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Literature Cited

Adams, V. M., D. M. Marsh, and J. S. Knox. 2005. Importance of the seed bank for population viability and population monitoring in a threatened wetland herb. Biological Conservation **124:**425–436.

Bainbridge, S. 2003. *Holocarpha macradenia* Green (Santa Cruz tarplant) demography and management studies. Report prepared for California Department of Fish and Game, Sacramento. Available from http://www.elkhornsloughctp.org/uploads/1108413913Bainbridge.pdf (accessed April 2005).

Barber, A. 2002. Conservation of a rare California wildflower: a case study of the Santa Cruz tarplant. B.S. thesis. Brown University, Providence, Rhode Island.

Carlsen, T. M., J. W. Menke, and B. M. Pavlik. 2000. Reducing competitive suppression of a rare annual forb by restoring native California perennial grasslands. Restoration Ecology **8:**18–29.

Collins, S. L., A. K. Knapp, J. M. Briggs, J. M. Blair, and E. M. Steinauer. 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. Science **280:**745–747.

D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics **23:**63–87.

Drayton, B., and R. B. Primack. 2000. Rates of success in the reintroduction by four methods of several perennial plant species in eastern Massachusetts. Rhodora **102:**299–331.

Facelli, J. M., and S. T. A. Pickett. 1991. Plant litter: its dynamics and effects on plant community structure. Botanical Review **57:**1–32.

Falk, D. A., C. I. Millar, and M. Olwell. 1996. Restoring diversity: strategies for reintroduction of endangered plants. Island Press, Washington, D.C.

Fiedler, P. L. 1991. Mitigation-related transplantation, relocation and reintroduction projects involving endangered and threatened, and rare plant species in California. Report FG-8611. California Department of Fish and Game, Sacramento.

Fowler, N. 1988. What is a safe site? Neighbor, litter, germination date, and patch effects. Ecology **69:**947–961.

Gregory, S. D., E. K. Espeland, and T. M. Carlsen. 2001. Demography and population biology of a rare tarplant, *Blepharizona plumosa* (Asteraceae), a California summer annual forb. Madroño **48:**272–285.

Grubb, P. J. 1986. Problems posed by sparse and patchily distributed species in species-rich plant communities. Pages 207–225 in J. Diamond and T. J. Case, editors. Community ecology. Harper & Row, New York.

Guerrant, E. O. Jr., and B. M. Pavlik. 1998. Reintroduction of rare plants: genetics, demography, and the role of *ex situ* conservation methods. Pages 80–108 in P. L. Fiedler and P. M. Kareiva, editors. Conservation biology. Chapman & Hall, New York.

Hayes, G. 1998. The saga of the Santa Cruz tarplant. Four Seasons **10:**18–21.

Hayes, G. F., and K. D. Holl. 2003*a*. Cattle grazing impacts on vegetation composition and structure of mesic grasslands in California. Conservation Biology **17:**1694–1702.

Hayes, G. F., and K. D. Holl. 2003*b*. Site-specific responses of native and exotic species to clipping frequency, litter accumulation and soil disturbance in a mesic grassland community. Applied Vegetation Science **6:**235–244.

Hickman, J. 1993. The Jepson manual. University of California, Berkeley.

Hobbs, R. J., and L. F. Huenneke. 1992. Disturbance, diversity, and invasion: implications for conservation. Conservation Biology **6:**324–337.

Hobbs, R. J. and H. A. Mooney. 1991. Effects of rainfall variability and gopher disturbance on serpentine annual grassland dynamics. Ecology **72:**59–68.

Hodgson, J. G., J. P. Grime, P. J. Wilson, K. Thompson, and S. R. Band. 2005. The impacts of agricultural change (1963–2003) on the grassland flora of Central England: processes and prospects. Basic and Applied Ecology **6:**107–118.

Hoekstra, J. M., T. M. Boucher, T. H. Ricketts, and C. Roberts. 2005. Confronting a biome crisis: global disparities of habitat loss and protection. Ecology Letters **8:**23–29.

Holmes, P. M., and D. M. Richardson. 1999. Protocols for restoration based on recruitment dynamics, community structure, and ecosystem function: perspectives from South African fynbos. Restoration Ecology **7:**215–230.

Howald, A. M. 1996. Translocation as a mitigation strategy: lessons from California. Pages 293–329 in D. Falk, C. I. Millar, and M. Olwell, editors. Restoring diversity. Island Press, Washington, D.C.

Huenneke, L. F., and H. A. Mooney. 1989. The California annual grassland: an overview. Pages 213–218 in L. F. Huenneke and H. A. Mooney, editors. Grassland structure and function: California annual grassland. Kluwer Academic Publishers, Dordrecht, Netherlands.

Kaye, T. N., K. L. Pendergrass, K. Finley, and J. B. Kauffman. 2001. The effect of fire on the population viability of an endangered species. Ecological Applications **11:**1366–1380.

Krauss, S. L., B. Dixon, and K. W. Dixon. 2002. Rapid genetic decline in a translocated population of the endangered plant *Grevillea scapigera*. Conservation Biology **16:**986–994.

Lennartsson, T. 2002. Extinction thresholds and disrupted plant-pollinator interactions in fragmented plant populations. Ecology **83:**3060–3072.

Lennartsson, T., and J. G. B. Oostermeijer. 2001. Demographic variation and population viability in *Gentianella campestris*: effects of grassland management and environmental stochasticity. Journal of Ecology **89:**451–463.

Levine, J. M., and M. Rees. 2004. Effects of temporary variability on rare plant persistence in annual systems. The American Naturalist **164:**350–363.

Loik, M. E., D. D. Breshears, W. K. Lauenroth, and J. Belnap. 2004. A multiscale perspective of water pulses in dryland ecosystems: climatology and ecohydrology of the western USA. Oecologia **141:**269–281.

Maze, D. 2004. The effect of mollusk herbivory on Santa Cruz tarplant. B.S. thesis. University of California, Santa Cruz.

McIntyre, S., and S. Lavorel. 1994. Predicting richness of native, rare, and exotic plants in response to habitat and disturbance variables across a variegated landscape. Conservation Biology **8:**521–531.

McIntyre, S., S. Lavorel, and R. M. Tremont. 1995. Plant life-history attributes: their relationship to disturbance response in herbaceous vegetation. Journal of Ecology **83:**31–44.

Menges, E. S. 2000. Applications of population viability analysis in plant conservation. Ecological Bulletins **48:**73–84.

Morgan, J. W. 1999. Have tubestock plantings successfully established populations of rare grassland species into reintroduction sites in western Victoria? Biological Conservation **89:**235–243.

Morgan, J. W. 2000. Reproductive success in reestablished versus natural populations of a threatened grassland daisy (*Ritidosis liptorrhynchoides*). Conservation Biology **14:**780–785.

Munz, P. A., and D. D. Keck. 1968. A California flora. University of California Press, Berkeley.

Myster, R. W. 1994. Contrasting litter effects on old field tree germination and emergence. Vegetatio **114:**169–174.

Noy-Meir, I. 1995. Interactive effects of fire and grazing on structure and diversity of Mediterranean grasslands. Journal of Vegetation Science **6:**701–710.

Noy-Meir, I., M. Gutman, and Y. Kaplan. 1989. Responses of Mediterranean grassland plants to grazing and protection. Journal of Ecology **77:**290–310.

Parker, I. M., S. K. Mertens, and D. W. Schemske. 1993. Distribution of seven native and two exotic plants in a tallgrass prairie in southeastern Wisconsin: the importance of human disturbance. American Midland Naturalist **130:**43–55.

Pavlik, B. M., and A. Enberg. 2001. Developing an ecosystem perspective from experimental monitoring programs. I. Demographic responses of a rare geothermal grass to soil temperature. Environmental Management **28:**225–242.

Pavlik, B. M., and E. K. Espeland. 1998. Demography of natural and reintroduced populations of *Acanthomintha duttonii,* an endangered serpentinite annual in northern California. Madroño **45:**31–39.

Pavlik, B. M., D. I. Nickrent, and A. M. Howald. 1993. The recovery of an endangered plant. I. Creating a new population of *Amsinkia grandiflora*. Conservation Biology **7:**510–525.

Reynolds, S. A., J. D. Corbin, and C. M. D'Antonio. 2001. The effects of litter and temperature on the germination of native and exotic grasses in a coastal California grassland. Madroño **48:**230–235.

Rincon, E., and J. P. Grime. 1989. Plasticity and light interception by six bryophytes of contrasted ecology. Journal of Ecology **77:**439–446.

Romermann, C., T. Dutoit, P. Poschlod, and E. Buisson. 2005. Influence of former cultivation on the unique Mediterranean steppe of France and consequences for conservation management. Biological Conservation **121:**21–33.

Satterthwaite, W. H. 2004. Dispersal in space and time and its importance to plant population dynamics. Ph.D. dissertation. University of California, Santa Cruz.

Savory, A. 1988. Holistic resource management. Island Press, Covelo, California.

Sternberg, M., M. Gutman, A. Perevolotsky, E. D. Ungar, and J. Kigel. 2000. Vegetation response to grazing management in a mediterranean herbaceous community: a functional group approach. Journal of Applied Ecology **37:**224–237.

Stromberg, M. R., P. Kephart, and V. Yadon. 2001. Composition, invasibility, and diversity in coastal California grasslands. Madroño **48:**236–252.

Tilman, D. 1993. Species richness of experimental productivity gradients: how important is colonization limitation? Ecology **74:**2179–2191.

USFWS (U.S. Fish and Wildlife Service). 2000. Endangered and threatened wildlife and plants; threatened status for *Holocarpha macradenia* (Santa Cruz tarplant). Federal Register **65:**14898–14908.