Effects of Established Perennial Grasses on Introduction of Native Forbs in California

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Abstract

Prairie restoration is not complete without the establishment of both grasses and forbs. However, if desirable forbs and grasses are seeded simultaneously, control of broadleaf weeds is problematic. If possible, a two-step process of introducing forbs after establishing grasses would allow use of broadleaf-specific herbicides at the critical early stages of grass growth. We conducted experiments to investigate methods for introducing forbs into previously restored native perennial grasslands on rural roadsides in the Sacramento Valley of California. In one experiment, we studied the effects of background vegetation (established perennial grasses or tilled ground) on seven native forb species planted from seed. In a second experiment, we evaluated the effects of background vegetation (existing perennial grasses or tilled ground) and container size (36 ml or 105 ml) with excavation technique (excavation by core removal [core] or by creating an impression [dibble]) on the growth of transplants of the native perennial forbs *Asclepias fascicularis* and *Sisyrinchium bellum*. The presence of established perennial grasses reduced the growth of seeded forbs, but did not affect transplants, indicating the vulnerability of seedling forbs to interference. When compared to control plots that had been tilled in the autumn, weed canopy cover was significantly lower in the presence of perennial grasses if seeded with forbs, but not in the presence of perennial grasses alone. Both transplanted species grew better in the large container/core treatment than the small container/dibble treatment; however, existing grasses eliminated these positive effects. *Asclepias fascicularis* performed better when grown in large containers than in small containers, but its growth was not affected by excavation method; *S. bellum* performed better when planted with the core method than the dibble method of excavation, but container size made no difference. We attribute differences in the responses of the species to interactions between phenological differences and expansive clay soils that naturally de-compact upon drying.

Key words: perennial grasses, California native species, forbs, prairie restoration, transplanting methods, seeding methods.

Introduction

Restoration of perennial grasslands along rural roadsides in the Sacramento Valley of California has been successfully practiced without including the herbaceous dicotyledon component (Bugg et al. 1997). Although forb species are an important part of the California prairie community, their initial exclusion has allowed the use of broadleaf-specific herbicides during establishment of the grasses. Introduction of native broadleaf species can be a second step in the restoration process. The most cost-effective method of introducing these species may be direct seeding. However, some California native perennial forbs can have relatively poor seedling vigor, and therefore may not be suitable for direct seeding into restoration sites with high densities of weed seed, or into established stands of vigorous perennial grasses. Alternatives to direct seeding include dividing and transplanting individuals from existing populations or planting container stock grown from seed. In either case, ease of production and transplantation and success of establishment in various settings are important criteria by which the techniques should be judged.

Here, we present two experiments investigating the introduction of forb species into established perennial grass stands. The first tested the effect of background vegetation on a mixture of direct seeded forb species. The species seeded included the annuals *Eschscholzia californica* A. Gray (California poppy), *Phacelia tanacetifolia* Benth. (tansy phacelia), *Lotus purshianus* Benth. (Spanish clover), *Lupinus succulentus* Koch (arroyo lupine), *Lupinus densiflorus* var. *microcarpus* Sims (chick lupine), and the perennials *Asclepias fascicularis* Decne. (narrowleaf milkweed) and *Sisyrinchium bellum* S. Watson (blue-

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eyed-grass). In the second experiment, we tested effects of production method, excavation technique, and background vegetation on the growth of *A. fascicularis*, a summer-growing rhizomatous perennial dicotyledon, and *S. bellum*, a winter-growing rhizomatous perennial monocotyledon.

These plants are desirable in rural roadside and other farmscape plantings for aesthetic and ecological reasons. *Asclepias fascicularis* is an important larval host plant for monarch butterfly (*Danaus plexippus* L., Lepidoptera: Danaidae), and attracts many nectarivorous and aphidophagous insects as well (Morse 1985). *Sisyrinchium bellum* produces blue flowers that many humans find beautiful, but which attract few insect visitors (C. D. Thomsen 1992, personal communication). *Lupinus* species and *Lotus purshianus* are nitrogen-fixing plants that can help increase soil fertility and are larval hosts to various butterflies (e.g., Lycaenidae). *Eschscholzia californica* is the state flower of California and attracts various solitary bees. As with many restoration sites, source populations of these and other native forb species were too distant to permit prompt natural dispersal and colonization.

Methods

Two trials were conducted within county road rights-of-way at Hedgerow Farms, approximately 8 km north of the town of Winters, Yolo County, California.

Seeded Forb Trial

The first trial tested establishment of forb species seeded into low-density perennial grasses that were planted in January 1992 across the topographic zones of the roadside (Fig. 1a). Experimental plots were approximately 7.62 m long (parallel to the traveled way) and approximately 7.62 m wide (across the topographic zones) (Fig. 1b). Plot width depended on how the area had been graded originally and proximity of the adjacent agricultural field. The experiment was a randomized complete block design with five blocks and three treatment levels, which are described below (15 plots total). Blocks I and II were located on Brentwood silty clay loam (fine, montmorillonitic, thermic Typic Xerochrepts [Class 1 agricultural soil]) and blocks III, IV, and V on Capay silty clay (fine, montmorillonitic, thermic Typic Haploxererts [Class 2 agricultural soil]). There were three background vegetation levels: (1) existing perennial grasses (grass alone); (2) existing perennial grasses seeded with forb mix (grass-with-forb mix); and (3) tilled plots seeded with forb mix (tilled-with-forb mix). Plots for the tilled-with-forb mix treatment were rototilled to a depth of 10–15 cm and hand cultivated to break up clods during the week before seeding. The grass-with-forb mix treatment plots were hand cultivated (2–3 cm deep) and the grass-alone plots were undisturbed.

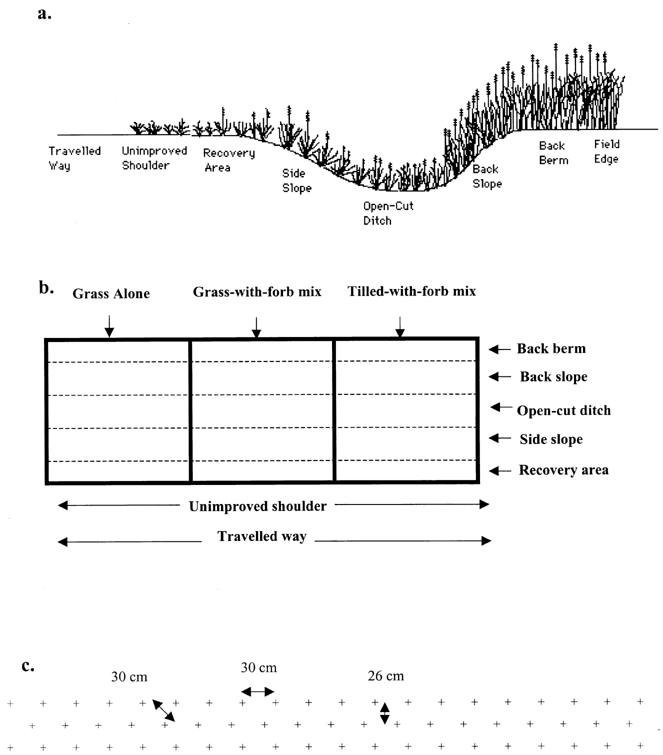

Figure 1. (a) Schematic diagram of roadside topographic zones. (b) Example layout of a single block of the seeded forb experiment. Locations of treatments were randomized within each block. (c) Layout of transplanted seedlings within a single background vegetation treatment. Each + represents a single plant. Two forb species and three container size/excavation technique treatment combinations were randomly assigned to each of the 60 locations (10 replicates of each treatment combination).

Forbs were planted by hand broadcasting a mixture of seed evenly across the grass-with-forb mix and tilled-with-forb mix treatment plots on 19 or 25 January 1993. Seeding density information is summarized in Table 1. The seed was mixed with commercial potting soil to aid in even distribution. The plots were divided into five sections and the appropriate subsample of seed was broadcast into each section. Seed was not incorporated after distribution.

Canopy cover and densities of perennial grasses for the grass alone and grass-with-forb mix treatment plots were estimated for all species but *Poa secunda* ssp. *secunda* before seeding the forbs on 24 September 1992. Because *Poa* remained dormant in the fall, this species was evaluated 16 December 1992 after it began to grow. Canopy cover was estimated using a slightly modified

Table 1. Forb species, seeding rates, and seed viability. Pure live seed values are based on commercial seed laboratory tests unless otherwise noted.

Common Name	*Scientific Name*	*Seeding Rate (kg/ha)*	*Pure Live Seed (%)*
Narrow-leaf milkweed	*Asclepias fascicularis*	1	65++
California poppy	*Eschscholzia californica*	2.2	67
Spanish clover	*Lotus purshianus*	2.2	60+
Chick lupine	*Lupinus microcarpus* ssp. *densiflorus*	6.7	94
Arroyo lupine	*Lupinus succulentus*	6.7	97*+
Tansy phacelia	*Phacelia tanacetifolia*	1.1	85*
Blue-eyed-grass	*Sisyrinchium bellum*	1.1	64

*Germination rather than pure live seed percentage because no estimate of purity was available for calculation.
+Estimates from tests with 100 seeds.
++Approximated from germination in greenhouse propagation of transplants.

Daubenmire (1959) method (i.e., 0 and trace categories were added) including eight cover classes (not present = 0%, trace = >0% and <1%, 1 = 1–5%, 2 = 5–25%, 3 = 25–50%, 4 = 50–75%, 6 = 95–100%). Midpoints of the cover classes were analyzed, as specified in Daubenmire (1959). A 0.5-m × 1.0-m quadrat was placed in two regularly spaced locations within each of three topographic zones (side slope, open-cut ditch, and back slope), percent cover was visually estimated, and the number of individuals of each species within the quadrat was counted. The response for each variable in a given topographic zone was the mean of the two subsamples. The perennial grass cover and density data are summarized in Table 2.

Forb densities were evaluated on 3 April 1993 using a 0.5-m × 0.25-m quadrat. Canopy cover of forbs, perennial grasses, and weeds (i.e., species that were not seeded) were estimated 2–14 May 1994 as described above in blocks I through IV. Due to experimenter error, canopy cover estimates were available only for the tilled-with-forb mix treatment in block V. To estimate cover, the quadrat was placed in three regularly spaced locations within each of three topographic zones (side slope, open-cut ditch, and back slope) and the mean of the nine subsamples was used as the plot response for each variable. Percent emergence (density of seedlings on April sampling date/density of viable seed planted) and percent cover (May sampling date) were separately evaluated using analysis of variance (ANOVA) of plot means for the mixture of forbs and for each individual forb species. The tilled-with-forb mix and grass-with-forb mix treatments were compared; grass alone treatments were not included. Due to inequality of variances that could not be corrected with transformation ($Y' = \arcsin[\sqrt{Y}]$ and $Y' = \log Y$), the ranks of the data were analyzed, resulting in distribution free tests (Conover & Iman 1984; Hora & Conover 1984; Iman et al. 1984).

The appropriate statistical model to analyze these data is a mixed model; blocks were random effects and other factors were fixed effects. Under such conditions, the background vegetation treatment effect might have been tested using the block-by-treatment interaction mean square error term (Bennington & Thayne 1994); however, there were insufficient degrees of freedom to estimate F-values using this error term. Furthermore, we did not expect there to be a significant interaction between block and background vegetation. Therefore, we used the residual mean square error term to test the background vegetation treatment effect (Neter et al.

Table 2. Canopy cover and density of perennial grass species for plots assigned the grass-with-forb treatment before seeding with forbs.

		Canopy Cover Class (%)			*Density (plants/m²)*		
Topographic Zone	*Seeded Species*	*Block I*	*Block II*	*Block III*	*Block I*	*Block II*	*Block III*
Recovery area	*Elymus multisetus*	1–5	trace	1–5	1.25	0.50	1.00
	Nassella cernua and *N. pulchra*	25–50	25–50	25–50	8.75	11.75	12.50
	Poa secunda ssp. *secunda*	trace	1–5	1–5	4.00	10.00	4.33
Open-cut ditch	*Elymus glaucus*	5–25	5–25	trace	3.50	3.25	0.50
	Elymus trachycaulus	5–25	5–25	1–5	1.13	1.13	0.63
	Hordeum brachyantherum ssp. *brachyantherum*	50–75	50–75	95–100	19.25	19.25	54.25
Back berm	*Elymus glaucus*	5–25	5–25	50–75	9.00	5.7	32.25
	Elymus trachycaulus	25–50	25–50	50–75	19.50	12.25	24.00
	Hordeum brachyantherum ssp. *brachyantherum*	1–5	1–5	1–5	0.75	1.25	1.00
	Nassella cernua and *N. pulchra*	0	trace	0	0.00	0.75	0.00

1990; Newman et al. 1997). According to some, this error term should be used to test these effects when blocks are considered fixed effects (Bennington & Thayne 1994), unlike our experiment. Using this error term also limits the ability to draw inferences about plots other than those included in the experiment (Bennington & Thayne 1994). SAS version 6.10 (SAS Institute Inc., Cary, NC) and JMP version 3.1 (SAS Institute Inc., Cary, NC) were used to conduct ANOVA and power analyses, respectively.

To evaluate the effect of the presence of seeded species on weeds, simple linear regression of transformed percent weed canopy cover versus percent perennial grass-with-forb mix canopy cover was performed (three topographic zones for each of four blocks; data on canopy cover in block V was missing for grass-with-forb mix treatments). Data were transformed as follows: 2(arcsine[square root {proportion cover}]) (Neter et al. 1990). SuperANOVA version 1.11 (Abacus Concepts, Inc., Berkeley, CA) was used to perform the regression analysis. ANOVA was also performed on transformed weed canopy cover data using JMP version 3.1.

Transplanted Forb Trial

A second trial tested the performance of perennial forbs grown in different size containers and transplanted into existing perennial grasses using different excavation techniques. The experimental plots were a subset of those used in an experiment on establishing and evaluating mixtures of California native perennial grasses along rural roadsides. The setting for this experiment is described in detail in Bugg et al. (1997) as trial II: polycultures. The transplanted forb trial was a factorial experiment with a split-plot, randomized complete block design with five blocks. Blocks I and II were situated on Brentwood silty clay loam and blocks III–V on Capay silty clay. Seedlings were planted into the back berm (as shown in Fig. 1c) of plots that were 3.1 m long (parallel to the traveled way) by 7.63–9.15 m wide (across topographic zones, width depended upon how the area was originally graded and proximity to the adjacent agricultural field). The main-plot factor was background vegetation (established perennial grasses, mainly *Elymus glaucus* Buckley [blue wildrye] and *E. trachycaulus* var. *trachycaulus* [Link] Shinn [slender wheatgrass] vs. tilled). Split-plots were assigned to combinations of the two crossed factors: (1) forb species; and (2) container size/excavation technique. There were 30 replications each of two forb species (*A. fascicularis* and *S. bellum*) per main-plot. There were 10 replications each of three container size/excavation technique treatment levels per main-plot: (a) forbs propagated in 7.5-cm deep containers (hereafter, small containers) (volume: 36 ml; interior diameter at top: 3 cm) (Plastomer, Inc., Barrie, Ontario, Canada) and transplanted into impressions made in the soil (hereafter, dibble); (b) forbs propagated in small containers and transplanted into holes created by removing a core of soil (hereafter, core); and (c) forbs propagated in 13.6-cm deep containers (hereafter, large containers) (volume: 105 ml; interior diameter at top: 3.6 cm) (Stuewe & Sons, Corvallis, OR) and transplanted into holes obtained by core removal.

The high-diversity native grass regime was established during 1992, as described by Bugg et al. (1997). This regime included 13 species, with a different mix of perennial grasses seeded into each of several roadside topographic zones. In the case of the present experiment, the topographic zone of interest and the one into which forbs were transplanted was the back berm zone, which was dominated by *Elymus glaucus* with lesser amounts of *E. trachycaulus* var. *trachycaulus* after early April 1992. Mean collective canopy cover by these two species was greater than 73%. On 21 November 1992, main plots assigned to the tilled (control) level of vegetational background were cultivated using a tractor-drawn rototiller to incorporate resident vegetation (resident vegetation described in detail by Bugg et al. 1997).

Seed of *A. fascicularis* was collected locally during 1992; seed of *S. bellum* was purchased from S & S Seeds, Inc., Carpinteria, California. Forbs were seeded on 10 or 29 October 1992, and grown in the greenhouse or in sheltered outdoor sites until planting. The soil employed was a commercial mix that included peat and vermiculite. Water was provided and forbs were thinned as needed during propagation. In the back berm zone of each main plot, levels of forb species and container size/excavation technique were randomly assigned to split-plots arrayed in a matrix with 3 rows and 20 columns (Fig. 1c). Consecutive rows were separated by 26 cm and consecutive columns by 30 cm. Columns were offset to provide uniform interplant distance of 30 cm. Excavation techniques employed two distinct tools: (1) a dibble (or surveyor's stake), which was a 2-cm $\times$ 4-cm stake beveled on two sides to form a point; and (2) a coring device constructed of a 4-cm interior diameter metal pipe attached to a handle with a horizontal foot lever for forcing the section of pipe into the soil to a depth of the container type assigned to the relevant location. The planting method entailed the following:

(1) Scrape the soil surface;
(2) Create a hole by either removing a core or inserting a dibble;
(3) Remove seedling from container;
(4) Place seedling in hole;
(5) Compress soil around seedling roots;
(6) Provide water equally to all seedlings immediately, and thereafter as needed during the first 14 days after planting.

Using indiscriminately chosen seedlings, blocks I and II were planted on 30 and 31 January, blocks III and IV on 29–30 March and block V on 4 April 1993. Performance in blocks I and II was assessed on 3 March and 4 April 1993. Blocks III–V were evaluated on 24 April and 14–16 May 1993. We did not assess simple survival of plants because this would have required destructive sampling to examine belowground shoots and roots. Instead, we evaluated the proportion of seedlings showing aboveground growth.

We also evaluated performance using a visual subjective rating for the vigor of each individual plant (hereafter, vigor). The scale of the vigor rating ranged from 0 to 3. We attempted to make the scale approximately linear and relatively objective by assigning the following classification criteria to particular values: 0 (dead or disappeared), 0.5 (uncertain if seedling was alive), 1 (alive but no leaves, having a green, turgid, flexible stem), 2 (new growth, little retention of old foliage), 3 (strong new growth, old foliage largely retained). When making these subjective evaluations of vigor, the observer did not know the container size/excavation technique treatments assigned to each individual. However, it was impossible for the observer to be unaware of the background vegetation treatment and forb species. Plant height was also evaluated as an indicator of plant performance. Transplant survival and vigor were estimated on both sampling dates, and plant heights were measured only at the second sampling date.

Data were assessed by appropriate analysis of variance (ANOVA) models using the factors forb species, plug size/excavation technique, and background vegetation as explanatory variables. Unequal error variances of response variables could not be corrected through transformation ($Y' = \text{arcsine}[\text{sqrt } Y]$ for proportion survival, and $Y' = \log Y$ for vigor and height); therefore, ranks of the data were analyzed. Qualitative results of ranked analyses did not differ from unranked results. Due to the split-plot design, F-tests for the fixed factor background vegetation were calculated using the mean square for block-by-background vegetation interaction as the denominator (treating block as a random factor). Differences among factor means were tested by Tukey's studentized range test or by planned single-degree-of-freedom linear contrasts. The following contrasts were applied to assess significant interactions between the factors species and plug size/excavation technique:

(1) small container/dibble versus small container/corer to isolate the effect of excavation technique
(2) small container/dibble versus large container/corer to compare the most and least resource and space intensive (i.e., most and least expensive) treatments
(3) small container/corer versus large containers/corer to isolate the effect of container size

Tests for equality of variances and ANOVA were conducted using SAS Version 6.12 (SAS Institute, Inc., Cary, NC). Exact probability levels are reported for the analyses of both experiments when available, unless referring to multiple tests, in which case the greatest acceptable probability of committing a type I error (α level) is stated.

Results

Seeded Forb Trial

Percent emergence was greater for the forb mixture seeded into tilled soil (11.0 ± 1.4) than into established perennial grasses (7.2 ± 2.5) ($p = 0.01$). *Lupinus microcarpus* var. *densiflorus* also had greater emergence in tilled treatments compared to perennial grass alone ($p = 0.02$). We did not detect differences between background vegetation treatments for other individual species; however, statistical power to detect differences was low (Table 3). The means presented in Table 3 indicate that *Eschscholzia californica* and *Sisyrinchium bellum* had poor emergence in both treatments and all species tended to have higher emergence when seeded into the tilled treatment than established perennial grasses.

Percent cover for the forb mixture was greater when forbs were planted into tilled soil (97.0 ± 12.8) than when they were planted into established perennial grasses (14.3 ± 3.4) ($p = 0.02$). This response was exhibited by individual species as well (Fig. 2), although *Asclepias fascicularis* and *S. bellum* did not become established in either the existing perennial grasses or the tilled treatments.

Weeds were reduced by the presence of perennial grasses with forbs. This was demonstrated by a significant negative correlative or regression relationship between perennial grass and forb mix canopy cover and weed canopy cover ($p = 0.04$) (Fig. 3) ($Y = 2.13–0.44[X]$). Forbs appeared to be an important component of this response because there was no significant relationship between canopy cover of perennial grasses alone and weed canopy cover ($p = 0.79$). In ANOVA, the background vegetation treatments did not affect weed cover ($p = 0.84$). However, this is a less powerful test than regression because there are fewer degrees of freedom in the error term.

Transplanted Forb Trial

When both species were included in the analysis, data from the first sampling date for proportion of seedlings with aboveground growth indicated non-significant effects for forb species ($p = 0.48$), container size/excavation technique ($p = 0.56$), and background vegetation ($p =$

Table 3. Mean percent emergence ± 1 SE and power to detect effect of established perennial grasses on percent emergence of individual forb species.

Species	*Background Vegetation*	*Percent Emergence*	*Power*	*Adjusted Power**
Asclepias fascicularis	Tilled	9.1 ± 1.6	0.57	0.16
	Established grasses	5.0 ± 1.6		
Eschscholzia californica	Tilled	0.2 ± 0.1	0.09	0.05
	Established grasses	0.05 ± 0.05		
Lotus purshianus	Tilled	20.0 ± 4.9	0.58	0.22
	Established grasses	18.5 ± 4.2		
Lupinus succulentus	Tilled	15.6 ± 5.9	0.07	0.05
	Established grasses	5.2 ± 2.8		
Phacelia tanacetifolia	Tilled	4.9 ± 1.4	0.37	0.14
	Established grasses	0.8 ± 0.6		
Sisyrinchium bellum	Tilled	0.8 ± 0.6	0.18	0.05
	Established grasses	0.0 ± 0.0		

*Adjusted power is calculated from sample estimates that are adjusted to have a more "proper expectation" by considering them random (JMP version 3.1 user's manual page 271).

0.08). The only significant interaction effect was block-by-background vegetation ($p = 0.02$).

When the species were analyzed separately, there was a significant effect of background vegetation for *A. fascicularis* ($p = 0.008$); this species performed better in the tilled treatment (0.97 ± 0.01) than the treatment with established grasses (0.93+0.03). For *S. bellum*, none of the experimental factors showed significant results either alone or in interaction with other factors.

Data for proportion of seedlings showing above-ground growth that were obtained during the second sampling date indicated a significant effect for forb species ($p = 0.02$) when both species were included in the analysis. *Sisyrinchium bellum* (0.87 ± 0.05) had greater mean survival than *A. fascicularis* (0.77 ± 0.06). There were non-significant effects of background vegetation ($p = 0.10$), container size/excavation technique ($p = 0.22$), and for all interaction terms involving forb species and container size/excavation technique. The only significant interaction effect was block-by-background vegetation ($p = 0.001$).

When the two species were analyzed separately, *A. fascicularis* showed a marginally non-significant response to background vegetation ($p = 0.06$) with slightly greater mean survival in tilled plots (19.53 ± 3.87) compared to plots with established grasses (11.47 ± 2.21). *Sisyrinchium bellum* demonstrated no tendency toward this response to background vegetation ($p = 0.32$). The only other factors with significant or near significant effects in the separate analyses of species were the block by background vegetation interactions ($p = 0.05$ and 0.0004 for *A. fascicularis* and *S. bellum*, respectively).

Response of vigor rating for the first sampling date varied with species and container size/excavation technique ($p = 0.007$) in the analysis including both species. We detected a significant effect of container size/excavation technique on *A. fascicularis* vigor when analyzed alone ($p < 0.0001$). This species performed better when grown in large containers compared to small containers (large container/corer > small container/corer, $p < 0.0001$) and the more expensive compared to the less expensive method (large container/corer > small container/dibble, $p < 0.0001$). However, we detected no difference between excavation techniques (small container/core vs. small container/dibble, $p = 0.56$) (Fig. 4a). Block-by-background vegetation interaction was significant ($p < 0.0001$) in this analysis of *A. fascicularis* alone. F-tests for all other main and interaction effects were non-significant.

Analyzed separately, *S. bellum* also responded to container size and excavation technique ($p < 0.0001$) (Fig.

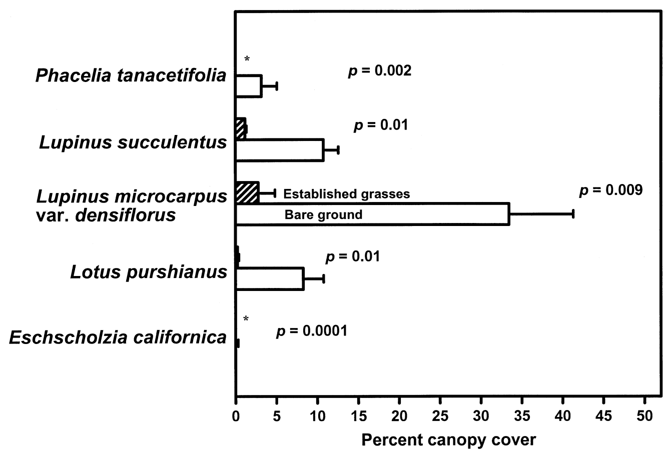

Figure 2. Canopy cover for individual species planted as seed into cleared and tilled soil or established perennial grasses. *Asclepias fascicularis* and *Sisyrinchium bellum* were not included because their cover values were zero for both treatments.

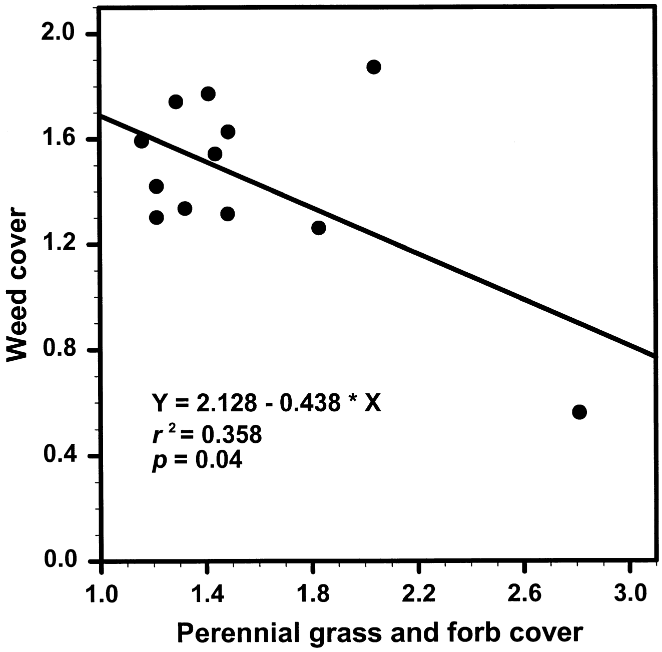

Figure 3. Regression of canopy cover of weeds against canopy cover of seeded perennial grasses and forbs. Cover values were transformed by 2(arcsine[square root{proportion cover}]). * Cover of forbs in established perennial grass treatment percent cover = 0.

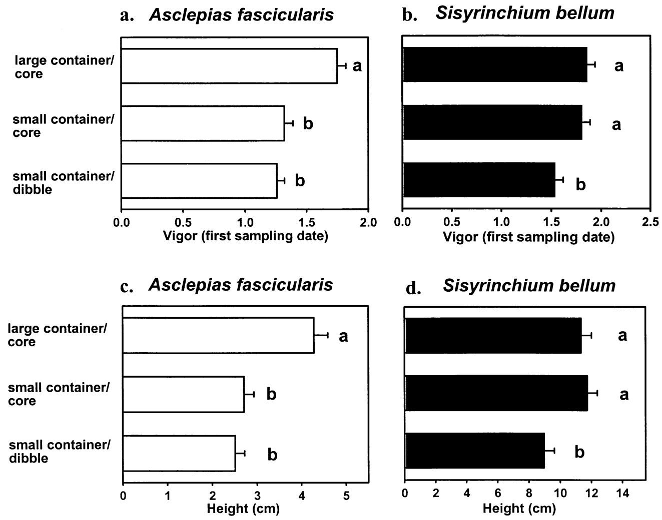

Figure 4. Responses of *Asclepias fascicularis* and *Sisyrinchium bellum* vigor (first sampling date) and height to container size/excavation technique demonstrate a significant interaction between species and propagation/planting method. Treatment means followed by different letters are significantly different according to planned linear contrasts ($p < 0.05$) (means $\pm$ 1 SE).

4b). It performed better in the most expensive propagation method treatment than in the least expensive (large container/corer > small container/dibble, $p < 0.0001$). However, it did not respond to container size (large container/corer > small container/corer, $p = 0.21$) and performed better when planted using the core method (small container/core > small container/dibble, $p = 0.0007$). F-tests for all other main and interaction effects were non-significant.

Vigor rating from the second sampling date produced highly significant effects due to forb species ($p < 0.0001$) and to container size/excavation technique ($p < 0.0001$). Mean values were greater for *S. bellum* (1.56 $\pm$ 0.05) than for *A. fascicularis* (1.10 $\pm$ 0.06). The effect of container size/excavation technique depended upon the background vegetation treatment; there was a significant interaction between background vegetation and container size/excavation technique ($p = 0.0008$). The block-by-background vegetation interaction was significant ($p < 0.0001$). F-tests for all other main effects and their interactions were non-significant.

Separate analyses of the two species showed similar results to the combined analysis reported above. However, there was a significant interaction between container size/excavation technique and background vegetation in the analysis of *A. fascicularis* alone ($p = 0.01$) (Fig. 5a), while the interaction between these factors in the analysis of *S. bellum* alone was non-significant ($p = 0.14$) (Fig. 5b). For the average across background vegetation treatments, *A. fascicularis* had the following vigor rating rankings: large container/corer (1.35 $\pm$ 0.11) > small container/corer (1.02 $\pm$ 0.09) = small container/dibble (0.94 $\pm$ 0.08) ($p < 0.05$). This ranking was apparent in the tilled plots but not the established grass plots, hence the significant interaction between planting method and background vegetation (Fig. 5a). Background vegetation appeared to eliminate the effects of container size/excavation technique for *A. fascicularis*. *Sisyrinchium bellum* had the following vigor rankings when averaged across background vegetation treatments: large container/corer (1.66 $\pm$ 0.09) = small container/corer (1.61 $\pm$ 0.09) > small container/dibble (1.40 $\pm$ 0.09) ($p < 0.05$) (Fig. 5b). The response was similar in the two background vegetation treatments, although it was more pronounced in the cleared and tilled plots.

When both species were included in the analysis, response of plant height to container size/excavation technique differed for the two species; the interaction between container size/excavation technique and species was significant ($p = 0.003$). The effects of species and container size/excavation technique and the interaction between block and background vegetation were also significant ($p < 0.01$) in this analysis.

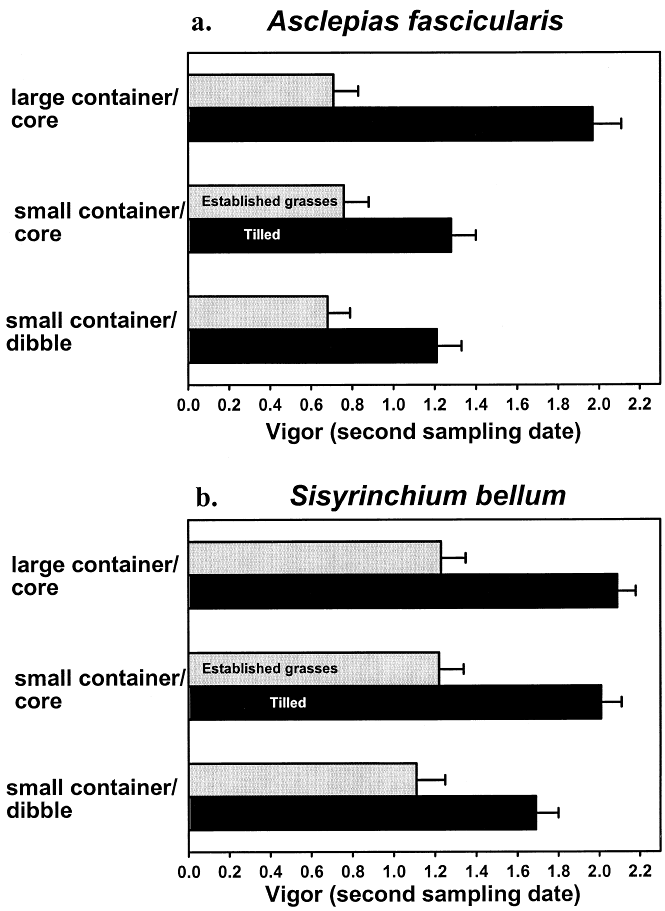

Figure 5. Vigor for the second sampling date illustrates a significant interaction between background vegetation and container size/excavation technique treatments for *Asclepias fascicularis* and a non-significant interaction for *Sisyrinchium bellum* (means ± 1 SE).

In separate analyses of the two species, *A. fascicularis* was taller when grown in large containers compared to small containers (large container/corer > small container/corer, $p < 0.0001$) and the more expensive compared to the less expensive method (large container/corer > small container/dibble, $p < 0.0001$) (Fig. 4c), but we detected no difference between excavation techniques (small container/core vs. small container/dibble, $p = 0.49$). There was also a significant background vegetation by block interaction in this analysis ($p < 0.0001$), but effects of other factors and their interactions were non-significant. *Sisyrinchium bellum* was also taller in the most expensive propagation method treatment (large container/corer > small container/dibble, $p = 0.0003$). However, it did not respond to container size (large container/corer > small container/corer, $p = 0.66$) and performed better when planted using the core method (small container/core > small container/dibble, $p < 0.0001$) (Fig. 4d).

Discussion

Several forb species established well from seed in the tilled treatment, including *Lupinus densiflorus*, *L. succulentus*, *Lotus purshianus* and *Phacelia tanacetifolia*. The emergence and cover of all species were lower in the presence of established perennial grasses than in the tilled treatment; most species produced little or no cover in the presence of established perennial grasses. Even the best performer, *L. densiflorus*, which had high emergence in both background vegetation treatments, achieved less than 5% cover in the established perennial grass treatment.

Species appeared to vary in their sensitivity to the effects of established perennial grasses before and after emergence. Although the emergence of all species was reduced by the presence of existing grasses, the reduction varied from 100% for *S. bellum* to only 10% for *L. purshianus*, with other species intermediate. *Eschscholzia californica* and *S. bellum* exhibited poor emergence and low cover in both tilled and established perennial grass treatments. Since both species had greater than 60% viable seed, we are unsure why they performed poorly in both background vegetation treatments. *Asclepias fascicularis* appeared to be particularly sensitive to the effects of existing grasses after emergence; despite having good emergence levels, it did not successfully establish. We suggest that this is largely because of the phenology of this species. *Asclepias fascicularis* does not begin rapid growth until the summer and was probably not able to garner enough resources, even in the tilled treatments, to survive through the spring due to the presence of cool-season growing forbs and grasses. This hypothesis was also supported by the performance of *P. tanacetifolia*, a cool-season forb, that had lower emergence than *A. fascicularis* yet achieved nearly 5% cover in the tilled treatment while *A. fascicularis* essentially disappeared. Although the observed pattern could also be explained by herbivory or disease that affected *A. fascicularis* more than *P. tanacetifolia* and other forb species, we did not observe evidence of such interactions.

These results suggest that differences among species in their germination biology, phenology, and competitive ability, and the interactions between the traits of seeded species and existing vegetation, were important factors that affected the performance of the seeded forb species in our experiment. We recommend considering such traits and their ecological interactions when selecting species for restoration projects because of their importance for establishment success.

Transplanting appeared to reduce a competitive disadvantage for forbs compared to seeding. Establishment of forbs from seed was consistently reduced by existing perennial grasses, whereas performance of transplanted forbs was not. This suggests that germination, emergence, and early growth are critical stages of establishment for forbs and that success can be improved by protecting plants from competition at these stages through transplantation or, for some species, tilling the soil. This may be particularly important when working with species that are known to have seedlings with low vigor, slow growth rates, or expensive or rare seed.

Weeds were reduced by the presence of established perennial grasses and forbs together, but not by perennial grasses alone. The significance of this relationship was influenced by a single plot (block I, tilled treatment). Weed cover was especially low in this plot and seeded forb cover was very high (mostly the two *Lupinus* species), which appears to be the primary cause for the significantly negative relationship between the cover of perennial grasses with forbs and the cover of weeds. The lack of relationship between the cover of existing perennial grasses alone and weed cover is in contrast with the result from a nearby experiment reported in Bugg et al. (1997) (trial II: monocultures) showing that weed canopy cover decreased with increasing perennial grasses canopy cover.

Reduced weed cover in plots with established grasses and seeded forbs may be an indication of one of the benefits of species diversity in plant communities. This response has been shown in other grasslands. For example, in a sand prairie in Minnesota, the number of seeded species that became established in grassland plots was negatively related to the number of species present before the addition of seed (Tilman 1997). The results from our experiments suggest that increasing the species richness of restored California grassland by including the forb component may help reduce the abundance of weedy species.

Mechanisms by which the incumbent perennial grasses suppressed forb growth were not assessed formally in this experiment. However, our observations suggest that shading was an important factor, inasmuch as transplanted forbs with immediately adjoining perennial grasses seemed to grow better if the former were in full sunlight than if overtopped by the adjacent perennial grass. In both cases, a forb seedling would be subjected to belowground effects of the perennial grass, but greater light availability improved performance noticeably. In plots with incumbent perennial grasses, proportions of seedlings with aboveground growth appeared lower, but statistically significant differences were not detected, perhaps because of the limited replication of the background vegetation treatment ($r = 5$). Mowing or burning of native grass stands prior to transplanting clonal forbs or planting forb seed might be expected to lead to better initial growth and establishment of forbs. The value of these techniques in promoting clonal forb establishment should be assessed in subsequent trials.

The data indicate that container size had a significant effect on the vigor and height of *A. fascicularis*, but not of *S. bellum* (for vigor at the second sampling date, the response of *A. fascicularis* was only detected in the tilled treatment). Specifically, *A. fascicularis* performed better when grown in larger containers, but either size appeared to suffice for *S. bellum*. This result may be related to different seasonal growth patterns of these two plants. Whereas *S. bellum* grew rapidly during the late winter and early spring when soil was moist, *A. fascicularis* appeared dormant in cold weather and only began rapid growth in late spring, when rainfall was lower and resident vegetation was already growing quickly. A deep, well-developed root system enabled by the large container may have conferred an advantage in the case of *A. fascicularis* due to probable scarcity of resources in very shallow soil when it began rapid growth. *Sisyrinchium bellum* was less likely to encounter this scarcity when it began growth earlier in the season.

Excavation technique had a significant effect on the vigor and height of *S. bellum*, but not *A. fascicularis*. We suggest that this result is due to an interaction between soil compaction caused by creating a hole with a dibble and the timing of plant growth. The dibble method, which involves making an impression in the soil with a solid object, is thought to be more likely to lead to soil compaction and reduced root growth than the excavation (core) method employed (Håkansson et al. 1988; Unger & Kaspar 1994; Whalley et al. 1995). However, the montmorillonitic clay and clay loam soils of Yolo County are well known to naturally de-compact through normal wetting and drying cycles (Ahmad 1983). In our experiment, any initial compaction caused by the dibble may have been relieved through time. When each species began rapid growth, the early-season species, *S. bellum*, may have experienced greater resistance to root growth than the late-season species, *A. fascicularis*, resulting in the differential responses we observed.

Both species performed better with the most expensive propagation method using large containers and the core method of excavation compared to the less expensive method using small containers and the dibble method of excavation. Note that this effect was not apparent for vigor estimates of either species in the presence of established perennial grasses at the second sampling date, although the effect on height was independent of background vegetation treatment at that time. Producing transplants in small containers was less expensive than large containers because there were twice as many cells in each tray of small containers. Each small container cell was approximately one-third the volume of each large container cell. Therefore, the small containers required 69% less soil to produce twice the number of plants in approximately the same amount of space as the large containers.

The dibble method is much faster than the core removal method because it only involves jabbing the dibble into the soil without having to take steps to remove soil from the implement as in the core removal method. However, as described above, this method may lead to greater soil compaction than core removal. Our results indicate that *S. bellum* may be propagated in the less expensive, small containers and still perform as well as if grown in large containers, if excavation for transplanting is core removal, not dibble. Our results also indicate that it was best to propagate *A. fascicularis* in the more expensive, large containers, and the less time-consuming dibble method of soil excavation may not have negatively affected its performance. This cannot be definitively determined because the experiment did not include a large container/dibble treatment.

Informal follow-up observations as late as 1996 indicated excellent persistence and vegetative spread of *S. bellum* and *A. fascicularis* that had been established amid *E. glaucus* and *E. trachycaulus*. The initial effects of propagation and excavation methods appeared to diminish over time. Once seedlings survived the first dry season, mortality was very low.

Diversity can confer some advantages in grassland ecosystems, in terms of improved community parameters of biomass production, nitrogen fixation, nitrate retention, and resistance to invasion (Tilman & Downing 1994; Tilman 1996; Tilman et al. 1996; Tilman 1997). There is also evidence that more species can coexist in some grasslands than do, primarily due to dispersal limitation that can be overcome by seed addition (Tilman 1997). The diversity of natural grassland communities is, in part, limited by the proximity of adult plants that contribute propagules to the community seed bank. In restoration projects, we have the opportunity to select the number of species and their identities, which may allow us to manipulate community level characteristics such as those listed above.

Although initial species richness can be controlled in restoration projects, there may be challenges to establishing multiple grass and forb species. Simultaneous seeding of grasses and forbs eliminates the possibility of using broadleaf-specific weed control during grass establishment. Approaching prairie restoration as a two-step process, as we have here, has different challenges. Fenner (1978) found that forb species differed in their abilities to establish from seed amid closed swards, as did we. We anticipate that different native perennial forbs may have varying optima and tolerances for site preparation and propagation methods, as suggested by the present study.

Other native clonal forb species that are being evaluated in the context of restoring native grasslands include: *Aster chilensis* Nees (Asteraceae), California goldenrod (*Solidago californica* Nutt., Asteraceae), hedge-nettle (*Stachys ajugoides* Benth., Lamiaceae), heliotrope (*Heliotropium curassavicum* L. var. *oculatum* (Heller) Jtn., Boraginaceae), *Lathyrus vestitus* Nutt. ex T. & G. (Fabaceae), western goldenrod (*Euthamia occidentalis* Nutt., Asteraceae), wild licorice (*Glycyrrhiza lepidota* Pursh., Fabaceae), and yarrow (*Achillea millefolium* L., Asteraceae). These should be evaluated for establishment and growth using various techniques, such as those reported here.

Acknowledgments

Thanks to John H. Anderson for providing the study site, to John Wayne McLean for technical assistance and advice, and to Ann Chandler of Cornflower Farms Nursery of Elk Grove, California, for assistance with plant propagation techniques. The manuscript was reviewed by Craig Thomsen. The research was in part supported by Wallace Genetic Foundation, Inc., the California Water Resources Control Board (under Inter-Agency Agreement 8-199-250-0), Elvenia J. Slosson Endowment Fund for Ornamental Horticulture, and Awards for Research Excellence in Wildlands (1992 Pacific Gas and Electric Company Gifts).

LITERATURE CITED

Ahmad, N. 1983. Pedogenesis and soil taxonomy. II. Pages 91–123 in L. P. Wilding, N. E. Smeck, and G. F. Hall, editors. Pedogenesis and soil taxonomy. Elsevier, Amsterdam.

Bennington, C. C., and W. V. Thayne. 1994. Use and misuse of mixed model analysis of variance in ecological studies. Ecology **75:**717–722.

Bugg, R. L., C. S. Brown, and J. H. Anderson. 1997. Restoring native perennial grasses to rural roadsides in the Sacramento Valley of California: establishment and evaluation. Restoration Ecology **5:**214–228.

Conover, W. J., and R. L. Iman. 1984. Rank transformations as a bridge between parametric and nonparametric statistics. Journal of the American Statistical Association **79:**124–133.

Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. Northwest Science **33:**43–64.

Fenner, M. 1978. A comparison of the abilities of colonizers and closed-turf species to establish from seed in artificial swards. Journal of Ecology **66:**953–963.

Håkansson, I., W. B. Voorhees, and H. Riley. 1988. Vehicle and wheel factors influencing soil compaction and crop response in different traffic regimes. Soil and Tillage Research **11:**239–282.

Hora, S. C., and W. J. Conover. 1984. The *F* statistic in the two-way layout with rank-score transformed data. Journal of the American Statistical Association **79:**668–673.

Iman, R. L., S. C. Hora, and W. J. Conover. 1984. Comparison of asymptotically distribution-free procedures for the analysis of complete blocks. Journal of the American Statistical Association **79:**674–685.

Morse, D. H. 1985. Milkweeds and their visitors. Scientific American **253:**112–119.

Neter, J., W. Wasserman, and M. H. Kutner. 1990. Applied linear statistical models. Irwin, Boston, Massachusetts.

Newman, J. A., J. Bergelson, and A. Grafen. 1997. Blocking factors and hypothesis tests in ecology: is your statistics text wrong? Ecology **78:**1312–1320.

Tilman, D. 1996. Biodiversity: population versus ecosystem stability. Ecology **77:**350–363.

Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. Ecology **78:**81–92.

Tilman, D., and J. A. Downing. 1994. Biodiversity and stability in grasslands. Nature **367:**363–365.

Tilman, D., D. Wedin, and J. Knops. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature **379:**718–720.

Unger, P. W., and T. C. Kaspar. 1994. Soil compaction and root growth: a review. Agronomy Journal **86:**759–766.

Whalley, W. R., E. Dumitru, and A. R. Dexter. 1995. Biological effects of soil compaction. Soil and Tillage Research **35:**53–68.