Native Perennial Grasses in Highway Medians: Pre- and Postplant Techniques for Establishment in a Mediterranean Climate

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Native Perennial Grasses in Highway Medians: Pre- and Postplant Techniques for Establishment in a Mediterranean Climate

Stephen L. Young and Victor P. Claassen*

Within highway rights-of-way, native perennial grasses provide desirable services to support natural and human constructed ecosystems. However, native perennial grass establishment in annual grass dominated roadsides of semiarid and Mediterranean climates of the western United States requires specific cultural and chemical management treatments to control weeds. In 2004, field studies were conducted in Sacramento Valley, California to determine the effect of herbicide, disc cultivation, and species selection on native perennial grass establishment and annual weed persistence. Perennial grass species mixes common to drier and wetter upland areas in northern California were drill seeded at two sites (I-5 North and I-5 South) that had been burned in 2003 and received weed control (i.e., herbicide, cultivation, mowing) in spring 2004. Herbicides were the most important treatments for native perennial grass establishment and weed reduction. Native perennial grass species persistence was largely unaffected by cultivation or native plant accessions at these sites. Native perennial grass density increased at I-5 North in the second year of growth (2006) resulting in a plant density totaled across all herbicide regimes of 3.9 plants m^{-1} compared to 2.5 plants m^{-1} at I-5 South. Vigorous native perennial grass growth in the more fertile and less droughty soils of I-5 North helped to limit annual weeds through competition, which is anticipated to reduce the need for chemical and mechanical control in years following early establishment.

Nomenclature: Chlorsulfuron; clopyralid; glyphosate; triclopyr.

Key words: Chlorsulfuron, clopyralid, highway rights-of-way, restoration, soil fertility, soil water holding capacity.

Weed management is required in the first few years after the establishment of native perennial grasses along roadsides in the arid (250 to 500 mm [9.8 to 19.3 in] precipitation per year) and Mediterranean climates (hot, dry summers and cool, wet winters) typical of the western United States (Wrysinski 1999). Roadside revegetation projects that receive little management for controlling weeds and promoting native perennial grasses have greater potential for reverting to stands of the preexisting weeds (see Rentch et al. 2005). Because of this common trend, successful native perennial grass establishment requires active weed control (Anderson and Long 1999).

Roadsides can be difficult locations for establishing native perennial grasses. Site conditions that can limit the success of any revegetation effort include topography (steepness, slope, aspect), soil (shallow, rocky, compacted, chemical imbalances), climate (region, seasonal variation), existing vegetation (competition, invasion), and continued impacts (traffic, maintenance activities). Brooks (1995) found revegetation treatments for visual impact mitigation were unsatisfactory on 72% of the cut slopes evaluated in the Tonto National Forest in central Arizona. In the Sacramento Valley of northern California, Bugg et al. (1997) report resident weeds influenced native perennial grass establishment, but plantings retaining 25% or greater native canopy cover were suitable for use in roadsides. In high elevation sites at a National Park in Glacier, roadside revegetation with native graminoids resulted in 9% native grass cover after 3 yr of management with a broadleaf selective herbicide (Tyser et al. 1998). On sites not conducive to native plant growth, inadequate pre- and postplant weed control results in planted vegetation reverting back to weeds in the years following a planting (Ivanovitch 1975). For example, Hallock et al. (2002) report poor establishment of vegetation on disturbed sites following surface applications (i.e., hydroseeding) due to

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Interpretive Summary

Weed management techniques are necessary to improve the establishment success of native perennial grasses in highway rights-of-way of many western states, such as California. The use of broad spectrum (preemergence) and selective herbicides (postemergence) are the most useful chemical management tools for weed reduction following a fall seeding of native perennial grasses. In addition, loam soils with adequate water holding capacity and fertility lead to faster and more vigorous establishment of native perennial grasses. Therefore, following initial site preparation (i.e., burn, herbicide, cultivation, mowing) we recommend the following order of considerations for successful establishment of native perennial grasses along roadsides in semiarid climates: (1) herbicide regime, (2) soil conditions, and (3) disc cultivation.

improper species selection, seeding at an inappropriate time, or improper seed mixes, fiber, and tackifier.

While pre- and postplant weed control is needed for establishing native perennial grasses along roadsides, persistence of native perennial grasses, once established, can occur with minimal management (O'Dell et al. 2007; Young and Claassen 2008). To increase the probability of establishment in the semiarid and Mediterranean climates of the western United States, weeds need to be prevented from going to seed for a year or more prior to planting native species to reduce the weed seed bank (Kimball and Lamb 1999; Wrysinski 1999). Although limitations in time and resources restrict the practice of pretreatment (e.g., herbicide, disc cultivation, seed mix selection), it is often the critical difference between success and failure for establishing a roadside stand of native perennial grasses.

Native perennial grasses have desirable characteristics in highway rights-of-way, including weed suppression, habitat, erosion control, and aesthetics. We have found little documented research that has provided guidelines for establishing native perennial grasses along highway rights-of-way in Mediterranean (summer dry/cool, wet winter) regions of northern California. Therefore, the objective of this large-plot study was to evaluate the effectiveness of herbicide and disc cultivation treatments for weed control and for establishment of native perennial grass seed mixes in annual weed dominated sections of highway rights-of-way.

Materials and Methods

Site and Treatment Description. Two sites (I-5 South and I-5 North) were identified in the median of Interstate 5 on California Department of Transportation (CalTrans) right-of-way in Colusa County, CA, about 80 km (50 mi) north of Sacramento. The 1.9-km-long I-5 South site was located 25 km from the southern border of Colusa County, while the 2.9-km-long I-5 North site was 24 km further north.

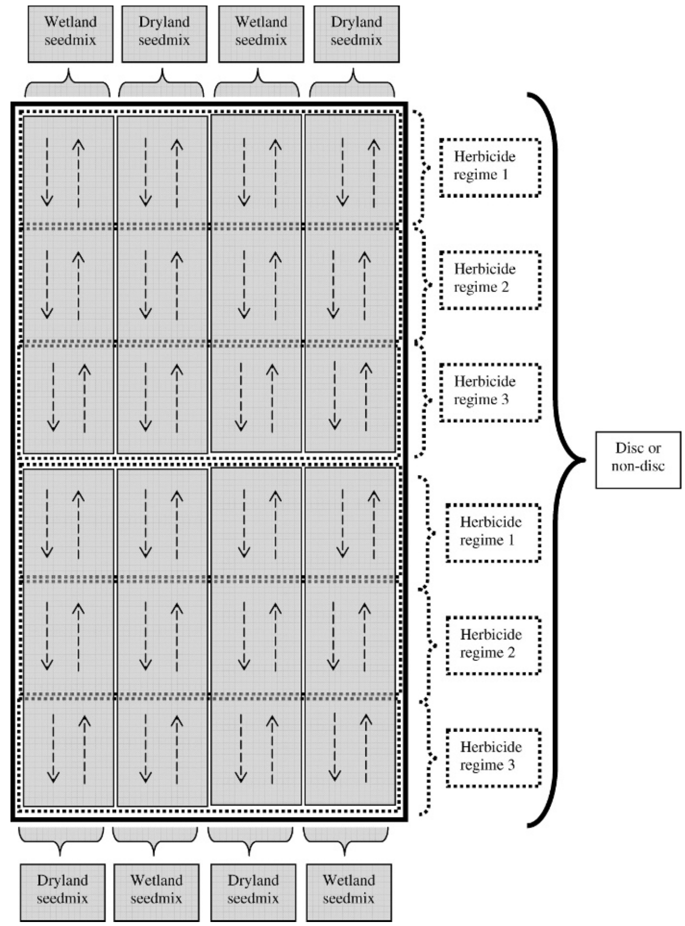

Figure 1. Layout of a single disc or nondisc plot and subplots of seeding and sub–subplots of herbicide regime used in the experimental design at I-5 North and South. Dashed lines with arrows indicate transects used for sampling plant density and the direction of sampling. The experimental layout was replicated four times in both the burn ½ and nonburn ½ of each site.

In summer 2003, wildfires had burned approximately half of each site, resulting in the uniform reduction of plant biomass in those areas. The burn areas of the flat and uniformly vegetated median area were delineated as a pretreatment burn. Due to lack of replication, however, burn and nonburn areas were not included as statistically analyzed treatments, but were interpreted as general trends. The experimental treatments were overlaid on burn or nonburn areas in a split–split–split plot design (Figure 1). A disc cultivation treatment was applied to control weeds and prepare the seedbed for drill seeding of two different seed mixes. Chemical treatments to control weeds in the two seed mix plantings included (1) postemergence, nonselective; (2) postemergence, broadleaf selective; and (3) preemergence, nonselective. Mowing was conducted uniformly across all plots—once in the spring and summer to maintain traffic safety and to control fuel loads.

Table 1. Seeding rates and germination for native perennial grasses.

Common name	Pure live seed (PLS)	PLS	Bulk seeding[a]
Dry site mix	%	——kg ha^{-1}——	
Meadow barley	66	4.5	6.8
Purple needlegrass	72	10.1	14.0
Squirrel tail	75	2.2	3.0
Blue wildrye	92	1.1	1.2
One-sided bluegrass	76	1.1	1.5
Wet site mix			
Meadow barley 1	87	3.4	3.9
Meadow barley 2	67	3.4	5.0
Creeping wildrye	82	5.6	6.9
Squirrel tail	75	2.2	3.0
Slender wheatgrass	85	1.1	1.3

[a] Bulk seeding rate = PLS kg/ha ÷ %PLS.

Native perennial grasses were drill seeded with a FlexII Series Grass Drill.[1] The native grass species selected were based on those most commonly found in the bioregions of northern and central California and most suitable for roadsides (e.g., plant height, tolerance to drought) (Table 1). Native perennial grass species in the dry site mix consisted of California barley (*Hordeum brachyantherum* ssp. *californicum* Nevski), purple needlegrass (*Nassella pulchra* Barkworth), squirreltail (*Elymus multisetus* M.E. Jones), blue wildrye (*E. glaucus* Buckley), and one-sided bluegrass (*Poa secunda* ssp. *secunda* J.S. Presl.), while the wet site mix included meadow barley (*Hordeum brachyantherum* Nevski; *Hordeum brachyantherum* Nevski ssp. *brachyantherum*), creeping wildrye [*Leymus triticoides* (Buckley) Pilger], squirreltail, and slender wheatgrass [*E. trachycaulus* (Link) Gould ex Shinners]. The general classification of a native perennial grass species as "wet site" or "dry site" was made based on observations of grass performance from other local stands in the Central Valley of California (J. A. Anderson, personal communication) and from field guides (DiTomaso 2005; Hickman 1993; Wrysinski 2000).

Annual weeds existing at the site consisted of dense stands of forb and grass species commonly found in the agricultural regions immediately adjacent to the highway. Yellow starthistle (*Centaurea solstitialis* L.), mustard (*Brassica* spp.), and redstem filaree [*Erodium cicutarium* (L.) L'Hér ex ait] were the dominant forbs, while the most common grasses were Italian ryegrass (*Lolium multiflorum* Lam.), wild oat (*Avena fatua* L.), and ripgut brome (*Bromus diandrus* Roth.). Soils were analyzed in the burn and nonburn sections of each site. Soil samples were collected from the upper 10 cm and sent to A & L Western Agricultural Laboratories of Modesto, CA, to determine soil fertility (S3C tests), including organic matter, extractable nitrogen, phosphorus, potassium, calcium, magnesium and sulfur, micronutrients, CEC, pH, and salts, as well as textural analysis.

Field Layout. Each site contained burn and nonburn median sections that extended for either 960 m (at I-5 South) or 1440 m (at I-5 North). At I-5 South, 120-m by 12-m disc and nondisc cultivation treatments (plots) were alternated four times (4 disc and 4 nondisc) within both the burn and nonburn sections. Within the 120-m disc and nondisc cultivation treatments, the two seeding mixes (subplots) were planted in adjacent bands of 60 m spanning across the 12-m-wide median in 3-m-wide strips. The wet site and dry site mixes were placed in alternate positions nearer or farther from the shallow central drain that temporarily saturates with water during rainy periods (Figure 1). The planting mix treatments received one of three herbicide regimes (sub–subplots) that were applied in 20-m by 12-m strips (Figure 1). Similarly at I-5 North, 180-m disc and nondisc cultivation treatments were overlaid with the two seeding mixes in 90-m by 3-m-wide strips. One of three herbicide regime treatments were applied in 30-m by 12-m-wide strips over each planting mix (Figure 1). Disc and nondisc cultivation treatments were replicated four times within both burn and nonburn sections, while seeding mix and herbicide regime were replicated 8 and 12 times, respectively.

Field Operations. Site treatment began in summer 2003 when wildfire burned approximately half of each large plot area. Both sites were sprayed uniformly with glyphosate at 2.24 kg ai/ha (2 lbs/ac) in the second year (March 2004), followed by cultivation (May 2004) and mowing (August 2004) to prevent weed seed production. Late season weeds like Russian thistle (*Salsola tragus* L.) were mowed again, and the first experimental disc cultivation treatment was conducted just before drill seeding the native perennial grass mixes in November 2004. Following drill seeding of the plant mixes, the first chemical treatment of glyphosate was applied at 1.12 kg/ha to all plots at both sites to control newly emerging weeds prior to the emergence of the seeded native grasses. In spring 2005, the second chemical treatment, consisting of clopyralid + triclopyr at 0.04 + 0.15 kg ae/ha, was applied over two-thirds of the plots, and the third and final chemical treatment of chlorsulfuron at 0.02 L ai/ha was applied to the remaining one-third of the plots in fall 2005. The first chemical treatment was for nonselective weed control, the second for selective control of broadleaf weeds, and the final treatment for selective control of germinating weed seed. The sites were mowed once or twice, depending on vegetative biomass, to maintain traffic safety. Except for the application of glyphosate, a similar herbicide regime was followed again in 2006.

Table 2. Soil fertility and texture for two highway medians in northern California.[a]

Site	Cation exchange capacity (CEC)	Nitrogen NO_3-N	Phosphorus $NaHCO_3$-P	Organic matter	Sand	Silt	Clay
	meq/100 g[b]	ppm		%			
I-5 North burn	22.7 a	12.7 a	8.3 c	4.4 a	27.0 d	33.3 a	39.7 a
I-5 North nonburn	16.0 b	17.0 a	15.7 b	4.4 a	38.3 c	37.3 a	24.3 b
I-5 South burn	12.2 b	23.7 a	23.7 a	2.7 a	66.3 a	16.0 c	17.7 c
I-5 South nonburn	12.6 b	10.3 a	9.7 bc	3.5 a	50.3 b	28.0 b	21.7 bc

[a] Values with the same letter in a column are not significantly different according to *t* tests (LSD) $P < 0.05$ ($n = 12$).

[b] meq/100 g, Milliequivalents of negative charge per 100 g of oven-dried soil (1 meq/100 g soil = 1 cmol/kg).

Data Collection. Plant density was measured within each sub–subplot or herbicide regime using paired transects placed parallel to the roadway (Figure 1). Transects of 16 m at I-5 South and 23 m at I-5 North were centered within and evenly spaced across the sub–subplot to avoid edge effects. Ten points were established at equal distances along transects at both sites, using randomly located starting points. At each measurement point, the presence of individual native perennial grass species, annual grass, annual forb, or bare ground was recorded. From burn and nonburn sections at each site, counts along transects, as shown in Figure 1, were conducted in three randomly selected disc and nondisc cultivation treatments in May 2005 and 2006.

Statistical Analysis. In burn and nonburn sections of each site, the effect of herbicide regime, disc cultivation, and seed mix on native perennial grass establishment and weed persistence was analyzed with ANOVA using the General Linear Model (GLM) procedure. Year-to-year variation prohibited statistical comparisons across years. Plant density differences due to weed control (i.e., herbicide, disc cultivation) and species mixtures were reported individually and in combination (e.g., disc · mix) for each plant group (i.e., annual grass, annual forb, and native perennial grass). Soil fertility and texture data were subjected individually to ANOVA for comparison between sites in either burn or nonburn locations. Significance of mean differences for each treatment was determined by Fisher's Protected Least Significant Difference (LSD) test at $P < 0.05$. All statistical analyses were conducted with SAS (SAS 2002).

Results and Discussion

Soil conditions were very different between the two sites (Table 2). At I-5 South, shallow, sandy textured soils prevailed, with large amounts of coarse fragments. The soils at I-5 North were finer in texture, which allowed for greater water holding capacity and nutrient availability. In addition, a gentle slope in the topography at I-5 South was in contrast to the relatively flat landscape at I-5 North.

Herbicides. Native perennial grass density increased in all herbicide regimes at I-5 North between 2005 and 2006 with the greatest increase occurring in nonburn sections containing the glyphosate + clopyralid + chlorsulfuron (G+C+C) herbicide regime (Figure 2). Similar to I-5 South, nonnative annual plant type at I-5 North changed from mostly forbs in 2005 to mainly grasses in 2006.

Annual grasses were the most dominant nonnative plant type, reducing native perennial grass density even in the high intensity herbicide regime at I-5 South (Figure 3). The change in nonnative annual plant type between 2005 and 2006 from forbs to grasses occurred after the disc cultivation and glyphosate (G) pretreatments in 2004. Disc cultivation and glyphosate applied once have only short-term residual effects and were probably no longer controlling the grasses. The shift to nonnative annual grasses resulted in an increase in density of annual weeds totaled across all herbicide regimes from 1.8 to 2.5 plants m^{-1} in burn sections and 1.7 to 2.8 plants m^{-1} in nonburn sections at I-5 South (Figure 3). A change in weed community from one plant type to another is not uncommon for land owners using native grasses in restoration efforts (Lulow et al. 2007). Selective measures for controlling target species that have similar growth and morphology to native perennial grasses is difficult without a broad spectrum of tools for weed control. Additionally, timing of treatment application can impact the selective ability of many chemical and cultural techniques for weed control, particularly following the establishment of native perennial grasses.

The densities of nonnative annual grasses at I-5 South were higher than I-5 North in 2006 possibly because of differences in soil organic matter and texture (Table 2). The soil textures at I-5 North were high in clay with few coarse fragments, while the I-5 South soils were sandy loams with 50 to 60% sand content. A compacted coarse soil may reduce the growth of deep rooted perennials, but

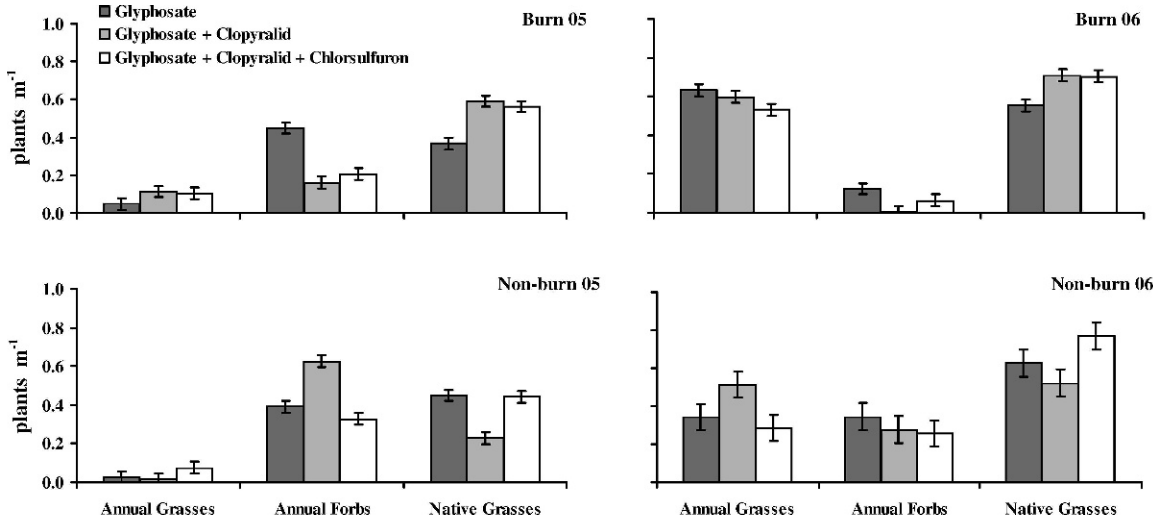

Figure 2. Establishment of native perennial grasses and persistence of nonnative species (plants m^{-1}) under three herbicide regimes at I-5 North. Error bars represent 1 standard deviation. Plant density was measured in burn and nonburn sections.

not affect a shallow rooting nonnative annual grass, particularly during the first season when frequent rains rewet the shallow soil. When observed for longer periods, however, native perennial grasses may have a competitive advantage due to deeper rooting, extended summer growth, perennial nature, and increased tolerance to harsh weather conditions (e.g., heat, low moisture) (Dyer and Rice 1999; Holmes and Rice 1996; Reever Morghan and Rice 2006).

Disc Cultivation. The disc cultivation treatment had a positive effect on native perennial grasses in 2005 at I-5 North, (i.e., lowered nonnative plant persistence and increased native perennial grass establishment) but by 2006, native grass densities were similar for disc and nondisc cultivation treatments (Table 3). Disc cultivating the soil brings up buried seed and causes a flush of newly germinating weeds (Canevari et al. 2002). We suspect disturbance effects (i.e., disc cultivation) were not a factor because of the superior soil conditions (i.e., nutrients and water) that ultimately led to the establishment of native perennial grasses in 2005 and further proliferation in 2006.

Seed Mixes. Native perennial grass density for dry and wet site seed mixes was different in burn and nonburn sections at I-5 South (Table 4), but not at I-5 North. The differences in plant populations within a seed mix indicates native perennial grasses, similar to all other plant types, are responsive to environmental conditions (e.g., climate, soil

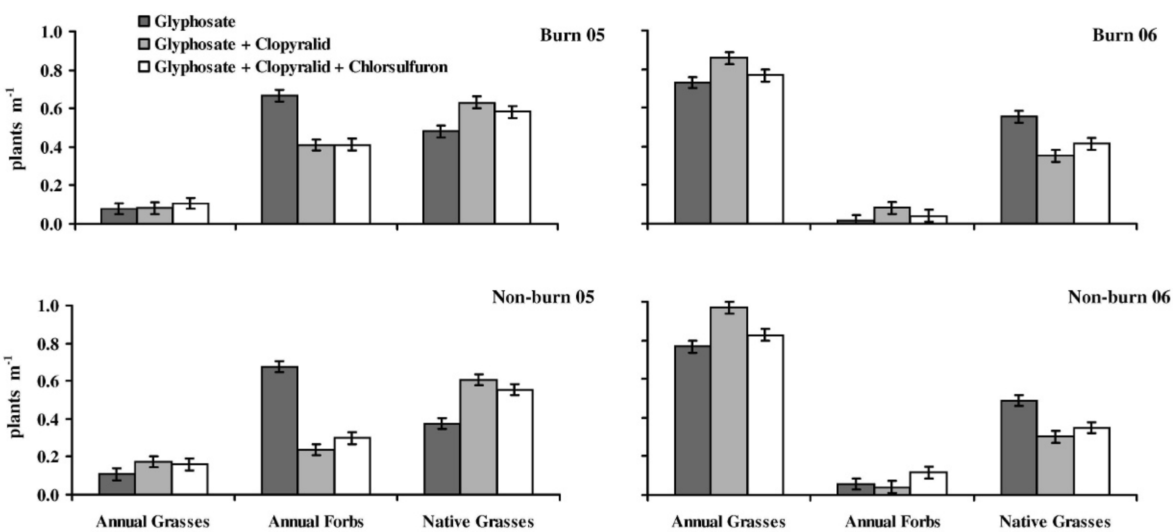

Figure 3. Establishment of native perennial grasses and persistence of nonnative annual species (plants m^{-1}) under three herbicide regimes at I-5 South. Error bars represent 1 standard deviation. Plant density was measured in burn and nonburn sections.

Table 3. Linear contrasts of weed control (Disc = tillage; Herbicide = herbicide regime) and species (Mix = Planting mixture) at I-5 North. In each row, underlined P-values indicate when disc, herbicide, and mix, individually and in combination, resulted in significantly lower weed (AG = annual grasses; AF = annual forbs) or higher native (NG = native perennial grasses) plant cover.[a]

Weed control and species mixture treatments	2005						2006					
	Burn			Nonburn			Burn			Nonburn		
	AG	AF	NG	AG	AF	NG	AG	AF	NG	AG	AF	NG
	P= 0.403	P < 0.0001	P=0.001	P=0.007	P < 0.0001	P < 0.0001	P= 0.594	P= 0.060	P= 0.291	P= 0.333	P= 0.999	P=0.732
	n = 72	*n* = 72	*n* = 72	*n* = 72	*n* = 72	*n* = 72	*n* = 72	*n* = 72	*n* = 72	*n* = 72	*n* = 72	*n* = 72
Disc	**P=0.021**	P=0.080	**P=0.003**	**P=0.006**	**P=0.030**	P=0.194	P=0.408	P=0.839	P=0.366	P=0.583	P=0.566	P=0.910
Herbicide	P=0.094	**P < 0.0001**	**P < 0.0001**	**P=0.004**	**P < 0.0001**	**P < 0.0001**	P=0.388	**P=0.005**	**P=0.050**	**P=0.025**	P=0.689	P=0.113
Mix	P=0.821	P=0.555	P=0.473	P=0.561	P=0.354	P=0.298	P=0.811	P=0.350	P=0.435	P=0.656	P=0.712	P=0.519
Disc · herbicide	P=0.989	P=0.969	P=0.964	P=0.187	P=0.716	P=0.309	P=0.399	P=0.140	P=0.784	P=0.406	P=0.964	P=0.553
Disc · mix	P=0.407	P=0.266	P=0.616	P=0.507	P=0.576	P=0.492	P=0.087	P=0.424	P=0.161	P=0.899	P=0.790	P=0.739
Herbicide · mix	P=0.979	P=0.507	P=0.677	P=0.639	P=0.187	**P=0.017**	P=0.660	P=0.400	P=0.448	P=0.826	P=0.902	P=0.689
Disc · herbicide · mix	P=0.833	P=0.173	P=0.382	P=0.258	P=0.757	P=0.499	P=0.631	P=0.508	P=0.454	P=0.345	P=0.907	P=0.704

[a] Bolded values are significant at P=< 0.05.

quality). Additionally, native perennial grass accessions from different geographical locations and elevations can result in different establishment densities (Annese et al. 2006; Knapp and Rice 1996), particularly in soils with low water holding capacity and nutrient availability.

Soil quality affects plant interactions and the ability to compete for available resources, particularly in soils with low fertility or water holding capacity (Grime 1979; Tilman 1988). Under poor soil conditions, the establishment of native perennial grasses can be difficult, even when using a wide range of plant accessions and different ecotypes. Soil conditions were better at I-5 North and probably negated any deleterious effects (e.g., poor germination, low vigor) from using a dry or wet site seed mix (Table 3).

Summary of Pre- and Postplant Techniques. Weeds are a major limiting factor for successful establishment of native perennial grasses (Barnes 2006; DiTomaso 2000; Lulow et al. 2007). We used burning, herbicide, cultivation, and mowing to control weeds prior to planting native perennial grasses along roadside rights-of-way. Following preplant weed control, 3 yr of cultural and chemical management was used to establish native perennial grasses. We found that at least two herbicide applications (nonselective after planting and broadleaf after establishment) provided control of annual weeds in burn areas of high soil organic matter and water holding capacity. Additionally, deep disc cultivation (> 8 cm) in fertile soils just prior to planting reduced nonnative annual grasses, thereby providing a competitive advantage for establishing native perennial grasses. In poorer soils, however, disc cultivation was associated with a significant increase in annual weeds possibly because of less vigorous native perennial grass seedlings. Because of the range of soil conditions for this study, wet versus dry site seed mix composition had little impact on native perennial grass establishment.

The reduction of weed populations is desirable along roadsides in preparation for planting native perennial grasses. Similar to Bugg et al. (1997), Tyser et al. (1998), and Wrysinski (1999), we found that cultural and chemical management techniques, especially in poor soil conditions, are necessary to improve the establishment success of native perennial grasses in the year before and the first 3 yr after planting along highway rights-of-way in regions of the western United States.

Sources of Materials

[1] FLEXII Series Grass Drill, Truax Company, 4300 Quebec Avenue North, New Hope, MN 55428.

Acknowledgment

Special thanks to R. O'Dell for helping with data collection and J. Anderson for site selection. This research was funded by

Table 4. Linear contrasts of weed control (Disc = tillage; Herbicide = herbicide regime) and species (Mix = Planting mixture) at I-5 South. In each row, underlined P-values indicate when disc, herbicide, and mix, individually and in combination, resulted in significantly lower weed (AG = annual grasses; AF = annual forbs) or higher native (NG = native perennial grasses) plant cover.[a]

	2005						2006					
	Burn			Nonburn			Burn			Nonburn		
	AG	AF	NG	AG	AF	NG	AG	AF	NG	AG	AF	NG
Weed control and species mixture	P= 0.274	P < 0.0001	P=0.120	P= 0.553	P < 0.0001	P=0.020	P=0.029	P=0.068	P=0.001	P=0.229	P=0.135	P=0.212
treatments	*n* = 72	*n* = 72	*n* = 72	*n* = 72	*n* = 72	*n* = 72	*n* = 72	*n* = 72	*n* = 72	*n* = 72	*n* = 72	*n* = 72
Disc	P=0.129	**P=0.002**	P=0.413	P=0.285	**P=0.001**	P=0.980	**P=0.003**	P=0.235	**P < 0.0001**	P=0.853	P=0.368	P=0.988
Herbicide	P=0.499	**P < 0.0001**	P=0.183	P=0.193	**P < 0.0001**	**P=0.002**	P=0.157	**P=0.030**	**P=0.012**	**P=0.006**	P=0.059	**P=0.017**
Mix	P=0.068	**P < 0.0001**	**P=0.001**	P=0.285	**P=0.034**	**P=0.022**	P=0.053	P=0.537	**P=0.017**	P=0.922	**P=0.047**	P=0.326
Disc · herbicide	P=0.870	P=0.225	P=0.841	P=0.869	P=0.307	P=0.816	P=0.358	P=0.556	P=0.131	P=0.472	P=0.285	P=0.290
Disc · mix	P=0.650	P=0.569	P=0.550	P=0.170	P=0.105	P=0.051	P=0.116	P=0.794	P=0.269	P=0.640	P=0.834	P=0.850
Herbicide · mix	P=0.335	P=0.745	P=0.705	P=0.745	P=0.512	P=0.416	P=0.935	P=0.014	P=0.693	P=0.687	P=0.322	P=0.516
Disc · herbicide · mix	P=0.779	P=0.491	P=0.974	P=0.526	P=0.856	P=0.899	P=0.454	P=0.842	P=0.753	P=0.635	P=0.511	P=0.488

[a] Bolded values are significant at $P < 0.05$.

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