RESEARCH ARTICLE

Why Pest Plant
Control and Native
Plant Establishment
Failed: A
Restoration Autopsy

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ABSTRACT: Explaining restoration failure can be as important as touting success. We used a series of studies to understand the failure of techniques commonly used to restore wetland prairies in the Willamette Valley of western Oregon. Burning, fallowing, and solarization (covering tilled plots with plastic sheeting to heat the soil) had pronounced first-year effects on several individual species, but either did not reduce overall pest plant abundance or reduced the abundance of native species as well. The 34% overall plant cover in solarized plots was the only significant difference from the 60% cover present in control plots. All first-year responses essentially disappeared by the second year. These measures had little lasting effect on pest and other exotic plants because many survived treatment and resprouted. In addition, treatments had little effect on the number of seeds in the soil, leaving a pool of immediate and potential regeneration. Specific control measures of target plants, such as hand removal and repeat maintenance after initial treatments, should prove more successful. In a second study, three mixtures of native species sown into fallowing treatment plots had low emergence rates of 1% - 7%, despite high seed viability, and produced only 0% - 3% cover. Native species should be selected and sown at densities high enough to lead to significant numbers of surviving seedlings, especially in the face of competition from surviving pest plants.

Index terms: pest-plant control, plant establishment, restoration, seeding, wetland prairies

INTRODUCTION

Two key elements of most restoration projects are pest-plant control (Berger 1993, Anderson 1995) and establishment of desired native species. An objective of pest-plant control is to allow the establishment and growth of native species by reducing competition from pest plants for soil resources or growing space (Fowler 1988, Montalvo et al. 1997). Many pest plants also quickly attain taller stature than the shorter, slower growing native species typical in Oregon's Willamette Valley (Wilson and Clark 2001). Thus, pest-plant control also releases desired species from suppression by shading.

Several pest-plant reduction techniques are widely used in attempts to restore native prairies. Because historically fire played a key role in maintaining many prairies (Boyd 1986, Collins and Wallace 1990), prescribed burning has been widely used for prairie improvement (Howe 1994, Anderson 1995, Brockway et al. 2002). Fallowing - tilling to reduce vegetation cover and to stimulate germination of buried seeds, followed by tilling to kill the resulting seedlings - is also widespread (Mohler 1993, Wilson and Gerry 1995). In solarization, tilled plots are covered with plastic sheeting to heat the soil and kill pest plants and seeds (Bainbridge 1990, Egley 1990, Schultz 2001).

Because weedy species often dominate the seed rain and the soil seed bank, pestplant control can lead to reinvasion and establishment of weedy species under these conditions of low competition and high resources (Hunneke et al. 1990, Davis 2000). One solution to this problem is to boost the abundance of native species. Broadcast sowing, seed drilling, and planting of seedlings can augment native plant populations (Luken 1990, Galatowitsch and van der Valk 1994, Biedenbender and Roundy 1996). Increasing cover of native species might also promote competitive suppression of pest and exotic species (Goodridge 2001).

Despite this array of techniques, many vegetation restorations fail, often with weedy plant species rapidly becoming dominant (D'Avanzo 1990, Kentula et al 1992, D'Antonio and Meyerson 2002). Progress in restoration requires not only reports of successes, but also analyses of failures. Such analysis requires both a statement of the outcomes and consideration of the ecological processes responsible for success or failure. Much as the medical autopsy seeks to explain the cause of death, the restoration autopsy might serve a diagnostic and prescriptive role in restoration, a field sometimes called "a healing art for nature." This paper evaluates the performance of several techniques commonly used to restore wetland prairies, explains the failure of these techniques, and identifies potential improvements.

STUDY SITE

We conducted the research at Horkelia Prairie, a degraded wetland prairie managed by the US Army Corps of Engineers in western Oregon's Willamette Valley (44°05'00" N, 128°14'25" W). Before Euro-American settlement of the area in the early 1800s, wetland prairies were widespread in poorly-drained, low-lying areas. Frequent burning by the native Kalapuya maintained these habitats by killing invasive, but more fire-susceptible, woody plants (Boyd 1986). More than 99% of the native wetland prairies of the Valley have been lost to agriculture, urbanization, invasion of exotic species, or natural succession to shrubland and forest. Management goals for Horkelia Prairie included restoring native vegetation, which would expand and protect an adjacent high-quality prairie remnant.

The dominant plant species at Horkelia Prairie included the natives Deschampsia cespitosa (L.) Beauv. and Panicum capillare L. and the exotics Agrostis capillaris L., Anthoxanthum odoratum L., and Hypochaeris radicata L. The Natroy silty clay loam soils of the site (Patching 1987) are poorly drained because of a thick clay pan close to the surface that causes seasonal perching of the water table (Scoles Associates 1994). As a result, Horkelia Prairie soils are saturated for at least two months at the beginning of the spring and summer growing season, having a surface-driven water regime; once spring rains stop, the soil dries by mid-summer (Scoles Associates 1994, Finley 1995).

METHODS

Pest-plant control techniques

We experimentally assessed three nonchemical weed control techniques commonly used in restoration projects, using a randomized complete block design with five replicate blocks. Blocks were established at random within five partitions of the study area that spanned the range of topographic and flooding conditions present. In the *fallow treatment*, we tilled 5-m × 5-m field plots first on May 12, 1992 by rototilling with a three-point 48" Howard HA Rotovator. This treatment was intended to kill vegetative plants of the undesirable species that dominated the site and to stimulate germination of their buried seeds. The second tilling on June 3, 1992 was designed to kill these emergent seedlings.

In the *solarization treatment*, 5-m × 5-m field plots were tilled twice as above, then covered tightly on June 3, 1992 with a sheet of 6-mil polyethylene treated with UV inhibitors. This treatment was intended to kill vegetative plants through tillage and to kill shallowly buried seeds and remaining vegetative plants with the hot and moist conditions under the polyethylene. The polyethylene sheets were removed October 21, 1992.

In the *burn treatment*, $5\text{-m} \times 5\text{-m}$ field plots were ignited with drip-torches on September 29, 1992, first on the downwind margin of each plot, then on all sides. Vegetation and litter provided continuous one-hour fuels through each plot. This procedure produced a rapid convection burn, lasting between 0.9 and 2.0 minutes with flame lengths 1.2 m to 2.7 m. This treatment was intended to kill vegetative plants with exposed buds and seeds on the soil surface.

No-manipulation plots served as controls

We recorded abundance (cover) for all plant species within each of eight 0.25m² sampling quadrats per treatment plot. Quadrats were located randomly and marked permanently within $3.5 - m \times 3.5 - m$ units centered within each plot, to allow a 0.75-m buffer of edge effects. Cover was estimated visually, using calibrated templates and the same observers to maintain consistency. Cover measurements were taken between June 7 and June 16 in 1993 and May 28 and June 11 in 1994. We also grouped species into categories of pests (plant species considered by restorationists to be undesirable or aggressive), natives (species present in similar ecosystems in the region before contact (Wilson et al. 1991)), and exotic species.

Treatment effects on plant cover were tested by analysis of variance and Dunnett's test for comparisons against controls ($\alpha = 0.05$) (Day and Quinn 1989). Rank transformations were applied as necessary to meet statistical assumptions (Conover 1980).

Seedling establishment and the soil seed bank

We examined both the short-term and the long-term capacity of buried seeds to contribute seedlings to aboveground vegetation. To estimate the short-term contribution, we recorded the density of seedlings emerging in the field and in the control plots during the first autumn, winter, and spring after fallow and solarization treatments. These seedlings arose in part from outside seed rain, which is almost entirely limited to the summer and early autumn seasons, and from non-dormant seeds already present in the soil seed bank. Emergence was recorded in five 15-cm × 15-cm quadrats per treatment area on October 12, 1992, and January 13, January 22, February 2, and April 20, 1993. To account for mortality and new emergence, we marked each seedling when first observed. We differentiated seedlings from vegetative sprouts by the presence of coleoptiles or cotyledons and the more vigorous growth of vegetative sprouts. Identification was limited to monocot vs. dicot.

Seedling emergence occurs only between the first rains after the summer drought and the following spring. Viable seeds remaining in the soil after this period of emergence constitute a pool of possible future seedlings. The density and composition of this persistent seed bank were determined by measuring seedling emergence from soil removed from the fallowed, solarized, and control plots in May, 1993 and placed under optimal germination conditions. Twelve $25\text{-cm}^2 \times 5\text{-cm}$ deep soil samples were removed from each experimental plot. Soil was stratified under cold (about 5 °C), moist conditions for 2.5 months. Soil was then spread in thin layers on growing flats in an Oregon State University greenhouse to allow germination as stratification and exposure to light are effective in breaking dormancy of most wetland prairie species (Gross 1990, Ingersoll and Wilson 1990).

Emergence was monitored once per week and seedlings were identified to species. Identification was aided by simultaneously growing seedlings from seeds of known taxonomic identity. Seedlings and vegetative sprouts were differentiated by the presence of coleoptiles or cotyledons, by the more vigorous growth of vegetative sprouts, and by excavation of roots.

Treatment effects on the soil seed bank were tested by analysis of variance and Dunnett's test for comparisons against controls ($\alpha = 0.05$) (Day and Quinn 1989). Rank or square-root transformations were

applied as necessary to meet statistical assumptions (Conover 1980).

Sowing

We selected seven desired native species for direct sowing: three native perennial grasses (*Deschampsia cespitosa*, *Hordeum brachyantherum* Nevski, and *Danthonia californica* Bolander), three native perennial forbs (*Wyethia angustifolia* (DC.) Nutt., *Eriophyllum lanatum* (Pursh) James Forbes, and *Microseris laciniata* (Hook.) Schultz-Bip.), and the native annual forb *Plagiobothrys figuratus* (Piper) Johnst.

Historically, *Deschampsia cespitosa* was the dominant species in Willamette Valley wetland prairies; the other six species are locally abundant. Ripe seeds were hand collected from nearby sites.

We also collected two bulk seed mixtures for sowing. The bulk seed mixtures were vacuum collected from two local sites that supported desired vegetation. The bulk mixture from one site was heavily dominated by *Carex* spp. (67% of the mixture) and *Eleocharis* spp. (99% of mixture), largely *E. acicularis* (L.) Roemer & Schultes (a perennial) and *E. ovata* (Roth) Roemer

Table 1. Average cover (%) of the 10 most abundant species one and two years after treatment and the analysis of variance for treatment effects on cover. N = native, E = exotic, P = pest (undesirable and aggressive). *: Treatments differed significantly from controls (Dunnett's test, $\alpha = 0.05$).

C.,		-	Tre	atments		F	D
Species		Burn	Fallow	Solarized	Control	F	P
Agrostis capillaris L. (E,Pe)	Year 1	26.8	2.9*	3.1*	12.0	11.5	< 0.01
	Year 2	11.7	17.2	14.5	6.7	0.9	0.49
Anthoxanthum odoratum L.	Year 1	6.3	3.2	10.8	9.1	1.1	0.39
(E,Pe)	Year 2	22.8	14.6*	20.7	28.2	5.1	0.02
Danthonia californica Bolander	Year 1	2.2	0.0*	0.0*	2.3	11.1	< 0.01
(N)	Year 2	2.7	0.3*	0.2*	1.8	11.3	< 0.01
Deschampsia cespitosa (L.)	Year 1	5.3	0.0*	0.4*	9.1	6.6	< 0.01
Beauv. (N)	Year 2	20.7	4.3	6.4	13.7	2.6	0.10
Grindelia integrifolia DC. (N)	Year 1	0.5	0.0*	0.0*	1.8	21.9	< 0.01
	Year 2	0.8*	0.2*	0.2*	4.6	13.3	< 0.01
Hypochaeris radicata L. (E,Pe)	Year 1	1.4	0.3*	0.0*	5.3	11.9	< 0.01
	Year 2	2.2	2.9	0.7	3.8	1.5	0.26
Juncus bufonius L. (N)	Year 1	0.5	56.9*	11.9*	0.1	38.5	< 0.01
	Year 2	0.0	2.1	2.1	0.0	4.1	0.03
Juncus marginatus Rostk. (E,Pe)	Year 1	0.2	2.2	0.7	0.2	1.0	0.42
	Year 2	0.0	5.9	1.3	0.0	5.7	0.01
Lotus purshianus F.E. & E.G.	Year 1	0.7	0.3	1.4	0.3	1.6	0.30
Clem. (N)	Year 2	1.0	1.1	5.9	0.9	2.5	0.11
Panicum capillare L. (N)	Year 1	3.6	0.3	1.8	5.6	1.7	0.23
	Year 2	3.4	8	8.7	6.5	0.9	0.46

& Schultes (an annual). All seeds were collected during the summer of 1992, and they were cleaned, dried, and kept in cold storage until testing in fall of 1992.

On October 21, 1992, we sowed three mixtures, each into two lightly raked 1250-cm² quadrats located at random in the fallowed plots. Mixture 1 was a monoculture of the seeds of *Deschampsia cespitosa* (100 filled seeds per quadrat). Mixture 2 was a combination of the seeds of seven native grasses and forbs (89 filled seeds per quadrat). Mixture 3 was a combination of the bulk collections (about 340 seeds per quadrat). After sowing, seeds were gently raked into the soil. The soil in the quadrats was essentially bare from tillage at the time of sowing.

We recorded seedling density on June 9 and June 16, 1993 and June 6 and June 10, 1994 in 35-cm × 35-cm microquadrats centered within each sowing quadrat. Seedling density of each species was adjusted by any emergence of that species in unsown microquadrats.

To help evaluate the sowing and establishment rates, we measured seed weight, viability, stratification requirement, and germination for each species. To determine seed weights, 5-19 replicates of 20 filled seeds per species were weighed. The number of replicates was set so that the coefficient of variation of estimated seed weight was < 16%.

We used three measures of seed vigor. Seed fullness was estimated visually. Seed viability was measured using the tetrazolium test (Moore 1985). Germination was recorded by holding 10 replicates of 20 seeds each at alternating temperature/light conditions of 4 °C/dark for 12 hours and 12 °C/light for 12 hours. The three species that did not readily germinate (*Carex* spp., *Hordeum brachyantherum*, and *Wyethia angustifolia*) were stratified by moistening 10 replicates of 20 seeds, holding them in sealed dishes at 3 °C for three months, and then exposing them to alternating 4 °C and 12 °C until germination.

RESULTS AND DISCUSSION

Pest-plant control techniques

One year after treatment, burned plots remained similar to control plots, with no significant differences in abundant species (Table 1) or species groups (Table 2). In contrast, the abundance of several species was less with fallowing or solarization. But cover was significantly lower for the desired native species Danthonia californica, Deschampsia cespitosa, and Grindelia integrifolia DC., as well as for targeted exotic pest plants such as Agrostis capillaris and Hypochaeris radicata. Woody pest plants, such as Rosa nutkana K. Presl and Fraxinus latifolia Benth., were not abundant enough on the site to see a treatment effect. In the first year after fallowing, the only significantly higher cover was that of Juncus bufonius L., a cosmopolitan and early successional annual. The significantly higher cover of native species and proportion of total cover constituted by native plants in fallowed plots (Table 2) was largely due to this species; without J. bufonius, native species cover was markedly lower in all treatments compared to controls.

Table 2. Average cover (%) of species groups one and two years after treatment and the analysis of variance for treatment effects. *: Treatments differed significantly from controls (Dunnett's test, $\alpha = 0.05$).

Group			<i>-</i>	D			
		Burn	Fallow	Fallow Solarized Control		F	P
All species	Year 1	62.1	68.2	34.0*	59.5	8.7	< 0.01
	Year 2	76.9	60.5*	68.0	79.8	5.4	0.01
Native species (non-pests)	Year 1	15.9	58.2*	15.7	24.1	13.7	< 0.01
	Year 2	31.9	18.4	27.5	32.0	2.4	0.12
Exotic species (non-pests)	Year 1	6.1	1.2	0.9	2.2	4.8	0.02
	Year 2	0.1	0.0	0.3	0.3	1.5	0.26
Pest species (undesirable	Year 1	40.1	8.8*	17.4	33.2	10.2	< 0.01
and aggressive)	Year 2	44.9	42.1	40.0	47.6	0.6	0.67
Natives ÷ total	Year 1	0.31	0.85*	0.53	0.44	15.5	< 0.01
	Year 2	0.42	0.32	0.41	0.42	0.6	0.62

By the second year after manipulation, many of these treatment effects had disappeared (Tables 1 and 2). The extremely high cover of *J. bufonius* in fallowed plots dropped from 57% to 2%, more in line with the other treatments. Both desired native species, such as *Deschampsia cespitosa*, and undesired pest species, such as *Hypochaeris radicata*, regained cover in fallowed and solarized plots. By the second year after treatment, the ratio of native cover to total cover was similar in all plots (Table 2).

Treatments had little lasting effect on vegetative cover because of rapid regeneration. Most of the perennial herbaceous species that dominated the site have a high capacity for resprouting from vegetative parts. Even after a temporary reduction in cover in the first year after fallowing and solarization, growth of survivors allowed these species to regain much of the former cover by the second year. Burning in the fall, as dictated by smoke management and fire safety regulations, means that nearly all plants were dormant aboveground. Poor propagation of heat into the soil (Maret 1996) left these plants essentially intact. Germination of buried seeds also contributed to the rapid regeneration of vegetation.

Seedling establishment and the soil seed bank

We recorded 280 to 1240 seedlings per m² in the fall, winter, and spring censuses (Table 3). The fallowing treatment stimulated the emergence of monocots. The solarization treatment caused a significantly lower emergence of dicots compared with controls. The overall emergence numbers were low compared with the potential of the persistent seed bank, but considerably higher than the number of seedlings obtained from sown seeds.

Soil from control plots contained more than 20,000 seeds per m², nearly 40% of which were exotic or pest species (Table 4). Seed numbers were significantly lower in soil from solarized and fallowed plots for the pests *Agrostis capillaris* and *Hypochaeris radicata* but not the seeds of pests as a group (Table 5). The unexpectedly negligible effect of fallowing on the density or

Table 3. Average number of emergents during the fall, winter, and spring after treatments, and the analysis of variance for treatment effects on seedling numbers. *: Treatments differed significantly from controls (Dunnett's test, $\alpha = 0.05$).

_		Treatments			
	Fallow	Solarized	Control	F	P
All species	1240	280	820	3.2	0.08
Monocots	1020*	250	140	6.2	0.01
Dicots	220	30*	680	6.5	0.01

species composition of the soil seed bank occurred possibly because unusually dry weather after spring tilling enforced seed dormancy (cf. Roberts and Potter 1980). Although seeds of individual native species were not significantly lower in solarized plots, native seed abundance as a group was just 63% of that in control plots (Table 4). Seeds of monocots were significantly reduced with solarization, but seeds of dicots were more abundant.

Sowing of native species

In mixture 1 (pure *Deschampsia cespitosa*), only 0.8% of the sown seeds were seedlings in the first year after sowing (Table 6), producing seedling densities (6-52 per m²) much lower than the number of seedlings of unsown species (280-1240 per m², Table 3).

The resulting average cover was very low, about 0.1%. The number of new seedlings of *D. cespitosa* in the second year was over twice that in the first year, even though no additional seeds were sown, and the 7.6% cover of second-year seedlings was also considerably higher than in the first year. *D. cespitosa* seedlings were uncommon outside of sowing plots (and seedlings in control plots were used to adjust establishment rates), so its increased cover was caused by vigorous growth of established seedlings or by delayed establishment of sown seeds.

In mixture 2 (multi-species), more than 7% of the sown seeds were seedlings in the first year (Table 6). The average cover of 2.8% was low, although much higher than in mixture 1. Results in the

Table 4. Average seed densities (number per m^2) for different categories of species in the persistent seed bank, one year after treatment, and the analysis of variance for treatment effects on seed densities. *: Treatments differed significantly from controls (Dunnett's test, $\alpha = 0.05$).

	Fallow	Solarized	Control	F	Р
All species	21660	15370	21150	1.7	0.24
Native species (non-pests)	14560	7160	11350	2.3	0.16
Exotic species (non-pests)	3820	3850	3680	0.3	0.76
Pest species	2430	3650	4320	1.3	0.32
Unknowns	1590	910	1890	1.1	0.37
Monocots	16860	7060*	14430	23.1	< 0.01
Dicots	4800	8310	6720	1.6	0.27

Table 5. Average seed densities (number per m^2) of the 10 most abundant species in the persistent soil seed bank, one year after treatment, and the analysis of variance for treatment effects on seed densities. N = native, E = exotic, Pe = pest. *: Treatments differed significantly from controls (Dunnett's test, $\alpha = 0.05$).

a ·		E	D		
Species	Fallow	Solarized	Control	F	P
Agrostis capillaris L. (E, Pe)	1350*	510*	3110	17.5	< 0.01
Briza minor L. (E)	610	200	540	0.7	0.52
Deschampsia cespitosa (L.) Beauv. (N) 200	300	740	2.9	0.11
Hypericum perforatum L. (E, Pe)	3110	3650	2990	0.0	0.96
Hypochaeris radicata L. (E, Pe)	70*	70*	740	9.4	< 0.01
Juncus bufonius L. (N)	8580	2970	5240	8.4	0.01
Myosotis discolor Pers. (N)	170	980	1320	4.0	0.06
Panicum capillare L. (N)	4160	1860	2870	1.6	0.25
Triodanis perfoliata (L.) Nieuwl. (N)	610	810	980	0.5	0.64
Unknown grass	300	340	640	4.2	0.06

second year were similar to those of the first. The best performing species were *Wyethia angustifolia* (highest emergence) and *Plagiobothrys figuratus* (highest cover in the first year). *Plagiobothrys* abundance dropped precipitously from dominance in the first year to a single seedling in the second.

In mixture 3 (bulk collection), only *Eleocharis*, of the two genera monitored (representing 90% of the seeds sown), was present in the first year, with a 2.7% seedling establishment rate and 2.7% cover (Table 6). No *Eleocharis* or *Carex* were found in the second year.

All sown species had viabilities > 60% except *Eleocharis* spp. and *Eriophyllum lanatum* (Table 7), yet emerged at low rates in the field. Low field emergence rates have also been reported from other grasslands (Glenn-Lewin et al. 1990, Thompson and Baster 1992, Reader 1993, Maret and Wilson 2000, Clark and Wilson 2003). The stratification requirement of *Carex* spp., *Hordeum brachyantherum*, and *Wyethia angustifolia* (Table 7) means

that spring sowing of these species would be unsuccessful.

The resulting low cover (0% to 8%) produced by the sowing mixtures was overwhelmed by the 45% to 58% cover of unsown species (Table 6). In contrast, Stevenson et al. (1995) found that sowing chalk grassland grasses and forbs at rates as low as 0.4 g/m² suppressed weeds, probably because agriculture and soil removal had greatly reduced weed abundance.

Conclusions and recommendations

The direct tests of restoration techniques (pest-plant control and sowing native species) and the supporting ecological studies (soil seed bank abundance and seedling establishment) suggest potential improvements for future restoration projects in similar wetland prairies. Plot tilling (as in the fallowing and solarized treatments) can be an effective method for reducing the following year's cover of exotic species, including pest species. Most of the pest-plant reduction in this study resulted from killing established plants, while the

soil seed bank was hardly affected. Yet by the second year, exotic pest plant cover had essentially recovered completely. Some dormant vegetative plants survived treatments, the undiminished soil seed bank served as a reservoir for new establishment, and the reduced competition in the first year after treatment allowed these survivors and seedlings to grow quickly. These results emphasize the need for several years of site preparation to reduce weed abundance or for the use of pest-plant control measures that continue in the years after sowing.

Fallowing and solarization treatments were as effective in reducing the cover of native species as in reducing the cover of exotic species. For restoration of similar wetland prairie sites with a significant component of native species worth saving, control techniques targeting exotic species, such as manual removal and spot herbicide application, might be a more effective—albeit expensive—alternative to broad-scale site preparation.

Prescribed burning is very useful in controlling woody species which are a major threat to wetland prairies in the Willamette Valley (Pendergrass et al. 1997, Wilson 1999, Clark and Wilson 2001). But in this study, burning was ineffective at reducing the abundance of herbaceous pest plants. Similarly poor control of herbaceous pest plants was found after prescribed burns in similar wetland prairies (Wilson et al. 1993, Pendergrass 1995, Wilson 1999). Moreover, prescribed burning should be used with caution in prairies having a large component of exotic species because seedling establishment of exotic species can be stimulated by burning (Maret and Wilson 2000, Morgan 2001).

Several of the sown species showed promise for use in future restoration projects. *Plagiobothrys figuratus* seeds were highly viable, emerged at a fairly high rate, and rapidly produced high cover. By the second year, however, cover of this annual was very low. These characteristics suggest that *Plagiobothrys* could be effective as an early site-dominating species. *Deschampsia cespitosa* seeds were moderately viable, but significant vegetative growth did not occur until the second year, at which time

Table 6. Sowing rates and average number and cover of emergents recorded in the first (June, 1993) and second (June, 1994) year after fallowing, for three sowing mixtures. All of the sown species are desired native species. Cover of unsown species in the sowing quadrats is listed for comparison.

	Sowing	rate	Year	1	Year	r 2
	seeds/m	g/m²	Emergents ±SE	Cover	Emergents ±SE	Cover
		M	fixture 1			
Deschampsia cespitosa (L.)	800	0.52	6.4±2.7	0.1%	16.8±6.4	7.6%
Unsown species				60%		55%
		N	fixture 2			
<i>Danthonia californica</i> Bolander	96	0.4	1.6±1.6	0.0%	0.0	0.1%
Deschampsia cespitosa (L.) Beauv.	240	0.16	0.0	0.0%	6.4±2.7	1.3%
Eriophyllum lanatum (Pursh) James Forbes	66	0.04	6.4±2.0	0.2%	2.4±1.0	0.4%
Hordeum brachyantherum Nevsk	96	0.39	0.0	0.0%	0.0	0.0%
Microseris laciniata (Hook.) Schultz-Bip.	96	0.18	1.6±1.0	0.1%	3.2±2.0	0.3%
Plagiobothrys figuratus (Piper) Johst.	96	0.07	15.2±8.9	1.7%	0.8 ± 0.8	0.0%
<i>Wyethia angustifolia</i> (DC.) Nutt.	25	0.35	27.2±7.3	0.8%	21.6±8.9	1.6%
Total of sown species	715	1.59	52.0±14.3	2.8%	34.4±8.4	3.7%
Unsown species				55%		58%
		N	fixture 3			
Carex spp.	1700	_	0.0	0.0%	0.0	0.0%
Eleocharis spp.	740	_	20.0±13.0	2.7%	0.0	0.0%
Total of sown species	2440	_	20.0±13.0	2.7%	0.0	0.0%
Unsown species				45%		55%
		Conti	ol quadrats			
Unsown species				59%		70%

it had the highest cover of all sown species. Sowing mixtures of rapidly growing native annuals and more slowly growing perennial dominants, such as *Plagiobothrys* with *Deschampsia*, could be effective in

establishing native cover and slowing weed invasion. *W. angustifolia* also performed well, with moderately high seed viability and the highest field emergence rate. Fall sowing or laboratory pretreatment is re-

quired when using species such as *Wyethia* that require stratification.

These findings suggest a two-step strategy for restoring sites with significant numbers

Table 7. Seed characteristics of the sown species.									
	Seed weight (mg±SE)	(%±SE)	of untreated	Germination after stratification (%)					
Carex spp.	_		0	60					
Danthonia californica Bolander	84±3	90±2	83						
Deschampsia cespitosa (L.) Beauv.	13±1	82±9	59						
Eleocharis spp.	_	1±1	0						
Eriophyllum lanatum (Pursh) James Forber	s 12±0	26±5	18						
Hordeum brachyantherum Nevsk	82±2	94±2	31	83					
Microseris laciniata (Hook.) Schultz-Bip.	37±1	90±2	85						
Plagiobothrys figuratus (Piper) Johst.	14±1	87±1	96						
Wyethia angustifolia (DC.) Nutt.	273±6	83±3	0	87					

of both exotic and native species. First, control measures should be implemented to reduce cover of undesirable species. In this study, the fallowing and solarization treatments were most successful in reducing vegetative cover, although prescribed burning can be an effective control measure for woody plants. Control measures should continue until there is ample open space for establishment of sown species, vegetative cover of exotic and pest species is low enough to reduce competitive pressure, and the soil seed bank of exotic and pest species is down to a manageable level. For wetland prairies such as Horkelia Prairie, we propose targets of < 30% cover of exotic pests and < 2000 viable seeds per m². The number of years needed for control can be determined by monitoring plant cover and seed bank densities; at least two years will probably be required under most circumstances.

Second, once adequate control has been reached and before exotic species can rebound, native species should be sown at densities high enough to lead to significant cover. Species with high rates of establishment, vigorous growth, and the ability to suppress exotic species will be more likely to attain significant cover. In this

study, species establishment rates ranged between 0% and 100%, and Goodridge (2001) found a 6-fold difference among wetland plant species in their ability to suppress weedy exotic species. Thus, establishment success can depend on selecting the proper species. This crucial step of species selection can be aided by models relating easily measured, inherent plant traits to field performance (Clark et al. 2001, Thompson et al. 2001).

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LITERATURE CITED

Anderson, P. 1995. Ecological restoration and creation: a review. Biological Journal of the Linnean Society 56 (Supplement):187-211.

Bainbridge, D.A. 1990. Soil solarization for restorationists. Restoration & Management Notes 8:96-98.

Berger, J.J. 1993. Ecological restoration and nonindigenous plant species: a review. Restoration Ecology 1:74-82.

Biedenbender, S.H., and B.A. Roundy. 1996. Establishment of native semidesert grasses into existing stands of *Eragrostis lehmanniana* in southeastern Arizona. Restoration Ecology 4:155-162.

Boyd, R. 1986. Strategies of Indian burning in the Willamette Valley. Canadian Journal of Anthropology 5:65-86.

Brockway, D.G., R.G. Gatewood, and R.B. Paris. 2002. Restoring fire as an ecological process in shortgrass prairie ecosystems: Initial effects of prescribed burning during the dormant and growing seasons. Journal of Environmental Management 65:135-152.

Clark, D.L., and M.V. Wilson. 2001. Fire, mowing, and hand-removal of woody spe-

- cies in restoring a native wetland prairie in the Willamette Valley of Oregon. Wetlands 21:135-144.
- Clark, D.L., and M.V. Wilson. 2003. Postdispersal seed fates of four prairie species. American Journal of Botany 90:730-735.
- Clark, D.L., M.V. Wilson, and J. Goodridge. 2001. Increasing the abundance of rare native wetland prairie species. Report to the US Bureau of Land Management. Washington, D.C. 19 pp.
- Collins, S.L. and L.L. Wallace, eds. 1990.
 Fire in North American Tallgrass Prairies.
 University of Oklahoma Press, Norman.
 175 pp.
- Conover, W.J. 1980. Practical Nonparametric Statistics, 2nd ed. John Wiley & Sons, N.Y. 493 pp.
- D'Antonio, C., and L.A. Meyerson. 2002. Exotic plant species as problems and solutions in ecological restoration: a synthesis. Restoration Ecology 10:703-71.
- D'Avanzo, C. 1990. Long-term evaluation of wetland creation projects. Pages 487-496 in M.E Kusler, J.A. and Kentula, eds., Wetland Creation and Restoration, Island Press, Washington.
- Davis, K.J. 2000. The effects of nitrogen manipulations and hydrology on the establishment and competitive abilities of wetland prairie species (western Oregon). Ph.D. Dissertation. Oregon State University, Corvallis. 93 pp.
- Day, R.W., and G.P. Quinn. 1989. Comparisons of treatments after an analysis of variance in ecology. Ecological Monographs 59:433-463.
- Egley, G.H. 1990. High-temperature effects on germination and survival of weed seeds in soil. Weed Science 38:429-435.
- Finley, K.K. 1995. Hydrology and related soil features of three Willamette Valley wetland prairies. M.S. Thesis. Oregon State University, Corvallis. 94 pp.
- Fowler, N.L. 1988. What is a safe site?: neighbor, litter, germination date, and patch effects. Ecology 69:947-961.
- Galatowitsch, S.M., and A.G. Van Der Valk. 1994. Restoring prairie wetlands: an ecological approach. Iowa State University Press, Ames. 246 pp.
- Glenn-Lewin, D.C., L.A. Johnson, T.W. Jurik,
 A. Akey, M. Leoschke, and T. Rosburg. 1990.
 Fire in central North American grasslands: vegetative reproduction, seed germination, and seedling establishment. Pages 28-45 in
 S.L. Collins and L.L. Wallace, eds., Fire in North American Tallgrass Prairies, University of Oklahoma Press, Norman.
- Goodridge, J.M. 2001. The effects of native

- plants on non-native plant abundance in a restoration setting: differences among native species and the predictive ability of species traits. M.S. Thesis. Oregon State University, Corvallis. 69 pp.
- Gross, K.L. 1990. A comparison of methods for estimating seed numbers in the soil. Journal of Ecology 78:1076-1093.
- Howe, H.F. 1994. Response of early- and late-flowering plants to fire season in experimental prairies. Ecological Applications 4:121-133.
- Hunneke, L.F., S.P. Hamburg, R. Koide, H. A. Mooney, and P. M. Vitousek. 1990. Effects of soil resources on plant invasion and community structure in California serpentine grassland. Ecology 71:478-491.
- Ingersoll, C.A., and M.V. Wilson. 1990. Buried propagules in an old-growth forest and their response to experimental disturbances. Canadian Journal of Botany 68:1156-1162.
- Kentula, M.E., J.C. Sifneos, J.W. Good, M. Rylko, and K. Kunz. 1992. Trends and patterns in section 404 permitting requiring compensatory mitigation in Oregon and Washington, USA. Environmental Management 16:109-119.
- Luken, J.O. 1990. Directing Ecological Succession. Chapman and Hall, London. 251 pp.
- Maret, M.P. 1996. Effects of fire on seedling establishment in upland prairies in the Willamette Valley, Oregon. M.S. thesis. Oregon State University, Corvallis. 159 pp.
- Maret, M.P. and M.V. Wilson. 2000. Fire and seedling population dynamics in western Oregon prairies. Journal of Vegetation Science 11:307-314.
- Mohler, C.L. 1993. A model of the effects of tillage on emergence of weed seedlings. Ecological Applications 3:53-73.
- Montalvo, A.M., S.L. Williams, K.J. Rice, S.L. Buchmann, C. Cory, S.N. Handel, G.P. Nabhan, R. Primack, and R.H. Robichaux. 1997. Restoration biology: a population biology perspective. Restoration Ecology 5:277-290.
- Moore, R.P., ed. 1985. Handbook on Tetrazolium Testing. The International Seed Testing Association, Zurich, Switzerland. 99 pp.
- Morgan, J.W. 2001. Seedling recruitment patterns over 4 years in an Australian perennial grassland community with different fire histories. Journal of Ecology 89:908-919.
- Patching, W. 1987. Soil Survey of Lane County Area, Oregon. US Department of Agriculture, Soil Conservation Service., Washington, D.C. 369 pp.
- Pendergrass, K.L. 1995. Vegetation composition and response to fire of native Willamette Valley wetland prairies. Master's thesis, Oregon

- State University, Corvallis. 241 pp.
- Pendergrass, K.L., P.M. Miller, and J.B. Kauffman. 1997. Prescribed fire and the response of woody species in Willamette Valley wetland prairies. Restoration Ecology 6:303-311.
- Reader, R.J. 1993. Control of seedling emergence by ground cover and seedling predation in relation to seed size for some old field species. Journal of Ecology 81:169-175.
- Roberts, H.A., and M.E. Potter. 1980. Emergence patterns of weed seedlings in relation to cultivation and rainfall. Weed Research 20:377-386.
- Schultz, C.B. 2001. Restoring resources for an endangered butterfly. Journal of Applied Ecology 38:1007-1019.
- Scoles Associates. 1994. Soils and hydrology. Report to Fishman Environmental Services and US Army Corps of Engineers.
- Stevenson, M.J., J M. Bullock, and L.K. Ward. 1995. Re-creating semi-natural communities: effect of sowing rate on establishment of calcareous grassland. Restoration Ecology 3:279-289.
- Thompson, K., and K. Baster 1992. Establishment from seed of selected Umbelliferae in unmanaged grassland. Functional Ecology 6:346-352.
- Thompson, K., J.G. Hodgson, J.P. Grime, and M. J. Burke. 2001. Plant traits and temporal scale: evidence from a 5-year invasion experiment using native species. Journal of Ecology 89:1054-1060.
- Wilson, M.V. 1999. Evaluating prescribed burning to improve prairie quality in the Willamette Floodplain Research Natural Area, W.L. Finley National Wildlife Refuge, Oregon. Final report to the US Fish and Wildlife Service, 25 pp.
- Wilson, M.V., and D.L. Clark. 2001. Controlling invasive *Arrhenatherum elatius* and promoting native prairie grasses through mowing. Applied Vegetation Science 4:129-138.
- Wilson, M.V., K.P. Connelly, and L.E. Lantz. 1993. Plant species, habitat, and site information for Fern Ridge Reservoir. Report to Waterways Experiment Station, US Army Corps of Engineers.
- Wilson, M.V., D.E. Hibbs, and E.R. Alverson. 1991. Native plants, native ecosystems, and native landscapes. Kalmiopsis 1:13-17.
- Wilson, S.D., and A.K. Gerry. 1995. Strategies for mixed-grass prairie restoration: herbicide, tilling, and nitrogen manipulation. Restoration Ecology 3:290-298.