

Restoration of Agricultural Fields to Diverse Wet Prairie Plant Communities in the Willamette Valley, Oregon

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Restoration of Agricultural Fields to Diverse Wet Prairie Plant Communities in the Willamette Valley, Oregon

Abstract

Restoring highly degraded sites in Oregon's Willamette Valley to diverse native prairie plant communities is an important component of regional conservation strategies. However, creating or reassembling desired native plant communities is a tremendous challenge for restoration practitioners, and useful practical approaches are needed. Here, we describe an implementation strategy we developed for restoring intensively managed agricultural sites to native wet prairie that integrates relevant scientific research and lessons learned from previous restoration experience, with a particular focus on sequencing disturbance, colonization, and competitive actions to achieve desired outcomes. Then, we report vegetation monitoring results from four projects where we used this implementation strategy to assess if progress is being made to achieve our two *a priori* project objectives: (1) establishing a plant community with 50 or more native plant species, and (2) establishing a plant community with > 70% absolute cover of native plant species. By the second growing season after seeding, all four projects had more than 40 native species and native cover exceeded 90%. For the two projects for which we have data during the fifth growing season, native species richness exceeded 50 and absolute native cover exceeded 100%. Furthermore, percent cover of native annuals decreased and percent cover of native perennials increased by the fifth growing season, consistent with predictions from succession. These results indicate that our implementation strategy can assist the efforts of landowners and managers to restore high diversity prairie communities from highly disturbed agricultural sites.

Introduction

Prairies in Oregon's Willamette Valley have been dramatically reduced in extent since Euro-American settlement and are now listed as critically endangered ecosystems (Noss et al. 1995, Christy and Alverson 2011). Historically, prairies covered 31% of the 13,539 km² Willamette Valley Ecoregion (Altman et al. 2001, Hulse et al. 2002, Whitlock and Knox 2002), but over 98% have been severely altered or destroyed by agricultural uses, urban development, invasion of exotic plants, and fire suppression (Johannessen et al. 1971, Towle 1982). The remaining prairie remnants are generally small (Altman et al. 2001, Alverson 2005) and isolated from one another, leading to degraded plant community structure and increased edge effects typically associated with highly fragmented habitats (Saunders et al. 1991, Andren 1994, Debinski and Holt 2000, Fisher and Lindenmayer 2007).

Willamette Valley prairie vascular plant communities are comprised of a diversity of forbs, sedges, rushes, and grasses (Alverson 2005, U.S. Fish and Wildlife Service 2006). Several of these plant species and one butterfly species are now listed under the federal Endangered Species Act of 1973 (U.S. Fish and Wildlife Service 2001, 2006, 2010). As a result, protecting the remaining remnant prairies is a high priority conservation goal (Defenders of Wildlife 1998, Oregon Department of Fish and Wildlife 2006, U.S. Fish and Wildlife Service 2006, 2010).

However, because there is so little remnant prairie left, and what remains is highly fragmented, meaningful long-term conservation of the Willamette Valley prairie ecosystem necessitates not only protection and management of prairie remnants, but also restoration of prairie habitat in highly altered sites (U.S. Fish and Wildlife Service 2010). Lands that are currently in production for grass seed, including annual ryegrass (Lolium multiflorum), perennial ryegrass (L. perenne), bentgrass (Agrostis spp.), and fescue (Festuca spp.) are suitable candidates for large-scale prairie restoration in the Willamette Valley for three reasons. First, almost all of these agricultural grasses are currently grown on lands that were previously prairie, so there is a high likelihood that the soil and hydrologic conditions would be suitable for restoring to native prairie. Second, there are currently 182,000 ha in the Willamette Valley in grass seed production (Oregon State University

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Extension Service 2010), representing approximately 50% of all agricultural lands in the Willamette Valley. Many of the most significant prairie remnants are surrounded by grass seed fields, so restoring strategically located grass fields to prairie could augment the size and function of existing remnants or serve as stepping stones between remnants. Third, the intensive farming practices used in grass seed production, particularly the aggressive elimination of non-crop species, have created conditions that make restoration easier than in other degraded sites. For example, in abandoned agricultural fields and prairie remnants with a mixed native and exotic community, the diversity and ubiquity of aggressive exotic plant species interspersed with natives can make it challenging to successfully eliminate exotic species while establishing or maintaining native species (Stanley et al. 2011).

Tremendous increases in germane prairie research and restoration experience, including in the Willamette Valley, make it an opportune time to integrate on-theground experience with scientific research results to advance the success of prairie restoration. Over the past 15 years governmental organizations at the local (e.g., City of Eugene) and federal level (e.g., U.S. Bureau of Land Management, U.S. Fish and Wildlife Service, U.S. Army Corps of Engineers), and private conservation organizations (e.g., The Nature Conservancy) have implemented numerous prairie restoration projects in the Willamette Valley. Included in this mix are multiple wet prairie restoration projects we have conducted through the West Eugene Wetlands Mitigation Bank. These projects have extensive quantitative vegetation monitoring data and annual monitoring reports associated with them (City of Eugene 2006, 2007, 2008, 2009, 2010); our analyses of these data have informed each subsequent project we conducted and allowed us to adaptively manage our portfolio of mitigation sites. In addition, abundant applied ecological research has been conducted in Willamette Valley prairies directed toward understanding the efficacy of various prairie restoration techniques (Pendergrass et al. 1999, Maret and Wilson 2000, Clark and Wilson 2001, Wilson and Clark 2001, Pfiefer-Meister 2008, Stanley et al. 2011) and species-specific biology (Schultz and Dlugosch 1999, Kaye et al. 2001, Schultz and Crone 2001, Schultz 2001, Schultz et al. 2003, Wilson et al. 2003, McIntire et al. 2007, Severns et al. 2006, Severns 2008).

We have refined our prairie restoration approaches through time as we learn from the results of our own projects as well as from the research and restoration results of other scientists and restoration practitioners. Table 1 summarizes key ecological lessons learned from our own prairie restoration work and related ecological research, and identifies restoration strategies that are associated with those findings. Table 2 outlines the specific restoration implementation strategy we developed based on the lessons learned. Three ecological processes that are highlighted repeatedly in Tables 1 and 2 are disturbance, colonization, and competition. For restoration practitioners, it is important to understand how the timing, duration, magnitude, and characteristics of each of these processes impact the trajectory of community assembly in a particular restoration setting.

Keeping in mind that the goals of ecological restoration are to recover native populations, communities, and ecosystem function in degraded habitats (Temperton et al. 2004, Walker et al. 2007a), it is best practiced with specific, explicitly stated a priori objectives (Pywell et al. 2002, Palmer et al. 2006, del Moral et al. 2007, Walker et al. 2007b). For the four prairie restoration projects described in this paper, we had two specific a priori objectives: (1) establishment of 50 or more native plant species, and (2) > 70% absolute cover of native plant species. The plant richness objective of 50 was selected because it represents an average of native diversity found in high quality prairie remnants in the southern Willamette Valley. Specifically, eight high quality remnants within 8 km of our study sites contained between 30 and 84 native species, with an average of 56 species (Pendergrass 1995, City of Eugene 2004). We typically have 70-80 native prairie species available as seed, so selecting a goal of 50 species to become established on a specific project site seemed ambitious but achievable. Furthermore, since increased site-level diversity can lead to increased resistance to invasion by exotics (Tilman 1997, Naeem et al. 2000, Kennedy et al. 2002, Piper et al. 2007, Funk et al. 2008, Middleton et al. 2010, Davies et al. 2011), we aspired to establish a high diversity of natives in our restoration projects. The objective of achieving > 70% cover of native species was selected to meet regulatory requirements that applied to these four restoration projects, which are part of the West Eugene Wetlands Mitigation Bank. This level of native cover is much greater than what is seen in high quality prairie remnants in the Willamette Valley, where native cover is typically < 40% (Pendergrass 1995, Stanley et al. 2011) and where exotic cover usually exceeds native cover (Pfeifer-Meister 2008, Stanley et al. 2011).

Here, we report the results of four wet prairie restoration projects at two sites, Dragonfly Bend and Coyote Prairie, where we apply the implementation strategy

TABLE 1. Lessons learned from previous restoration experience in the Willamette Valley or from ecological research results, associated restoration strategies, and selected references.

Ecological Lesson Learned	Associated Restoration Strategy	Selected References
1. Dispersal and colonization of native species is severely limited.	Seed and plant a high density and diversity of native species.	Tilman 1997, Pywell et al. 2002, Pywell et al. 2003, Foster and Tilman 2003, Seabloom et al. 2003a, Seabloom et al. 2003a, Seabloom et al. 2004, Walker et al. 2006, Foster et al. 2007, Dickson and Busby 2009, Collinge and Ray 2009, Middleton et al. 2010, Stanley et al. 2011
2. Multiple colonization events lead to greater chance of establishment.	Seed native species for multiple years. Phase the introduction of native species.	Pywell et al. 2003, Walker et al. 2004, Collinge and Ray 2009
3. Increased site-level diversity can lead to increased resistance to invasion by exotics.	Seed native species that cover as many spatial, temporal, and functional roles as possible. Create specific seed mixes for different microsites within the project area to maximize establishment success.	Tilman 1997, Naeem et al. 2000, Kennedy et al. 2002, Foster et al. 2007, Piper et al. 2007, Funk et al. 2008, Davies et al. 2011
4. Plant community composition changes significantly during initial years of restoration.	Use seed mixes that will facilitate desired successional trajectory. Phase the introduction of desired species. For example, emphasize early-successional species (e.g., annuals) in initial seed mixes.	Pywell et al. 2003, Walker et al. 2004, Foster et al. 2007, Piper at al. 2007, Trowbridge 2007, Walker et al. 2007a, Pfeifer-Meister 2008
5. Seed bank is extensive and dominated by exotics.	Minimize soil disturbance to avoid surfacing buried seeds. Use no-till disturbance techniques such as fire, mowing, and herbicide.	U.S. Army Engineer Waterways Experiment Station et al. 1995, Walker et al. 2004, Andreu 2005
6. Order of arrival is important, priority effects exist.	Seed species with known, undesired priority effects after other species have established. For example, seed grasses (particularly <i>Deschampsia cespitosa</i>) after forbs. Consider spatially separating certain species across the project site, or sowing species with undesired priority effects at low densities.	Schramm 1992, Pywell et al. 2003, Ejrnaes et al. 2006, Piper et al. 2007, Collinge and Ray 2009, Dickson and Busby 2009
7. Exotic colonization is extensive and some species are highly competitive.	Aggressive exotic control is needed for first 2 years following initial seeding and planting of natives to prevent exotics from outcompeting natives.	Walker et al. 2004, Andreu 2005, Pfeifer-Meister 2008
8. Disturbance regimes can alter community assembly trajectory in desired and undesired directions, depending on how they are implemented.	Restoration efforts can be improved by increasing or decreasing the frequency, intensity, or duration of disturbance events. For example, 4-5 years after initial seeding and planting, prescribed fire followed by overseeding can increase species richness by opening space for annuals and less aggressive forbs.	Seabloom et al. 2003b, Pfeifer-Meister 2008, Stanley et al. 2011

TABLE 2. Major management actions for the first five years of the Dragonfly Bend and Coyote Prairie restoration projects. Each action is listed sequentially by year and season, followed by the ecological process the action manipulates. The 'year' is from fall to fall rather than a calendar year.

Step	Year	Season	Action	Ecological Process
1	0	Fall	Mow and burn or mow and hay final year of grass seed production	Disturbance
2	0	Spring	Apply glyphosate	Disturbance & Competition
3	0	Summer	Hydrologic manipulation/restoration	Disturbance
4	1	Fall	Seed and plant forbs, sedges, and rushes	Colonization
5	1	Spring and Summer	Apply grass-specific herbicide twice	Competition
6	1	Spring and Summer	Spot spray or hand weed exotic forbs	Competition
7	2	Fall	Seed and plant forbs, sedges, and rushes	Colonization
8	2	Spring and Summer	Grass-specific herbicide if needed	Competition
9	2	Spring and Summer	Spot spray or hand weed exotic forbs	Competition
10	2	Spring and Summer	Collect quantitative vegetation data	
11	3	Fall	Seed grasses and additional forbs, sedges, and rushes	Colonization
12	3	Fall	Seed areas disturbed by weed control methods	Colonization
13	3	Spring and Summer	Spot spray or hand weed exotic grasses and forbs	Competition
14	4	Fall	Seed areas disturbed by weed control methods	Colonization
15	4	Fall	Prescribed burn, mow, or mow and hay	Disturbance
16	4	Spring and Summer	Spot spray or hand weed exotic grasses and forbs	Competition
17	5	Fall	Seed areas disturbed by weed control methods and prescribed burns	Colonization
18	5	Spring and Summer	Spot spray or hand weed exotic grasses and forbs	Competition
19	5	Spring and Summer	Collect quantitative vegetation data	

outlined in Table 2 to restore agricultural grass fields to native wet prairie. We describe the specific steps we undertook during restoration implementation, present vegetation data from the second growing season after initial seeding and planting for all projects, and present vegetation data from the fifth growing season after initial seeding and planting for two projects. We assess if progress is being made to achieve our two *a priori* project objectives: (1) establishing a plant community with 50 or more native plant species, (2) establishing a plant community with > 70% absolute cover of native plant species.

Methods

Study Sites

The two restoration sites, Dragonfly Bend (T17S R4W S20) and Coyote Prairie (T18S R5W S01), are located within 5 km of each other in west Eugene, Oregon, USA. Historically, both sites were Willamette Valley wet prairie, a seasonally-flooded plant community. In wet prairie communities, grasses represent the dominant cover; however, a wide variety of forbs, sedges, and rushes are also present and comprise the majority of plant richness (Alverson 2005, U.S. Fish and Wildlife Service 2010), similar to what is observed in the tall-grass/mixed-grass prairies of the Midwest (Turner and

Knapp 1996, Collins et al. 1998, Dickson and Busby 2009). Dragonfly Bend and Coyote Prairie each have inclusions of emergent, vernal pool, and upland prairie plant communities due to subtle variations in topography and depth and duration of inundation, which is common for wet prairies in the Willamette Valley. These inclusions were mapped for use in creating seed mixes suitable for each plant community type. Typical for the plant community and the region (Finley 1995), both sites have Dayton and/or Natroy clay soils (Patching 1987) derived from ash fall deposits from the eruption of Mt. Mazama, now Crater Lake (Baitis and James 2005). With an average annual precipitation of 124 cm, falling primarily between October and May, soils are saturated or shallowly inundated from November through April (Finley 1995). Prior to restoration, these wetland restoration sites were in agricultural use for at least several decades, most recently cropped with annual ryegrass (Lolium multiflorum) or tall fescue (Festuca arundinacea) for seed production.

Two restoration projects at each of the Dragonfly Bend and Coyote Prairie restoration sites are the focus of this paper. Of the four projects described herein, Dragonfly Bend Phase 1 is 16.2 ha, Dragonfly Bend Phase 2 is 3.2 ha, Coyote Prairie Phase 1 is 10.5 ha, and Coyote Prairie Phase 2 is 15.3 ha.

Restoration Timeline

Our restoration implementation at these two sites occurred over a five year period and involved 19 steps (Table 2). We refer to the year that we conducted site preparation as Year 0. For the purposes of this paper, a year starts in the fall, since that is when our implementation began. Year 0 for Dragonfly Bend Phase 1 was 2004, Dragonfly Bend Phase 2 was 2005, Coyote Prairie Phase 1 was 2006, and Coyote Prairie Phase 2 was 2007. Given these starting dates, we have second year results to present for Coyote Prairie, and second and fifth year results for Dragonfly Bend. During Year 0, we removed the existing above-ground vegetation by either mowing and burning or mowing and haying each project area (Table 2, step 1). We then treated each project area two to three times with a broadcast application of a glyphosate-based post-emergent herbicide as successive flushes of annual ryegrass germinated from the soil seed bank (Table 2, step 2). Although both sites were repeatedly tilled, and sometimes leveled, during agricultural production, Dragonfly Bend Phase 1 was the only project where hydrologic enhancement was necessary. We removed shallow ditching that had been constructed to facilitate drainage (Table 2, step 3). Seeding and planting (Table 2, steps 4, 7, and 11) began early in Year 1 and is described in detail below. In Years 1 and 2, control of invasive exotic plant species included broadcast applications of grass-specific (sethoxydim-based or clethodim-based) herbicide to further eliminate annual ryegrass and other exotic grasses (Table 2, steps 5 and 8), and hand weeding and spot herbicide application of broad-leaf exotics, using glyphosate-based or triclopyr-based herbicide (Table 2, steps 6 and 9). In Years 3-5, additional hand weeding and spot spraying occurred at lower, maintenance levels (Table 2, steps 13, 16, and 18). A prescribed burn was implemented during Year 4 of Dragonfly Bend Phase 1 and Year 3 of Dragonfly Bend Phase 2, while Coyote Prairie Phase 1 was mowed during Year 4 (Table 2, step 15). Areas that were disturbed through weed control actions or prescribed burning were subsequently seeded with a mixture of native species (Table 2, steps 12, 14, and 17).

Planting Plans and Seed Mixes

We determined the species and seeding rates to include in a given seed mix by reviewing data from prairie remnant reference sites in the southern Willamette Valley (Pendergrass 1995, Taylor 1999, Jancaitis 2001), the experience of local ecologists, seed availability, and past establishment success in our wetland prairie restorations (City of Eugene 2003, 2004, 2005, 2006). We took care to develop seed mixes containing a high diversity of species to fill different niches (Hutchinson 1958). For example, hydrologic conditions vary across the site, throughout the season, and from year to year. Including a high diversity of native species with different hydrologic tolerances may improve the chances that native species, rather than exotics, will become established (Tilman 1997, Naeem et al. 2000, Kennedy et al. 2002, Piper et al. 2007, Funk et al. 2008, Middleton et al. 2010, Davies et al. 2011). The species composition and sowing densities of our mixes are shown in Tables 3 and 4.

At each project site, we created a planting plan with multiple seed mixes corresponding to each plant community type (emergent, vernal pool, and wet prairie) based on topographic and hydrologic conditions found within the site. Since over 35 mixes were seeded over the four projects, general mixes for emergent/vernal pool and vernal pool/wet prairie plant communities are reported here in Tables 3 and 4. We calculated the general mixes by averaging all the seeding rates for a particular species by plant community type. Forbs, sedges, and rushes were sown in Years 1-3 (Table 2, steps 4, 7, and 11), while grasses were sown during Year 2 at Dragonfly Bend and Year 3 at Coyote Prairie (Table 2, step 11). The first and second year mixes of forbs, sedges, and rushes ranged from 4317 to 4884 g ha⁻¹ each and contained an average of 30 species (Table 3). The seed mixes introducing grasses were between 2457 and 4345 g ha⁻¹ and contained an average of 5 species (Table 4). Year 1 forb, sedge, and rush seed mixes had higher rates of annual to perennial ratios than subsequent year mixes. Seeding was always done in the fall of each year, usually in October. Forbs, sedges, and rushes were broadcast seeded using either a Truax ATV-mounted Electric Operated Seed Slinger or with a Lely Land Wheel Driven WFF broadcast seeder pulled by an ATV. Grasses were seeded using a Truax FLEXII-812 no-till drill.

In addition to sowing seed, we planted plugs, bulbs, and bare root stock of 41 species across each project site (Table 2, steps 4 and 7). The species we planted were ones that we had found difficult to establish from seed on previous projects, or that are long-lived perennial species that take many years to reach reproductive status when sown as seed. The planted species and planting rates are shown in Appendix 1.

Vegetation Sampling

To evaluate the trajectory of the developing plant community in our restoration sites, we quantitatively sampled

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TABLE 3. Average seeding rate of forb, sedge, and rush species seeded in emergent/vernal pool and vernal pool/wet prairie seed mixes in grams per hectare. Limited seed availability resulted in numerous species with grams per hectare of less than ten. Abbreviations: A = annual, P = perennial; G = grass, F = forb, R = rush, S = sedge; approximate flowering period by month where. 4 = April, 5 = May, etc.; wetland indicator status for Region 9 (U.S. Fish and Wildlife Service 1988, U.S. Fish and Wildlife Service 1993) OBL = obligate wetland, FACW = Facultative Wetland, FAC = Facultative, FACU = Facultative Upland, ---- = no designation provided. "+" indicates a frequency toward the higher end of the category (more frequently found in wetlands), "-" indicates a frequency toward the lower end of the category (less frequently found in wetlands), "*" identifies tentative assignments based on limited information from which to determine the indicator status.

		Habit	at Type	Plant Traits			
Num.	Species	Emergent/ Vernal Pool (g ha ⁻¹)	Vernal Pool/ Wet Prairie (g ha ⁻¹)	Life History	Growth Habit	Flowering Period	Wetland Indicator Status
1.	Achillea millefolium var. borealis	0	123	P	F	7	FACU
2.	Alisma plantago-aquatica	371	148	P	F	5	OBL
3.	Allium amplectens	0	13	P	F	6	
4.	Asclepias speciosa	0	27	P	F	7	FAC+
5.	Brodiaea coronaria	0	2	P	F	7	
6.	Brodiaea elegans	0	7	P	F	7	FACU
7.	Camassia leichtlinii var. suksdorfii	0	89	P	F	5, 6	FACW-
8.	Camassia quamash var. maxima	0	87	P	F	5, 6	FACW*
9.	Cardamine penduliflora	0	1	A	F	4	OBL
10.	Carex densa	152	99	P	S	5	OBL
11.	Carex feta	0	7	P	S	5	FACW
12.	Carex obnupta	213	86	P	S	6	OBL
13.	Carex pellita	0	1	P	S	6	
14.	Carex stipata	124	79	P	S	7	OBL
15.	Carex unilateralis	105	85	P	S	5	FACW
16.	Carex vesicaria	0	2	P	S	5	OBL
17.	Castilleja tenuis	0	2	A	F	6	
18.	Cicendia quadrangularis	0	1	A	F	4	
19.	Clarkia amoena ssp. lindleyi	0	74	A	F	7	
20.	Clarkia purpurea ssp. quadrivulnera	0	116	A	F	7	
21.	Collomia grandiflora	0	106	A	F	6	
22.	Dichelostemma congestum	136	10	P	F	6, 7	
23.	Downingia elegans	136	184	A	F	5	OBL
24.	Downingia yina	148	91	A	F	5	OBL
25.	Eleocharis acicularis	10	0	A	S	5	OBL
26.	Eleocharis obtusa	35	5	A	S	5	OBL
27.	Eleocharis palustris	103	10	P	S	5	OBL
28.	Epilobium densiflorum	340	300	A	F	7, 8	
29.	Eriophyllum lanatum var. leucophyllum	0	118	P	F	7	
30.	Eryngium petiolatum	62	54	P	F	6	OBL
31.	Galium trifidum	99	41	P	F	5	FACW+
32.	Gentiana sceptrum	7	7	P	F	6	OBL
33.	Geum macrophyllum var. macrophyllum	12	25	P	F	7, 8	FACW-*
34.	Gratiola ebracteata	107	30	A	F	5	OBL
35.	Grindelia integrifolia	144	231	P	F	7	FACW
36.	Juncus acuminatus	105	72	P	R	5	OBL
37.	Juncus bolanderi	42	11	P	R	5	OBL
38.	Juncus effusus var. pacificus	92	68	P	R	5	FACW
39.	Juncus ensifolius	55	9	P	R	5	FACW
40.	Juncus occidentalis	0	37	P	R	6	
41.	Juncus oxymeris	54	11	P	R	5	FACW+
42.	Juncus patens	74	14	P	R	5	FACW

continued, next page

TABLE 3, continued

	_	Habit	at Type	Plant Traits			
Num.	Species	Emergent/ Vernal Pool (g ha ⁻¹)	Vernal Pool/ Wet Prairie (g ha ⁻¹)	Life History	Growth Habit	Flowering Period	Wetland Indicator Status
43.	Lasthenia glaberrima	53	64	A	F	4	OBL
44.	Lomatium nudicaule	0	159	P	F	6	
45.	Lotus formosissimus	0	7	P	F	5	FACW+
46.	Lotus unifoliolatus var. unifoliolatus	0	108	A	F	6	
47.	Ludwigia palustris var. pacifica	165	0	A	F	5	OBL
48.	Lupinus polyphyllus	0	26	P	F	6	FAC+
49.	Lupinus rivularis	0	139	A	F	6	FACU
50.	Luzula comosa	0	32	P	F	4	FAC*
51.	Madia elegans	0	68	A	F	7	
52.	Madia glomerata	115	48	A	F	6	FACU+
53.	Madia sativa	0	51	A	F	7	
54.	Microseris laciniata	0	152	P	F	6	
55.	Microsteris gracilis	51	29	A	F	5	FACU
56.	Montia linearis	22	17	A	F	4	
57.	Myosotis laxa	63	7	A	F	6	OBL
58.	Navarretia intertexta ssp. intertexta	83	44	A	F	7	FACW
59.	Nemophila menziesii var. atomaria	0	6	A	F	4	
60.	Orthocarpus bracteosus	0	6	A	F	6	
61.	Perideridia oregana	0	82	P	F	7, 8	
62.	Plagiobothrys figuratus	278	149	A	F	5, 6	FACW
63.	Plectritis congesta	0	107	A	F	6	FACU
64.	Polygonum hydropiperoides	124	0	A	F	5	OBL
65.	Potentilla gracilis var. gracilis	0	204	P	F	7	FAC
66.	Prunella vulgaris var. lanceolata	0	175	P	F	7	FACU+
67.	Ranunculus alismifolius	0	49	P	F	5	FACW
68.	Ranunculus occidentalis var. occidentalis		41	P	F	5	FAC
69.	Ranunculus orthorhynchus	124	53	P	F	5	FACW-
70.	Rorippa curvisiliqua	75	48	A	F	5	OBL
71.	Rumex salicifolius var. salicifolius	132	77	P	F	7, 8	FACW
72.	Saxifraga oregana	0	9	P	F	4	FACW+
73.	Schoenoplectus tabernaemontani	79	0	P	F	6	OBL
74.	Sidalcea cusickii	0	16	P	F	6	FACW-
75.	Sisyrinchium hitchcockii	13	0	P	F	6	
76.	Sisyrinchium idahoense var. idahoense	0	8	P	F	6	FACW
77.	Sparganium emersum	5	0	P	F	5	OBL
77. 78.	Symphyotrichum hallii	0	144	P	F	8	
79.	Thalictrum fendleri var. polycarpum	0	17	P	F	5	FAC
80.	Triteleia hyacinthina	0	15	P	F	6	FACU
81.	Veronica peregrina var. xalapensis	45	37	A	F	6	OBL
82.	Veronica scutellata	185	25	A	F	6	OBL
83.	Wyethia angustifolia	0	155	A P	F	7	FACU
84.	Zigadenus venenosus var. venenosus	0	155	P P	г F	6, 7	FACU*
				Г	Г	0, /	racu"
Average	e total grams per hectare	4,317	4,884				

absolute vegetation cover in June during the second and fifth years following the first seeding of native plant species (Table 2, steps 10 and 19). To measure vascular plant cover, we established two to four macroplots within

each project and sampled plants using the point-intercept method (Elzinga et al. 1998). Macroplots were large enough (typically 50 x 50 m or 50 x 80 m) to ensure we could collect at least 200 sample points within each plot.

TABLE 4. Average seeding rate of each grass species seeded in emergent/vernal pool and vernal pool/wet prairie seed mixes in grams per hectare. See Table 3 for explanation of column coding.

		Habita	at Type	Plant Traits			
Num.	Species	Emergent/ Vernal Pool (g ha ⁻¹)	Vernal Pool/ Wet Prairie (g ha ⁻¹)	Life History	Growth Habit	Flowering Period	Wetland Indicator Status
1.	Agrostis exarata	0	260	P	G	5	FACW
2.	Beckmannia syzigachne	3,295	402	A	G	5	OBL
3.	Danthonia californica	0	295	P	G	6	FACU*
4.	Deschampsia cespitosa	0	390	P	G	6	FACW
5.	Deschampsia danthonioides	0	64	A	G	5	FACW-
6.	Dichanthelium acuminatum var. fasciculatum	0	36	P	G	6	FAC
8.	Glyceria occidentalis	371	159	P	G	5	OBL
9.	Hordeum brachyantherum	680	828	P	G	5	FACW-*
Averag	ge total grams per hectare	4,345	2,457				

The number of macroplots in each project was based on its size. We sampled the same macroplots in Years 2 and 5 for each project. Macroplot placement at Dragonfly Bend was similar to releve plot placement, where macroplots were selectively placed to represent the most common vegetation condition. This was done because the focus of data collection was to assess the projects' progress towards meeting mitigation bank vegetation standards. Beginning in 2008, to both measure progress toward meeting mitigation bank standards and improve our ability to use inferential statistics to compare sites in the future, we began using random placement of macroplots, after stratifying by hydrologic condition. Thus, at Coyote Prairie macroplots were established following a stratified random design. Within each macroplot, transects were randomly located at 2-5 m spacing perpendicular to a baseline along the plot's long axis. The distance between points along transects was 3 m at Dragonfly Bend and 4 m at Coyote Prairie. Given the relatively small size of the herbaceous vegetation, this distance was deemed sufficient to consider each point an independent sample. We sampled vegetation using a tripod and a 2 m long, 1.2 cm diameter steel pole with a sharpened tip. As the pole was lowered vertically through the vegetation, each species touched by the tip was recorded. Since multiple species could be touched with each lowering of the pole, cover can exceed 100%. We calculated the percent absolute cover of each species as well as the percent absolute cover of native and exotic species for each macroplot, and then calculated the mean and standard deviation of each measure for all the macroplots in the project. All percent cover statistics are descriptive and the results are reported with no assignment of statistical significance between projects.

To gather data on species richness, we walked each project area twice during the second and fifth years following the first seeding and planting, and recorded all vascular plant species observed (Table 2, steps 10 and 19). The exact timing of each visit varied with annual precipitation patterns, but the first generally occurred between late May and early June and second between mid-June and early July. Native and exotic species richness for each project is reported as count data. Species richness results are reported as descriptive statistics with no assignment of statistical significance between projects.

Species nomenclature follows the USDA plant database (U.S. Department of Agriculture, Natural Resources Conservation Service, 2010). Nativity follows the 'Vascular Plants of Lane County, Oregon: An Annotated Checklist' (Simpson et al. 2002).

Results

Second Growing Season Following Initial Seeding and Planting

By the second growing season after the initial seeding and planting, all four projects showed high total and native cover with correspondingly low exotic cover (Figure 1) as well as high native species richness (Table 5). Total cover ranged between $128\% \pm 3\%$ (SD) and $177\% \pm 21\%$ and native cover ranged between $91\% \pm 9\%$ and $174\% \pm 20\%$. Exotic cover ranged between $4\% \pm 2\%$ and $15\% \pm 5\%$, except Dragonfly Bend Phase 2 ($37\% \pm 6\%$) where populations of the exotic grasses *Vulpia myuros* and *V. bromoides* established by the second growing season, but substantially declined by the fifth growing season. Greater than 40 native species were present on all projects (Table 5), while

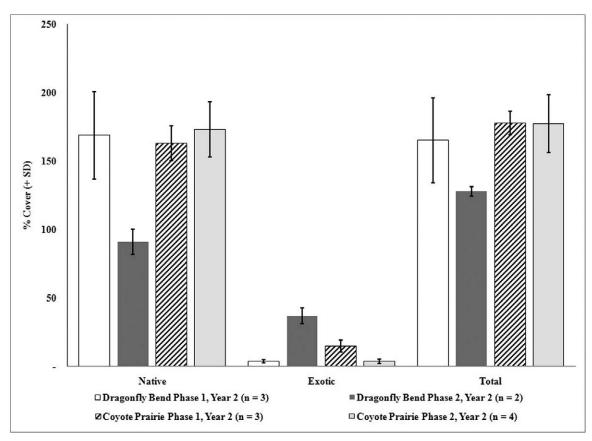


Figure 1. Native, exotic, and total percent cover for each project two years following the initial seeding and planting.

TABLE 5. Species richness of each project with the project name and size.

			Year 2		Year 5		
Project	Phase	Size (ha)	Native	Exotic	Native	Exotic	
Dragonfly Bend	1	16.9	66	33	74	38	
Dragonfly Bend	2	3.2	45	21	58	28	
Coyote Prairie	1	10.5	67	25	N/A	N/A	
Coyote Prairie	2	15.4	42	13	N/A	N/A	

exotic species richness was consistently less than half of native species richness (Table 5).

The planting of bulbs, plugs, and bare root stock does not seem to have had an effect on the percent cover of most species. This was determined by comparing the percent cover of each planted species at projects where it was planted to projects where it was not planted. With one exception, the percent cover of the planted species was very similar to projects where these species were only seeded. Carex unilateralis was the one exception. It only reached percent covers greater than 10% in projects where it was both planted and seeded.

A number of native species consistently established in the restorations by the second growing season after

the initial seeding. Seeded native annual forb species that were present the second growing season with greater than 10% cover in at least one macroplot in all four projects were Epilobium densiflorum, Madia elegans, Madia sativa, and Plagiobothrys figuratus. Native annual species not seeded, but meeting the criteria above, were Epilobium brachycarpum, Epilobium ciliatum, Gnaphalium palustre, and Juncus bufonius. Native perennial species seeded that were present the second growing season with greater than 10% cover in at least one macroplot included Achillea millefolium, Agrostis exarata, Carex unilateralis, Deschampsia cespitosa, Grindelia integrifolia, Juncus occidentalis, and Prunella vulgaris var. lanceolata. As noted above, Carex unilateralis likely would not have reached

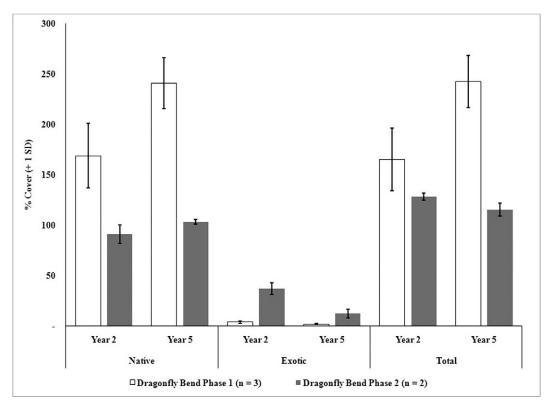


Figure 2. Native, exotic, and total percent cover for Dragonfly Bend Phases 1 and 2 two and five years following the initial seeding and planting.

10% cover if it had not been both planted and seeded. Only two exotic species had cover greater than 10%: the annual grasses *Vulpia myuros* and *V. bromoides* in Dragonfly Bend Phase 2. However, cover of these species was less than 3% by the fifth growing season following grass-specific herbicide applications.

The absolute cover of unseeded native species ranged from $14\% \pm 3\%$ to $63\% \pm 24\%$ among the four projects. Macroplots on the wetter end of the hydrologic spectrum tended to have a higher cover of unseeded species and 8 of the 11 unseeded native species recorded were annuals. The unseeded native perennial species were *Alopecurus geniculatus*, *Salix* spp., and *Fraxinus latifolia*, where each was less than 2% cover in any macroplot.

The percent cover of native and exotic annuals exceeded native and exotic perennials in all four projects by a low of $30\% \pm 48\%$ at Dragonfly Bend Phase 1 to a high of $157\% \pm 13\%$ in Coyote Prairie Phase 1. Of native species, the percent cover of annuals exceeded perennials by between $27\% \pm 47\%$ and $154\% \pm 11\%$. Two macroplots did have a higher cover of native perennials than native annuals. One, at Dragonfly Bend Phase 1, had a higher cover of native perennials largely because of one species, *Grindelia integrifolia*, which

had a cover of 31%. The second macroplot was at Coyote Prairie Phase 1, where *Prunella vulgaris* var. *lanceolata* had a cover of 33%.

Fifth Growing Season Following Initial Seeding and Planting

We have data for the fifth growing season following initial seeding and planting for the two projects at Dragonfly Bend. Between Year 2 and Year 5, total native cover increased (Figure 2), exotic cover decreased (Figure 2), and species richness increased (Table 5). Native cover for Dragonfly Bend Phase 1 increased from $168\% \pm 32\%$ to $240\% \pm 25\%$ while native cover for Dragonfly Bend Phase 2 increased from 91% ± 9% to $103\% \pm 3\%$. Absolute cover of unseeded native species at Dragonfly Bend Phase 1 decreased from $27\% \pm 7\%$ to $4\% \pm 5\%$, while it increased in Phase 2 from $10\% \pm 5$ to $20\% \pm 2$. The increase of unseeded species in Phase 2 is likely due to the emergence of Juncus bufonius in openings created by removal, via herbicide application, of exotic Vulpia spp. Exotic cover decreased at Phase 1 from $4\% \pm 1\%$ to $2\% \pm 1\%$ and from $37\% \pm 6\%$ to $12\% \pm 4\%$ at Phase 2. Total cover increased on Phase 1 (165% \pm 31% to 243% \pm 26%), but decreased on Phase 2 (128% \pm 4% to 116%

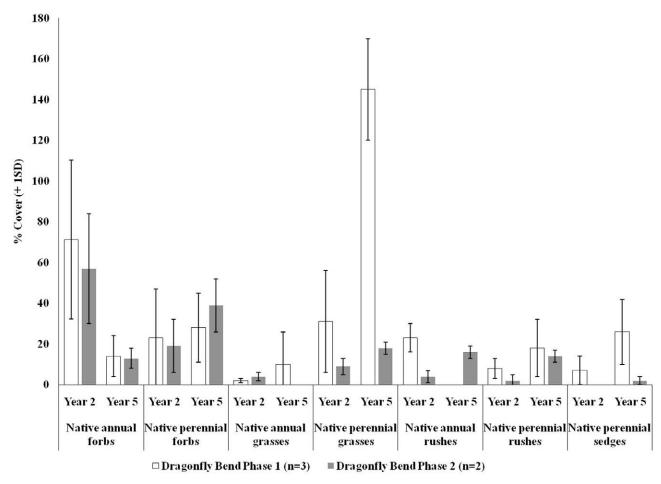


Figure 3. Percent cover of native plant guilds for Dragonfly Bend Phases 1 and 2, two and five years following the initial seeding and planting.

± 6%) because of the substantial decrease in exotic cover. Native species richness increased between Year 2 and Year 5 on Phase 1 by 8 (66 to 74) and 13 (45 to 58) species at Phase 2 while exotic species richness increased by 5 (33 to 38) species on Phase 1 and by 7 (21 to 28) species at Phase 2.

The percent cover of annual and perennial species shifted between the second and fifth growing seasons at Dragonfly Bend (Figure 3), with a trend of decreasing annuals and increasing perennials by the fifth growing season. Percent cover of native annual forb species decreased from $71\% \pm 39\%$ to $14\% \pm 10\%$ in Phase 1 and from $57\% \pm 27\%$ to $13\% \pm 5\%$ in Phase 2, while native perennial forbs remained fairly stable in Phase 1 ($23\% \pm 24\%$ to $28\% \pm 17\%$) and increased in Phase 2 ($19\% \pm 13\%$ to $39\% \pm 13\%$). Native perennial grasses increased in Phase 1 ($31\% \pm 25\%$ to $145\% \pm 25\%$) and Phase 2 ($9\% \pm 4\%$ to $18\% \pm 3\%$), with the grasses *Deschampsia cespitosa* and *Agrostis exarata* accounting for the vast majority of the increase. Native

annual rushes decreased from $23\% \pm 7\%$ to undetectable in Phase 1 and increased from $4\% \pm 3\%$ to $16\% \pm 3\%$ in Phase 2. Native perennial rushes increased between the second and fifth growing seasons in both Phase 1 ($8\% \pm 5\%$ to $18\% \pm 14\%$) and Phase 2 ($2\% \pm 3\%$ to $14\% \pm 3\%$). Native perennial sedges increased from $7\% \pm 7\%$ in the second growing season to $26\% \pm 16\%$ in the fifth growing season in Phase 1. Perennial sedges were not detected the second growing season in Phase 2 but were in the fifth growing season ($2\% \pm 2\%$). No native annual sedges were observed within the project areas.

A total of ten species, none of which were exotic, had at least 10% cover in one of the macroplots by the fifth year after initial seeding and planting. Of those ten species, one was an annual forb (*Plagiobothrys* sp.), three were perennial forbs (*Grindelia integrifolia, Prunella vulgaris* var. *lanceolata*, and *Rumex salicifolius* var. *salicifolius*), one was an annual grass (*Deschampsia danthonioides*), two were perennial grasses (*Agrostis*

exarata and Deschampsia cespitosa), one was a sedge (Carex unilateralis) and two were rushes (Juncus bufonius* and Juncus occidentalis). As noted above, Carex unilateralis likely would not have reached 10% cover without it having been planted in addition to seeded. An asterisk indicates species that was not seeded.

An additional six species had at least 5% cover in one of the macroplots by the fifth year after initial seeding and planting. Of those six species, three were annual forbs (*Epilobium brachycarpum**, *Epilobium densiflorum*, *Gnaphalium palustre**), two were perennial forbs (*Eriophyllum lanatum* var. *lanatum* and *Microseris laciniata*,), and one was a perennial grass (*Hordeum brachyantherum*). An asterisk indicates species that were not seeded.

Discussion

These results demonstrate that the restoration approach we used was successful at meeting our two a priori restoration objectives on lands that had been intensively used for agricultural grass seed production for decades: (1) establishing a plant community with 50 or more native plant species; and (2) establishing a plant community with > 70% absolute cover of native plant species. The results also show that over the first five years, plant community composition changed in ways consistent with what one would expect in the early stages of succession and that the plant community at each site is on a desired trajectory. For example, between Year 2 and Year 5 at Dragonfly Bend, native cover increased (Figure 2), exotic cover decreased (Figure 2), species richness increased (Table 5), cover of annuals decreased (Figure 3), and cover of perennials increased (Figure 3).

The restoration implementation strategy we used (Table 2) was developed specifically to achieve our restoration goals and to apply the most relevant ecological information and practical experience we had about Willamette Valley prairies and wet prairie restoration. The three ecological processes that are highlighted repeatedly in our lessons learned (Table 1) and implementation strategy (Table 2) are disturbance, colonization, and competition. For restoration practitioners, it is important to consider how the timing, duration, magnitude, and characteristics of each of these processes impact the trajectory of community assembly. For the agricultural grass seed fields that were the starting point at Dragonfly Bend and Coyote Prairie, we used a no-till disturbance regime (mow, burn, broadcast herbicide), followed by multiple years of colonization events (strategic seeding and planting) to fill as many niches as possible. While we were able to partially control colonization

through seed addition and planting, propagule arrival of natives and exotics from off-site and emergence from the existing seed bank also contributed to the plant community. Thus, we complemented this colonization strategy with aggressive manipulation of the competitive regime, using herbicides and manual control methods to strategically remove undesired species for several years following initial site preparation. By thoughtfully managing the timing, duration, magnitude, and character of disturbance, colonization, and competitive actions in an integrated way, this implementation strategy resulted in a community assembly trajectory consistent with our pre-project goals.

Our restoration approach differed significantly from our previous work (City of Eugene 2004, 2003), as well as most other prairie restoration projects we are aware of in the Willamette Valley (e.g., Clark and Wilson 2001, Wilson and Clark 2001, Schultz 2001, Pfeifer-Meister 2008, Stanley et al. 2011), in how we managed colonization. Our colonization approach differed from other projects in four key ways. First, we did not seed any grasses during the first year or two of the projects. Second, we seeded the sites over multiple growing seasons. Third, our seed mixes changed composition over time, with a greater representation of annuals in the first year mixes compared to later year mixes. Fourth, we seeded a high diversity of species on the sites. Each of these four differences is described in more detail below.

There were two key reasons why we did not seed any grasses during the first year (at Dragonfly Bend) or two (at Coyote Prairie) of the projects. First, we wanted the ability to use grass-specific herbicides (sethoxydim-based and clethodim-based) to eliminate the annual ryegrass that had been cultivated on these sites for decades. Use of grass-specific herbicides allowed concurrent establishment of forbs, sedges, and rushes and control of annual ryegrass and other exotic grasses. Second, we knew that at least one native grass species, Deschampsia cespitosa, would competitively exclude many native forbs if seeded at the same time as the forbs. The highly competitive nature of certain grasses in restoration settings has led other prairie researchers to conclude that native grasses should: (a) be sown at very low seeding densities (Dickson and Busby 2009), (b) be spatially segregated from forbs (Schramm 1993, Dickson and Busby 2009), or (c) phased in over time to allow establishment of less competitive species (Pywell et al. 2003). Our strategy was most like the phased approach recommended by Pywell et al. (2003).

Our colonization strategy involved seeding for multiple years to counter germination and establishment variations driven by annual climatic variability, stochastic events, planned disturbance events, and anticipated successional patterns (e.g., annuals establishing earlier than perennials). Thus, the multi-year colonization strategy is a "bet-hedging" or "spread the risk" strategy, as well as a way to manipulate succession. If we had not seeded over multiple years, species that did not fare well during a single seeding event may not have established at all.

Our seed mixes also changed composition over time, with a greater representation of annuals in the first year mixes compared to later year mixes. Our initial seed mixes (Year 1 and Year 2) had a high density of native annuals because we wanted native species that could establish and reproduce rapidly, thereby increasing the on-site native seed rain and competitively excluding exotics. As discussed above, our initial seed mixes also contained no grasses because we have observed significant priority effects with, and competitive exclusion by, one native grass, *Deschampsia cespitosa*. This appears to have limited overall site diversity, including diversity of forbs, at other sites, which is consistent with the findings of Schramm (1992), Pfeifer-Meister (2008), and Dickson and Busby (2009). We also wanted the ability to use a grass-specific herbicide during years one and two to kill any of the agricultural or exotic grasses that germinated from the seed bank (Andreu 2005). Later seed mixes (e.g., Year 2) emphasized later successional species and desired species that had not yet established. Eventually, grasses were also seeded (e.g., in Year 2 or 3).

In contrast to most other prairie restoration projects in the Willamette Valley, we seeded a high diversity of species on the sites. In other prairie systems, native plant species dispersal within prairie remnants (Tilman 1997, Seabloom et al. 2003a, Foster and Tilman 2003, Zeiter et al. 2006, Stanley et al. 2011) or from remnants to abandoned fields (Pywell et al. 2002, Foster et al. 2007, Middleton et al. 2010) has been shown to be limited; in all these cases, manual seeding of native species substantially increased richness and percent native cover over plots that were unseeded. Therefore, we expected that the few native species that would emerge from the seed bank, or disperse from field edges, would be inadequate to achieve our a priori diversity goal of at least 50 species. Because of this, we seeded a high diversity of species onto the sites over multiple growing seasons and also planted a diversity of bulbs, plugs, and bare root stock.

Our rationale for wanting 50 or more native species in our prairie restoration sites was three-fold. First, Willamette Valley prairies were historically very diverse (Alverson 2005, U.S. Fish and Wildlife Service 2006) and provided habitat for a wide variety of animals, including insects, many of which are important pollinators. It seems reasonable to expect that the more diverse the restored plant community, the more likely we would provide habitat for the wide variety of other community members (e.g., fungi, animals) that depend on the plants (Siemann et al. 1998, Haddad et al. 2001). Second, a long-term goal of our restoration projects is for them to be resistant to invasion by exotic species. At the site level, higher diversity plant communities have been found to be more resistant to invasion by exotics than lower diversity communities (Tilman 1997, Naeem et al. 2000, Kennedy et al. 2002, Piper et al. 2007, Funk et al. 2008, Middleton et al. 2010, Davies et al. 2011, but see Stohlgren et al. 2003 for examples to the contrary, especially at larger spatial scales). Therefore, to the extent that we can establish a diverse plant community that is comprised of species that can more effectively fill available niches, the more likely the plant community will be resistant to invasion of exotics (Tilman 1997, Naeem et al. 2000, Kennedy et al. 2002, Piper et al. 2007, Funk et al. 2008, Middleton et al. 2010, Davies et al. 2011). Third, a more diverse community of native species will be tolerant of a wider range of environmental conditions, and therefore, likely be more resilient to disturbances than a lower diversity community (Seabloom 2007). This may become increasingly important with potential future rapid changes in climate (Bachelet et al. 2011).

We complemented our seeding with planting of bulbs, plugs, and bare root stock of 41 species that we expected to grow slowly or be difficult to establish from seed. Of the planted stock, only Carex unilateralis appeared to lead to increases in cover relative to what would have been achieved with seeding only. While we were able to determine that planted stock, with the exception of Carex unilateralis, did not substantially influence percent cover results, our monitoring design was not well suited for determining percent survival of planted stock or its influence on species richness in the projects. Middleton et al. (2010) found that prairie restorations using both seeds and propagated plants had higher species richness, higher native plant density, and more closely resembled prairie remnants after four years than restorations using only seeds. In the future, we will continue to depend on seeds as our primary method of establishing diverse native prairie communities. However, we will more closely examine the role that planted stock could have in meeting our objectives of restoring wet prairie communities with high native diversity, high native cover, and low exotic cover.

Despite the desired vegetation results described above, the restored prairies at Dragonfly Bend and Coyote Prairie have very low abundance of some plant species commonly found in high quality prairie remnants. For example, Allium amplectens, Brodiaea elegans, Camassia leichtlinii var. suksdorfii, Camassia quamash var. maxima, Potentilla gracilis var. gracilis, Wyethia angustifolia, and Zigadenus venenosus are much less frequent at Dragonfly Bend and Coyote Prairie than in high quality remnants, despite seeding them, and for several species planting them, at these sites. Future studies could examine whether this is due to competition, insufficient seeding or planting rates, order of arrival, incompatible disturbance events, or other factors. In addition, the grasses Danthonia californica, Agrostis exarata, and Hordeum brachyantherum have not established well when seeded in Year 2 or Year 3. For future projects, we are considering adding these grasses in Year 2, when more niche space is available for colonization, and only delay introduction of our most competitive native perennial grass, Deschampsia cespitosa, until Year 3. Alternately, we may continue to initially seed these grasses in Year 3, but use higher seed densities. We will continue to experiment with seed mixes and seeding plans, for example, by seeding areas where certain species can establish with limited competition (Schramm 1992, Dickson and Busby 2009) or introducing species in different order and in different densities. In addition, future research could be directed at determining if different disturbance events, such as fire or mowing, would alter abiotic or biotic conditions in a way that would facilitate establishment of these species.

These four projects are the first ones we have implemented where we significantly surpassed our objective of having > 70% absolute native cover five years after the initial seeding. In previous projects, we regularly exceeded the 70% absolute native cover objective, but usually by less than 10% (City of Eugene 2003, 2004, 2005, 2006). In the four projects discussed here, we exceeded the 70% native cover objective after five years by 33% at Dragonfly Bend Phase 2 and 107% at Dragonfly Bend Phase 1 (Figure 2). The two projects at Coyote Prairie greatly exceeded the 70% native cover objective after two years (Figure 1), and we expect that they will continue this trajectory of high native cover and low exotic cover.

The desired combination of high native cover, low exotic cover, and high native diversity exhibited by these four restoration projects is uncommon for prairie restoration projects in the Willamette Valley. Other prairie restoration projects with high native cover often had low species richness; this is true in the Willamette Valley (Pfeifer-Meister 2008) and in other prairie systems (Schramm 1992, Pywell et al. 2003, Dickson and Busby 2009). Common to all of these examples is the competitive dominance of perennial grasses, including Deschampsia cespitosa in the Willamette Valley, which exclude other species. In addition, these four projects exhibited low exotic cover after two and five years (Figures 1 and 2), which contrasts greatly with remnant sites, where exotic cover often exceeds native cover (Pfeifer-Meister 2008, Stanley et al. 2011). Through the integrated strategy of manipulating disturbance, colonization, and competition described here, we were able to achieve restorations with the desired outcome of high native cover, low exotic cover, and high native species richness.

The ability of other restoration practitioners in the Willamette Valley to implement projects with the colonization approach we used is currently limited by the inability to commercially purchase seed of most native Willamette Valley prairie species. Lack of seed dispersal to restoration sites is a key factor limiting assembly of diverse prairie communities (Tilman 1997, Pywell et al. 2002, Pywell et al. 2003, Foster and Tilman 2003, Seabloom et al. 2003a, Seabloom et al. 2003b, Walker et al. 2004, Zieter et al. 2006, Foster et al. 2007, Dickson and Busby 2009, Middleton et al. 2010, Stanley et al. 2011). In addition, colonization by a wide diversity of native species plays a key role in generating high diversity plant communities and in conferring resistance to invasion of exotics (Tilman 1997, Naeem et al. 2000, Kennedy et al. 2002, Piper et al. 2007, Funk et al. 2008, Middleton et al. 2010, Davies et al. 2011). Therefore, the success of wet prairie restoration projects on a meaningful spatial scale in the Willamette Valley will require a broader availability of seed from a diverse set of native species, particularly forbs. We encourage restoration practitioners from private organizations and government agencies to collaborate to substantially expand the production of both the number of native species, as well as the quantity of each species, available for commercial purchase.

Our integrative approach resulted in restoring Willamette Valley wet prairie plant communities with 50 native plant species and greater than 70% native cover to sites that had been in intensive agricultural grass seed

production for decades. Less than 2% of prairies remain in the Willamette Valley, and regional conservation plans (Defenders of Wildlife 1998, Oregon Department of Fish and Wildlife 2006) and species recovery plans (U.S. Fish and Wildlife Service 2010) call for restoration of currently degraded habitat. Since agricultural grass fields currently occupy over 182,000 ha in the Willamette Valley, much of which was formerly prairie, the restoration approach we described here can assist the efforts of landowners and managers to restore high diversity prairie communities.

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APPENDIX 1. Species and quantity of propagated plants installed in the restoration projects. Quantities are shown as units ha⁻¹. DB1 = Dragonfly Bend Phase 1, DB2 = Dragonfly Bend Phase 2, CP1 = Coyote Prairie Phase 1, CP2 = Coyote Prairie Phase 2. Flats are 38 x 38 x 10 cm deep. In some years, bulbs were planted by the flat, rather than individually. Each bulb flat has approximately 80 to 300 small bulbs.

		Quantity (units ha ⁻¹)				
Species	Plant Material Type (unit)	DB1	DB2	CP1	CP2	
(non Liliaceae)						
Achillea millefolium var. borealis	plugs	98	143	0	0	
Asclepias speciosa	plugs	14	6	0	0	
Aster hallii	plugs	7	78	0	0	
Carex densa	bare root	592	0	0	0	
Carex stipata	plants (2 gallon)	0	0	0	7	
Carex unilateralis	bare root and plugs	266	453	138	0	
Delphinium menziesii	plugs	0	15	0	0	
Dichanthelium acuminatum	plugs	7	0	0	0	
Eleocharis palustris	bare root	473	0	0	0	
Festuca roemeri	plugs	169	178	0	0	
	bare root	0	0	238	136	
Fragaria virginiana		0	0			
Gentiana sceptrum	plugs		78	1 24	0	
Juncus acuminatus	bare root and plugs	296			0	
Juncus bolanderi	bare root and plugs	178	313	143	0	
Juncus bolanderi	flats of plants	0	0	0	4	
Juncus effusus var. pacificus	bare root	30	0	0	0	
Juncus ensifolius	bare root	192	0	0	0	
Juncus ensifolius	flats of plants	0	0	0	2	
Juncus nevadensis	bare root and plugs	592	31	57	0	
Juncus oxymeris	bare root	30	0	48	0	
Juncus patens	bare root	30	0	0	0	
Lomatium nudicaule	potted tubers	0	0	3	4	
Lupinus rivularis	plugs	29	63	0	0	
Perideridia spp.	bare root	0	0	11	0	
Potentilla gracilis var. gracilis	plugs	67	104	0	0	
Prunella vulgaris var. lanceolata	plugs	49	110	0	0	
Ranunculus occidentalis						
var. occidentalis	plugs	8	0	0	0	
Rumex salicifolius	plugs	22	0	0	0	
Saxafraga oregana	bare root and plugs	0	0	31	0	
Sidalcea cusickii	plugs	1	0	0	0	
Sisyrinchium idahoense	bare root	0	0	286	0	
Thalictrum occidentale	plugs	0	5	0	0	
Wyethia angustifolia	plugs	57	88	0	0	
Tryenna angusiyona	prago	37	00	· ·	· ·	
Liliaceae		0.0	0.0	220.0	22.0	
Allium amplectens	bulbs	0.0	0.0	220.0	32.0	
Allium amplectens	flats of bulbs	0.9	0.6	0.0	0.4	
Brodiaea coronaria	bulbs	0.0	0.0	282.0	0.0	
Brodiaea coronaria	flats of bulbs	0.8	0.3	0.0	0.0	
Brodiaea elegans	bulbs	0.0	0.0	81.0	2.0	
Bulb mix (Allium amplectens,						
Triteleia hyacinthina, Camas spp.)	bulbs (salvaged)	0.0	0.0	0.0	197.0	
Camassia leichtlinii var. suksdorfii	bulbs	0.0	0.0	0.0	32.0	
Camassia leichtlinii var. suksdorfii	flats of bulbs	1.1	0.3	0.0	0.1	
Camassia quamash var. maxima	bulbs	0.0	0.0	14.0	32.0	
Camassia quamash var. maxima	flats of bulbs	1.2	0.6	0.0	0.6	
Camassia spp.	bulbs (salvaged)	0.0	0.0	0.0	10.0	
Dichelostemma congestum	bulbs	0.0	0.0	217.0	0.0	
Dichelostemma congestum	flats of bulbs	0.2	0.3	0.0	0.0	
Triteleia hyacinthina	bulbs	0.0	0.0	0.0	3.0	
Triteleia hyacinthina	flats of bulbs	1.0	0.9	0.0	0.4	
Zigadenus venenosus var. venenosus	bulbs	0.0	0.0	76.0	0.0	
Zigadenus venenosus var. venenosus	flats of bulbs	1.0	0.6	0.0	0.0	

Literature Cited

- Altman, B., M. Hayes, S. Janes, and R. Forbes. 2001. Wildlife of westside grassland and chaparral habitats. In D. H. Johnson and T. A. O'Neil (managing directors), Wildlife Habitat Relationships in Oregon and Washington. Oregon State University Press, Corvallis. Pp. 261-291.
- Alverson, E. 2005. Preserving prairies and savannas in a sea of forest: a conservation challenge in the Pacific Northwest. Plant Talk 40:23-27.
- Andren, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71:355-366.
- Andreu, A. G. 2005. Effects of fall prescribed fire on regeneration from the seed bank of two western Washington grasslands. M.S. Thesis, University of Washington, Seattle.
- Bachelet, D., B. R. Johnson, S. D. Bridgham, P. V. Dunn, H. E. Anderson, and B. M. Rogers. 2011. Climate change impacts on western Pacific Northwest prairies and savannas. Northwest Science 85:411-433.
- Baitis, K., and M. James. 2005. Willamette Valley clay linked to thick blankets of Mount Mazama airfall. Current Archaeological Happenings in Oregon 30:14-19.
- Christy, J. A., and E. R. Alverson. 2011. Historical vegetation of the Willamette Valley, Oregon, circa 1850. Northwest Science 85:93-107.
- City of Eugene. 2010. West Eugene Wetlands Mitigation Bank: Annual Report 2009. Available online at http://www.eugeneor.gov/nrlibrary.
- City of Eugene. 2009. West Eugene Wetlands Mitigation Bank: Annual Report 2008. Available online at http://www.eugeneor.gov/nrlibrary.
- City of Eugene. 2008. West Eugene Wetlands Mitigation Bank: Annual Report 2007. Available online at http://www.eugeneor.gov/nrlibrary.
- City of Eugene. 2007. West Eugene Wetlands Mitigation Bank: Annual Report 2006. Available online at http://www.eugeneor.gov/nrlibrary.
- City of Eugene. 2006. West Eugene Wetlands Mitigation Bank: Annual Report 2005. Available online at http://www.eugeneor.gov/nrlibrary.
- City of Eugene. 2005. West Eugene Wetlands Mitigation Bank: Annual Report 2004. Available online at http://www.eugeneor.gov/nrlibrary.
- City of Eugene. 2004. West Eugene Wetlands Mitigation Bank: Annual Report 2003. Available online at http://www.eugeneor.gov/nrlibrary.
- City of Eugene. 2003. West Eugene Wetlands Mitigation Bank: Annual Report 2002. Available online at http://www.eugeneor.gov/nrlibrary.
- Clark, D. L., and M. V. Wilson. 2001. Fire, mowing, and handremoval of woody species in restoring a native wetland prairie in the Willamette Valley of Oregon. Wetlands 21:135-144.
- Collinge, S. K., and C. Ray. 2009. Transient patterns in the assembly of vernal pool plant communities. Ecology 90:3313-3323.
- Collins, S. L., A. K. Knapp, J. M. Briggs, J. M. Blair, and E. M. Steinauer. 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. Science 280:745-747.
- Davies, K. F., J. Cavender-Bares, and N. Deacon. 2011. Native communities determine the identity of exotic invaders even at scales at which communities are unsaturated. Diversity and Distributions 17:35-42.
- Debinski, D. M., and R. D. Holt. 2000. Review: a survey and overview of habitat fragmentation experiments. Conservation Biology 14:342-355.

- Defenders of Wildlife. 1998. Oregon's Living Landscape: Strategies and Opportunities to Conserve Biodiversity. Defenders of Wildlife, Lake Oswego, Oregon.
- del Moral, R., L. R. Walker, and J. P. Bakker. 2007. Insights gained from succession for the restoration of landscape structure and function. In L. R. Walker, J. Walker, and R. J. Hobbs (editors), Linking Restoration and Ecological Succession. Springer Science+Business Media, New York, New York. Pp. 19-44.
- Dickson, T. L., and W. H. Busby. 2009. Forb species establishment increases with decreased grass seeding density and with increased forb seeding density in a northeast Kansas, U.S.A., experimental prairie restoration. Restoration Ecology 17:597-605.
- Ejrnaes, R., H. H. Bruun, and B. J. Graae. 2006. Community assembly in experimental grasslands: suitable environment or timely arrival? Ecology 87:1225-1233.
- Elzinga, C. L., D. W. Salzer, and J. W. Willoughby. 1998. Measuring and Monitoring Plant Populations. USDI Bureau of Land Management, National Business Center, Denver, CO.
- Finley. K. K. 1995. Hydrology and related soil features of three Willamette Valley wetland prairies. M.S. Thesis, Oregon State University, Corvallis.
- Fisher, J., and B. D. Lindenmayer. 2007. Landscape modification and habitat fragmentation: a synthesis. Global Ecology and Biogeography 16:265-280.
- Foster, B. L., C. A. Murphy, K. R. Keller, T. A. Aschenbach, E. J. Questad, and K. Kindscher. 2007. Restoration of prairie community structure and ecosystem function in an abandoned hayfield: a sowing experiment. Restoration Ecology 15:652-661.
- Foster, B. L., and D. Tilman. 2003. Seed limitation and the regulation of community structure in oak savanna grassland. Journal of Ecology 91:999-1007.
- Funk, J. L., E. E. Cleland, K. N. Suding, and E. S. Zavaleta. 2008. Restoration through reassembly: plant traits and invasion resistance. Trends in Ecology and Evolution 23:695-703.
- Haddad, N. M., D. Tilman, J. Haarstad, M. Ritchie, and J. M. H. Knops. 2001. Contrasting effects of plant richness and composition on insect communities: a field experiment. The American Naturalist 158:17-35.
- Hulse, D. W., S. V. Gregory, and J. P. Baker (editors). 2002. Willamette River Basin: Trajectories of Environmental and Ecological Change. Oregon State University Press, Corvallis.
- Hutchinson, G. E. 1958. Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology 22:415-427.
- Jancaitis, J. E. 2001. Restoration of a Willamette Valley wet prairie: an evaluation of two management techniques. M.S. Thesis, University of Oregon, Eugene.
- Johannessen, C. L., W. A. Davenport, A. Millet, and S. McWilliams. 1971. The vegetation of the Willamette Valley. Annals of the Association of American Geographers 61:286-302.
- Kaye, T. N., K. L. Pendergrass, K. Finley, and J. B. Kauffman. 2001. The effect of fire on the population viability of an endangered prairie plant. Ecological Applications 11:1366-1380.
- Kennedy, T. A., S. Naeem, K. M. Howe, J. M. H. Knops, D. Tilman, and P. Reich. 2002. Biodiversity as a barrier to ecological invasion. Nature 417:636-638.
- Maret, M. P., and M. V. Wilson. 2000. Fire and seedling population dynamics in western Oregon prairies. Journal of Vegetation Science 11:307-314.
- McIntire, E. J. B., C. B. Schultz, and E. E. Crone. 2007. Designing a network for butterfly habitat restoration: where individuals, populations and landscapes intersect. Journal of Applied Ecology 44:725-736.

- Middleton, E. L., J. D. Bever, and P. A. Schultz. 2010. The effect of restoration methods on the quality of the restoration and resistance to invasion by exotics. Restoration Ecology 18:181-187.
- Naeem, S., J. M. H. Knops, D. Tilman, K. M. Howe, T. Kennedy, and S. Gale. 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. Oikos 91:97-108.
- Noss, R. F., E. T. LaRoe III, and J. M. Scott. 1995. Endangered Ecosystems of the United States: A Preliminary Assessment of Loss and Degradation. Department of the Interior, U.S. National Biological Service, Washington, D.C.
- Oregon Department of Fish and Wildlife. 2006. The Oregon Conservation Strategy. Oregon Department of Fish and Wildlife, Salem, Oregon.
- Oregon State University Extension Service. 2010. 2009 Oregon County and State Agricultural Estimates. Special Report 790-09.
- Palmer, M. A., D. A. Falk, and J. B. Zedler. 2006. Ecological theory and restoration ecology. *In D. A. Falk, M. A. Palmer*, and J. B. Zedler (editors), Foundations of Restoration Ecology. Island Press, Washington, D.C. Pp. 1-10.
- Patching, W. R. 1987. Soil Survey report of Lane County Area, Oregon. USDA, Soil Conservation Service. Washington, DC.
- Pendergrass, K. L. 1995. Vegetation composition and response to fire of native Willamette Valley wetland prairies. M.S. Thesis, Oregon State University, Corvallis.
- Pendergrass, K. L., P. M. Miller, J. B. Kauffman, and T. N. Kaye. 1999. The role of prescribed burning in maintenance of an endangered plant species, *Lomatium bradshawii*. Ecological Applications 9:1420-1429.
- Pfeifer-Meister, L. 2008. Community and ecosystem dynamic in restored and remnant prairies. Ph.D. Dissertation, University of Oregon, Eugene.
- Piper, J. K., E. S. Schmidt, and A. J. Janzen. 2007. Effects of species richness on resident and target species components in a prairie restoration. Restoration Ecology 15:189–198.
- Pywell, R. F., J. M. Bullock, A. Hopkins, K. J. Walker, T. H. Sparks, M. J. J. Burke, and S. Peel. 2002. Restoration of species-rich grassland on arable land: assessing the limiting processes using a multi-site experiment. Journal of Applied Ecology 39:294-309.
- Pywell, R. F., J. M. Bullock, D. B. Roy, L. Warman, K. J. Walker, and P. Rothery. 2003. Plant traits as predictors of performance in ecological restoration. Journal of Applied Ecology 40:65–77.
- Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology 5:18-32.
- Schramm, P. 1992. Prairie restoration: a twenty-five year perspective on establishment and management. *In* D. D. Smith and C. A. Jacobs (editors), Proceedings of the Twelfth North American Prairie Conference 1990. University of Northern Iowa, Cedar Falls. Pp. 169-177.
- Schultz, C. B. 2001. Restoring resources for an endangered butterfly. Journal of Applied Ecology 38:1007-1019.
- Schultz, C. B., and E. E. Crone. 2001. Edge-mediated dispersal behavior in a prairie butterfly. Ecology 82:1879-1892.
- Schultz, C. B., and K. M. Dlugosch. 1999. Nectar and hostplant scarcity limit populations of an endangered Oregon butterfly. Oecologia 119:231-238.
- Schultz, C. B., P. C. Hammond and M. V. Wilson. 2003. The biology of the Fender's blue butterfly, an endangered species of western Oregon native prairies. Natural Areas Journal 23: 61-71.

- Seabloom, E. W., E. T. Borer, V. L. Boucher, R. S. Burton, K. L. Cottingham, L. Goldwasser, W. K. Gram, B. E. Kendall, and F. Micheli. 2003a. Competition, seed limitation, disturbance, and reestablishment of California native annual forbs. Ecological Applications 13:575-592.
- Seabloom, E. W., W. S. Harpole, O. J. Reichman, and D. Tilman. 2003b. Invasion, competitive dominance, and resource use by exotic and native California grassland species. Proceedings of the National Academy of Science 100:13384-13389.
- Seabloom, E. W. 2007. Compensation and the stability of restored grassland communities. Ecological Applications 17:1876-1885
- Severns, P. M. 2008. Exotic grass invasion impacts fitness of an endangered prairie butterfly, *Icaricia icariodes fenderi*. Journal of Insect Conservation 12:651-661.
- Severns, P. M., L. Boldt, and S. Villegas. 2006. Conserving a wetland butterfly: quantifying early lifestage survival through seasonal flooding, adult nectar, and habitat preference. Journal of Insect Conservation 10:361-370.
- Siemann, E., D. Tilman, J. Haarstad, and M. Ritchie. 1998. Experimental tests of the dependence of arthropod diversity on plant diversity. The American Naturalist 152:738-750.
- Simpson, C., J. Koenig, J. Lippert, R. Love, B. Newhouse, N. Otting, S. Sundberg, D. Wagner, and P. Warner. 2002. Vascular Plants of Lane County, Oregon: An Annotated Checklist. Emerald Chapter of the Native Plant Society, Eugene, Oregon.
- Stanley, A. G., T. N. Kaye, P. W. Dunwiddie. 2011. Multiple treatment combinations and seed addition increase abundance and diversity of native plants in Pacific Northwest prairies. Ecological Restoration 29:35-44.
- Stohlgren, T. J., D. T. Barnett, and J. T. Kartesz. 2003. The rich get richer: patterns of plant invasions in the United States. Frontiers in Ecology and the Environment 1:11-14.
- Taylor, T. 1999. Long-term vegetation response to fire of Willamette Valley wet prairie species. M.S. Thesis, University of Oregon, Eugene.
- Temperton, V. M., R. J. Hobbs, T. Nuttle, and S. Halle (editors). 2004. Assembly Rules and Restoration Ecology. Island Press, Washington, DC.
- Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. Ecology 78:81-92.
- Towle, J. C. 1982. Changing geography of Willamette Valley woodlands. Oregon Historical Quarterly 83:66-87.
- Trowbridge, W. B. 2007. The role of stochasticity and priority effects in floodplain restoration. Ecological Applications 17:1312-1324.
- Turner, C. L., and A. K. Knapp. 1996. Responses of a C_4 grass and three C_3 forbs to variation in nitrogen and light in tallgrass prairie. Ecology 77:1738-1749.
- U.S. Army Engineer Waterways Experiment Station and Oregon State University. 1995. Studies of plant establishment limitations in wetlands of the Willamette Valley, Oregon. Technical Report WRP-RE-13, U.S. Army Engineer Waterways Experiment Station, Vicksburg, MS.
- U.S. Department of Agriculture, Natural Resources Conservation Service. 2010. The PLANTS Database. National Plant Data Center, Baton Rouge, LA 70874-4490 USA. Available online at http://plants.usda.gov/ (accessed 25 July 2010).
- U.S. Fish and Wildlife Service. 2010. Recovery plan for the prairie species of western Oregon and southwestern Washington.
 U.S. Fish and Wildlife Service, Portland, Oregon.
- U.S. Fish and Wildlife Service. 2006. Endangered and threatened wildlife and plants; Designation of critical habitat for the Fender's blue butterfly (*Icaricia icariodes fenderi*), *Lupinus*

- sulphureus spp. kincaidii (Kincaid's lupine), and Erigeron decumbens var decumbens (Willamette Daisy). Final rule. Federal Register 71:63862-63977.
- U.S. Fish and Wildlife Service. 2001. Endangered and threatened wildlife and plants; Endangered status for Erigeron decumbens var decumbens (Willamette Daisy) and Fender's blue butterfly (Icaricia icariodes fenderi) and Threatened status for Lupinus sulphureus spp. kincaidii (Kincaid's lupine). Final rule. Federal Register 65:3875-3890.
- U.S. Fish and Wildlife Service. 1993. 1993 supplement to list of plant species that occur in wetlands: Northwest (Region 9). Supplement to U.S. Fish & Wildlife Service Biological Report 88 (26.9).
- U.S. Fish and Wildlife Service. 1988. National list of vascular plant species that occur in wetlands. U.S. Fish & Wildlife Service Biological Report 88 (26.9).
- Walker, K. J., P. A. Stevens, D. P. Stevens, J. O. Mountford, S. J. Manchester, and R. F. Pywell. 2004. The restoration and recreation of species-rich lowland grassland on land formerly managed for intensive agriculture in the UK. Biological Conservation 119:1-18.

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- Walker, L. R., J. Walker, and R. J. Hobbs (editors). 2007a. Linking Restoration and Ecological Succession. Springer Science+Business Media, New York, New York.
- Walker, L. R., J. Walker, and R. G. del Moral. 2007b. Forging a new alliance between succession and restoration. In L. R. Walker, J. Walker, and R. J. Hobbs (editors), Linking Restoration and Ecological Succession. Springer Science+Business Media, New York, New York. Pp. 1-18.
- Whitlock, C., and M. A. Knox. 2002. Prehistoric burning in the Pacific Northwest: human versus climatic influences. In T. R. Vale (editor), Fire, Native Peoples, and the Natural Landscape. Island Press, Washington, D. C. Pp. 195-231.
- Wilson, M. V., and D. L. Clark. 2001. Controlling invasive Arrenatherum elatius and promoting native prairie grasses through mowing. Applied Vegetation Science 4:129-138.
- Wilson, M. V., T. Erhart, P. C. Hammond, T. N. Kaye, K. Kuykendall, A. Liston, A. F. Robinson, C. B. Schultz, and P. M. Severns. 2003. The biology of Kincaid's lupine (Lupinus sulphureus spp. kincaidii), a threatened species of western Oregon native prairies. Natural Areas Journal 23:72-83.
- Zeiter, M., A. Stampfli, and D. M. Newbery. 2006. Recruitment limitation constrains local species richness and productivity in dry grassland. Ecology 87:942-951.