California
Native
Grasslands
Association

GRASSLANDS

Published quarterly by the California Native Grasslands Association

Vol. 24, No. 4 Fall 2014

Constraints on Direct Seeding of Coastal Prairie Species: Lessons Learned for Restoration

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Introduction

California coastal prairies have been adversely affected by agriculture, development, and changing disturbance regimes, and they are the focus of extensive restoration efforts given the high number of species of concern they host (Stromberg et al. 2001, Ford and Hayes 2007). Grassland restoration throughout California generally involves reducing exotic cover and reintroducing native species, given that many native grasses and forbs are absent from both the seed bank and standing vegetation community and dispersal is limited (Seabloom et al. 2003, DiVittorio et al. 2007, Stromberg et al. 2007). One frequently suggested and implemented strategy for reintroducing native propagules is seeding, as the associated costs are often less than planting seedlings (Moore et al. 2011). Some past studies in both interior and coastal California grasslands have suggested that seeded grasses can establish (Buisson et al. 2008) and outcompete exotics over a period of a few years (Kephart 2001, Seabloom et al. 2003, Stromberg et al. 2007). A much larger number of studies, however, suggests that establishment from seed is highly unpredictable (Dyer et al. 1996, Hamilton et al. 1999, Orrock et al. 2008, Hayes and Holl 2011, Seabloom 2011), which the authors attribute to variable rainfall, competition with exotic species, and seed predation.

Here, we summarize results from three studies in the vicinity of Santa Cruz, California, that tested seeding of native grass and forb species into weed-dominated coastal prairies combined with different management regimes designed to reduce exotic grass and forb cover. Our results show low rates of establishment for most species seeded into existing weedy coastal prairie, which suggests that this approach has limited utility for coastal prairie restoration. All study sites were located in coastal terrace prairies within 2 km of the ocean that were dominated by exotic grasses and forbs. Seeds were collected locally when possible or obtained from commercial suppliers of seed from the closest available source population. Seeding rates varied across studies based on seed availability, viability (percent pure live seed or germination), and size (fewer seeds of larger-seeded species), and all fell in the middle to high end of the range of seeding rates typically used for California grasslands (Stromberg et al. 2007).

Case Study 1

We seeded a number of grass and forb species as part of a study designed to test the effect of mowing on the balance between native and exotic vegetation (Hayes and Holl 2011). The study was conducted at three sites: UC Santa Cruz (UCSC) campus (36° 59' 5.5" N, 122° 3' 0.9" W), Swanton Pacific Ranch (37° 4' 13.4" N; 122° 15' 0.0" W), and land owned by the Elkhorn Slough Foundation (36° 52' 4.3" N, 121° 44' 23.8" W). All sites had sandy loam soils >1 m deep and slopes of <10°. All sites were likely lightly surface tilled (<5 cm) in the early 1900s and grazed periodically between the 1950s and the start of the study. The sites were dominated by exotic grasses (primarily *Brachypodium distachyon, Bromus* spp., *Festuca myuros,* and *Festuca perenne*) and exotic forbs (largely *Erodium* spp., *Geranium dissectum, Plantago lanceolata,* and *Trifolium* spp.). See Hayes and Holl (2011) for a detailed description of site conditions and species composition.

We manually broadcasted seeds in nine 3 × 3 m plots at Swanton and UCSC without removing the existing vegetation cover or taking any additional management actions (e.g., raking in seeds or providing supplemental watering). In fall 2003, we seeded 500 seeds m^{-2} of each of five species: *Danthonia californica* and *Stipa pulchra* (native perennial grasses), *Castilleja exserta* spp. *exserta* and *Gilia capitata* (native annual forbs), and *Sisyrinchium bellum* (native perennial forb). In fall 2004, we reseeded the same species, as well as *Calandrinia ciliata, Eschscholzia californica,* and *Lupinus nanus* (native forbs), at a density of 500 seeds m^{-2} per species. Since most species seeded in 2003 and 2004 had very low or no establishment, we tried again to enhance species richness in these plots by seeding five annual and one perennial (*Achillea millefolium*) forb species in fall 2009 and 2010 at one to three sites (Table 1); some species were not seeded at all sites due to the presence of existing populations of the species or limited seed. We recorded the number and cover of seedlings beginning the spring following seeding through spring 2012 for all species. We also conducted greenhouse germination tests for seeds used in 2009 and 2010 to assess viability.

We recorded no establishment of seedlings in the first growing season following the 2003 seeding, during which annual rainfall was

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Table 1. Seeding and germination rates in the greenhouse and field for forb seedlings in fall 2009 and 2010 in Case Study 1. All species are annuals except *A. millefolium*. Values are means ± 1 SE. Seedling density in the field is reported for the growing season after seeding (either spring 2010 or 2011) and spring 2012.

Species	Year Seeded	No. of sites	Seeds m^{-2}	Greenhouse germination (%)	Seedlings m^{-2} in spring following seeding	% yield	Seedlings m^{-2} in spring 2012
Achillea millefolium	2009	2	65	66.0 ± 4.9	0	0	0
Clarkia davyi	2010	3	700	26.8 ± 8.4	1.7 ± 0.7	0.1	0.6 ± 0.3
Deinandra corymbosa	2009	1	245	33.3 ± 0.6	0	0	0
	2010	1	60	11.0 ± 6.4	0	0	0
Madia sativa	2009	1	75	30.5 ± 0.7	1.8 ± 1.2	2.4	1 seedling*
Navarretia squarrosa	2009	2	500	81.8 ± 8.4	0.3 ± 0.3	<0.1	1 seedling*
Trifolium willdenovii	2009	3	200	no data	0	0	0
	2010	3	500	49.2 ± 8.1	0	0	0
TOTAL	2009		585				
	2010		1260				

*Only 1 seedling was observed in all the quadrats surveyed.

Direct Seeding *continued*

close to average (Hayes and Holl 2011). Two species (*Stipa pulchra* and *Sisyrinchium bellum*) had higher cover in seeded vs. non-seeded plots at one or both of the sites 2–4 years following the 2004 seeding, during which rainfall was above average (Hayes and Holl 2011). Two species (*Eschscholzia californica* and *Gilia capitata*) had higher establishment in seeded plots in the first growing season, but not thereafter. The remaining four species showed little (<4 seedlings total at all sites) or no establishment in seeded plots. There was no difference in exotic species composition in seeded vs. unseeded plots, and inter-annual variation in vegetation composition is described in detail in Hayes and Holl (2011). In 2012 (7.5 years after seeding), both *Stipa pulchra* and *Sisyrinchium bellum* cover remained higher in seeded vs. unseeded plots (*Stipa*—seeded: 11.4 ± 2.5%, unseeded: 1.9 ± 2.5, F = 11.0, p = 0.0022; *Sisyrinchium*—seeded: 2.2 ± 0.7%, unseeded: 0.0 ± 0.0, F = 7.4, p = 0.0107, Fig. 1), which shows that these two species were able to establish successfully from seed.

Of the six species seeded in 2009 and 2010, only half established in the field experiments (Table 1) and only one (*Madia sativa*) had a yield rate (number of seedlings per number of seeds) of >0.1%. Viability was not likely to be the limiting factor in this case, as 11–82% of the seeds germinated in the greenhouse (Table 1). Rainfall was below average in fall 2009, whereas rainfall was well above average throughout the 2010–2011 growing season.

Figure 1. UCSC experimental plots from Case Study 1. Note *Stipa pulchra*, one of the few species that established from seed. *Photo: Lewis Reed*

Case Study 2

In a second study, we either used controlled burns (conducted in late September 2007 using a burn box) to reduce above-ground vegetation or scraped off the top 5 cm of soil to reduce competition by removing vegetation and the exotic annual forb and grass seed bank (Buisson et al. 2006), as well as to create optimal habitat for recruitment of the endangered Ohlone tiger beetle (*Cicindela ohlone*). Each treatment was replicated in two blocks of ten 2 × 2 m plots in two different areas of coastal prairie with sandy loam soils on the UCSC campus (n = 40 per treatment). Vegetation prior to treatments and in control plots consisted of a dense cover (~90%) of exotic grasses (primarily *Avena barbata, Briza maxima, Bromus hordaceous,* and *Festuca myuros*) and forbs (mostly *Medicago polymorpha, Plantago lanceolata,* and *Erodium botrys*). Native perennial grasses and forbs made up ~10% of the cover and consisted of species such as *Danthonia californica, Ranunculus californicus, Stipa pulchra, Chlorogalum pomeridianum, Eschscholzia californica,* and *Sisyrinchium bellum*. The plots were seeded at a rate of 1,150 seeds m^{-2} with seven native annual forbs in fall 2007 (Table 2) to try to enhance the diversity of this guild, and no supplemental water was provided. We monitored establishment of seeded species for the two subsequent growing seasons (spring 2008 and 2009). Seed viability was not tested in the greenhouse, so it is possible that low viability may have affected establishment.

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Table 2. Seeding rate and annual forb seedling density in scraped plots for the first growing season following seeding for Case Study 2. Values are means ± 1 SE.

Species	Seeds m^{-2}	Seedlings m^{-2}	% yield
Castilleja densiflora	113	0.0 ± 0.0	0.0
Clarkia rubicunda	465	1.9 ± 0.6	0.4
Lasthenia californica	276	1.2 ± 0.4	0.4
Layia platyglossa	41	0.7 ± 0.2	1.7
Lepidium nitidum	32	0.5 ± 0.2	1.4
Lupinus nanus	15	0.4 ± 0.2	2.5
Triphysaria eriantha	212	0.4 ± 0.1	0.2
TOTAL	1154	5.0 ± 1.2	0.4

Direct Seeding *continued*

One individual of *Lasthenia californica* was the only seedling from seeded species observed in burned plots in the first growing season when annual rainfall was close to average, and no seeded individuals were observed in burned plots in the second growing season. Only a few individuals of six of the seven species were observed in scraped plots in the first growing season (Table 2), despite the fact that scraping substantially reduced exotic cover and increased bare ground in scraped plots (46.5 ± 2.4%), as compared with burn (9.4 ± 0.9%). By the second growing season, there were only a few individuals of *Layia platyglossa, Lasthenia californica,* and *Lupinus nanus* in some scraped plots, at which time approximately half of these plots were still ~25% bare of vegetation.

Case Study 3

The third study was conducted in a weedy, moist, formerly coastal prairie site that had been used for several decades for agriculture and then had been abandoned for over 20 years at the UC Younger Lagoon Reserve located in Santa Cruz, California (+36° 57' 00.75", -122° 03' 47.80"). At the time of the study site initiation, it was covered by nearly 100% exotic species, dominated by exotic grasses (primarily *Festuca perenne* and *Bromus diandrus*) and exotic forbs (such as *Raphanus sativus, Medicago polymorpha,* and *Helminthotheca echioides*). In summer 2011, plots were mowed to reduce the cover of standing thatch and fenced to minimize herbivory from rabbits. During October 2011 following the first rain and emergence of annual weeds, the site was treated with a broad-spectrum herbicide (2.5% glyphosate). Immediately prior to seeding in November 2011, any exotic regrowth was treated with herbicide and then the thatch was raked off the plots. In five 10 × 10 m plots, we seeded each of eight coastal prairie grasses and forbs (Table 3) into a single, 10-m long row consisting of two hand-cut furrows. Seeds were hand-buried to a depth of 7–10 mm to simulate drill seeding and manually tamped to improve seed–soil contact. Given the small size of the plots, a regular drill seeder was not used. Due to unusually dry conditions, the plots received supplementary water in December to help ensure germination and survival of germinated seedlings. We planted the same species as plugs in rows in five additional 10 × 10 m plots in January 2012. In April–May 2012 and 2013, each seeded row was surveyed for planted seedlings, and plant survival was recorded in planted plots. We also conducted greenhouse germination studies to assess seed viability.

In the greenhouse, most species had germination rates >50%; however, *Symphyotrichum chilense* and *Juncus patens* had very low germination (Table 3). Two forb species, *Trifolium willdenovii* and *S. chilense*, were not observed in the field during the first year. For the remaining three forb species (*Achillea millefolium, Clarkia davyi,* and *Grindelia stricta*), percent yield (seedlings/live seed planted ×100) was 1–2% in Year 1 (Table 3), but no individuals of the two perennial species survived until the second year. In the field, the grasses and one rush species planted could not be distinguished from the large number of exotic grass seedlings (Fig. 2) and, therefore, were not quantified; but even by the second year we did not record identifiable individuals of those species, and the sites retained a dense cover of the exotic grasses and forbs present prior to the initiation of the experiment. As a comparison, 72% of planted plugs survived in Year 1 and 40% in Year 2, ranging in survival from 64% for *Hordeum brachyantherum* to 13% for *S. chilense* in Year 2 (Tang 2013).

Figure 2. Recently germinated *Clarkia davyi* seedling underneath dense exotic grass cover at Younger Lagoon Reserve (Case Study 3). *Photo: Lewis Reed*

Discussion and Conclusions

The results of the three case studies presented, as well as Buisson et al. (2006), show extremely low establishment rates in coastal prairie from seed with yields of 1–2% at best in the first year and numbers

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Table 3. Seeding and germination rates in the greenhouse and the first year in the field for Case Study 3.* Values are means ± 1 SE. Note that units of germination in the field are per meter of drill-seeded row.

Species	Growth form	Seeds m^{-2}	Greenhouse germination (%)	Mean ± seedlings m^{-1}	SE % yield
Clarkia davyi	Annual forb	135	50 ± 4.5	3.0 ± 1.1	2.1
Trifolium willdenovii	Annual forb	90	36 ± 4.9	0	0
Symphyotrichum chilense	Perennial forb	180	10 ± 0.4	0	0
Achillea millefolium	Perennial forb	180	76 ± 4.7	2.6 ± 0.7	1.4
Grindelia stricta	Perennial forb	135	85 ± 2.4	1.7 ± 0.6	1.2
Bromus carinatus	Perennial grass	135	61 ± 3.7	no data	
Hordeum brachyantherum	Perennial grass	135	65 ± 2.7	no data	
Stipa pulchra	Perennial grass	135	46 ± 3.8	no data	
Juncus patens	Perennial sedge	180	<2	no data	
TOTAL		1305			

*It was impossible to reliably identify recently germinated native grass and rush seedlings in the field from the huge number of recently germinated exotic grass seedlings; no native grass and rush seedlings were observed in larger size classes.

declining in subsequent years. Of the many species we seeded, only *Stipa pulchra* and *Sisyrinchium bellum* established populations (and only at one site) that were observed in any abundance after the first 2 years. We reiterate, however, that we were unable to reliably identify native grass seedlings in the third Case Study, and some seed may have germinated after the second year of Case Studies 2 and 3. There are several reasons for such low yield rates: highly variable rainfall typical of California, which often results in seedling desiccation (Hamilton et al. 1999, DeFalco et al. 2012); competition with abundant exotic grasses, the seeds of which often outnumber and germinate before natives (DiVittorio et al. 2007, Abraham et al. 2009, Wainwright et al. 2012); and high levels of herbivory (Orrock et al. 2008, Maze 2009, DeFalco et al. 2012). These factors also present challenges to restoring coastal prairies by planting seedlings, but outplanting larger seedlings overcomes losses due to seed predation, failed germination, and mortality of recently germinated seedlings, which are typically quite high (Clark et al. 2007, James et al. 2011).

We note that results of direct seed-sowing may be more favorable when seeds are 1) drill seeded into recently abandoned agricultural lands where weeds have been controlled for many years, thereby reducing the exotic seed bank and competition, and/or 2) extensive exotic control measures are undertaken after seeding (Lulow 2008, Nyamai et al. 2011, Watsonville Wetland Watch 2013). Typically, efforts to improve seed–soil contact, such as drill seeding, tamping, or using a heavy roller, improve establishment from seed (Rotundo and Aguiar 2005, Desimone 2011, DeFalco et al. 2012). The low establishment from our simulated drill seeding likely resulted from a low rainfall year combined with high cover of exotic grasses (particularly *Festuca perennis*), although it is important to note that we found low establishment from seed in years that annual rainfall spanned from below to well above the average.

One important consideration is the relative cost of seeding vs. other revegetation methods. Typically, seeding is much less expensive than planting seedlings, due to nursery propagation and outplanting costs for seedlings (Moore et al. 2011). Relative costs, however, vary greatly depending on 1) whether seed is purchased from a seed supplier with propagation fields or locally hand collected, 2) germination rates, and 3) labor costs, particularly if volunteer labor is available for small restoration planting efforts. For example, in our third Case Study, the contract for collecting and processing seed was double that for producing plugs for a similar area of land, and the project had substantial volunteer labor support to reduce the cost of planting plugs. Moreover, plug planting resulted in much higher cover of native grasses and forbs than did seeding (Tang 2013).

In summary, our results from multiple studies demonstrate that sowing seeds into weed-dominated coastal prairies, where exotic plant competition is high and rainfall is unpredictable, is likely to have a low success rate. Further research on the prospective value of direct seeding in coastal prairies should focus on pre-planting site preparation and post-planting weed control, which ameliorates exotic plant competition and methods for overcoming drought stress during initial years of establishment.

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