American Journal of Botany 98(5): 801–811. 2011.

Serpentine soils harbor some of the Earth's most unique and unusual vegetation (Whittaker, 1954; Brooks, 1987; Kruckeberg, 2002). Found on every continent, serpentine soils are derived from ultramafic parent material and are notable for their lack of essential nutrients; high concentrations of potentially toxic heavy metals such as nickel, chromium, and cadmium; and low Ca^{2+}/Mg^{2+} ratios (Kruckeberg, 1984; Alexander et al., 2006). These characteristics generally result in vegetation with physiaboveground biomass after fire. The relatively small number of studies regarding the effects of fire on serpentine vegetation, however, limit any generalizations that can be made for how *Darlingtonia* fen vegetation will respond to wildfire.

Our study assessed the impact of fire on *Darlingtonia* fen plant assemblages by taking advantage of the 2002 Biscuit Fire, a lightening-ignited fire that burned ~202 000 ha in northern California and southwestern Oregon (USDA Forest Service and BLM, 2004). Because the fire burned across many different vegetation types, including numerous *Darlingtonia* fens, it provided an unparalleled opportunity to study the effects of fire on various taxonomic groups and ecosystem processes (Ratchford et al., 2005; Donato et al., 2006; Sanders et al., 2007; Thompson et al., 2007, Fontaine et al., 2009; Wittman et al., 2010). In the study presented here, we used a set of eight unburned and eight burned fens to examine the effects of burning on plant cover, species density and diversity, evenness, and community composition. Although the unpredictable timing of the Biscuit Fire did not allow for preburn data to be collected, our study analyzes data from fixed plots for vascular plants over the course of 5 yr (2003–2007) after the fire. We predicted that the life histories of plants in *Darlingtonia* fens (i.e., perennials with well-developed underground storage organs) coupled with low site productivity and high summertime moisture would minimize species losses and changes in community structure and composition resulting from fire.

MATERIALS AND METHODS

Study sites—We studied the vegetation in unburned and burned *Darlingtonia* fens on the serpentine soils straddling the border of northern California and southwestern Oregon (see also Ratchford et al., 2005; Sanders et al., 2007; Wittman, 2010). The area is characterized by a Mediterranean climate with warm, dry summers and mild, wet winters (Whittaker, 1960). On average, the region experiences ~154 cm precipitation annually, though only ~4 cm falls between June and August. Common serpentine plant associations in the Klamath Mountains include Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.) savanna, knobcone pine (*P. attenuata* Lemmon) forest, mixed conifer forest, and serpentine meadows and barrens (Whittaker, 1960). Within our study area, *Darlingtonia* fens are found across an elevational range of 200–1300 m, though the majority of fens occur between 350 m and 600 m (Frost et al., 2004). In addition to the dominant *D. californica*, the distinct vegetation of *Darlingtonia* fens is composed mainly of perennials such as

To estimate evenness, we used Hurlbert's (1971) probability of an interspecific encounter (PIE):

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value of *AvgTrend* means the slopes of temporal change for most species in the assemblage are large. A large value of

the first year after the fire (Fig. 1). During the first year after the fire, burned fens had, on average, 10% fewer species recorded. Overall differences in species density between fen type were marginally significant ($F_{1,\ 137.4} = 3.79$, $P = 0.074$). Species density varied significantly over the 5 yr ($F_{4,\ 21.9} = 13.21$, $P < 0.001$), with average species density peaking 3 yr after the fire for both unburned and burned fens (Fig. 1). Site characteristics, as described by the first principal component, were strongly related to species density ($F_{1,\ 510.3} = 14.05$, $P = 0.002$).

True diversity did not differ between unburned and burned fens ($F_{1,\ 0.81} = 0.077$, $P = 0.785$; Fig. 1). Diversity increased significantly over the 5 yr of the study ($F_{4,\ 7.16} = 8.399$, $P < 0.001$), though unburned and burned fens changed similarly through time ($F_{4,\ 0.518} = 0.607$, $P = 0.659$). Site characteristics had a marginally significant impact on diversity ($F_{1,\ 36.56} = 3.51$, $P = 0.084$). Interestingly, sampling in only 1 yr would have led to differing results: sampling in 2006 or 2007 would have yielded marginally higher diversity in burned fens (2006: $t = 1.82$, df = 14, $P = 0.090$; 2007: $t = 1.76$, df = 14, $P = 0.109$). Evenness was greater in burned fens, though the differences were marginally significant ($F_{1,\ 0.01} = 3.017$, $P = 0.106$). Differences in evenness between unburned and burned fens were greatest in the last 2 yr of the study (Fig. 1). Evenness varied significantly among the 5 yr of the study ($F_{4,\ 0.003} = 6.367$, $P < 0.001$), though interannual differences were similar among unburned and burned fens ($F_{4,\ 0.001} = 0.395$, $P = 0.811$). Evenness was lowest for both unburned and burned fens in the first year after the fire (Fig. 1). As with species diversity, sampling evenness would have yielded significant differences only in the last 2 yr of the study (2006: $t = 2.29$, df = 14, $P = 0.038$; 2007: $t = 1.85$, df = 14, $P = 0.085$).

A high level of concordance existed in the ranks of species between unburned and burned fens in all 5 yr (for all years $\tau \geq 0.6$, $P < 0.001$). That is, common species in burned fens tended to be common in unburned fens also. However, the order of dominance differed for several of the most abundant species between unburned and burned fens, and differences between unburned and burned fens were variable among species (Figs. 2, 3). For instance, *S. officinalis* remained the dominant species in both fen types, and its abundance did not differ significantly between fen types ($F_{1,\ 47.0} = 0.44$, $P = 0.517$). Similarly, the abundances of *N. californicum* and *R. californica* did not differ between fen types ($F_{1,\ 175.1} = 18.88$, $P = 0.370$; $F_{1,\ 62.8} = 0.452$, $P = 0.513$; respectively). *Rudbeckia californica*, usually the fourth most dominant plant in unburned fens, was reduced to the tenth most abundant plant in burned fens, though this is likely to be an artifact of one unburned fen that had 3–5× more *R. californica* cover than other unburned fens, depending on the year. *Darlingtonia californica* was always one of the four most abundant plants, regardless of fen type, but we detected at best a marginally significant difference between unburned and burned

Fig. 2. Rank abundance curves for vegetation in unburned (n = 8) and burned (n = 8) *Darlingtonia* fens for the years 2003–2007. Bars indicate mean cover found in the eight fens of each type, and error bars indicate ±1.0 SEM. Colors indicate individual species and are intended to highlight both temporal changes and differences among fen type for seven dominant species.

in the amount of variance in species responses over the 5 yr (Fig. 5). In other words, the amount of change that occurred was quite similar in burned fens assemblages, whereas unburned fens showed more variable temporal patterns of change among fens. This indicates that the fire homogenized these plant assemblages and, perhaps more importantly, restricted their trajectories within relatively narrow bounds.

Cover in burned *Darlingtonia* fens was, on average, 39% the year after the Biscuit Fire, whereas cover in unburned fens was approximately 55% (Fig. 1). The difference in cover between fen types gradually diminished during the course of our study, and by 2007, 5 yr after the fire, burned fens had 54% cover and unburned fens had 62% cover (Fig. 1). Importantly, differences between cover in unburned and burned fens were not significant. However, had we conducted our study during only a single year, we would have detected differences in cover between burned and unburned fens only in 2003 and 2005. Interestingly, another study of *Darlingtonia* fens burned during the Biscuit Fire (Cramer, 2005), conducted 2 yr after the fire in 2004, did not detect differences in herbaceous cover. It is possible that differences were largely diminished by 2004 in Cramer's (2005) study fens, of which only three of their 24 were used in our study. In addition, Cramer's (2005) use of broad cover values (i.e., a modified Daubenmire scale) may have reduced her ability to detect differences. Given the results of our work, it appears that the influence of fire on cover of these unique perennial herbaceous plant communities is immediate and temporary, and it can persist for approximately 3 yr.

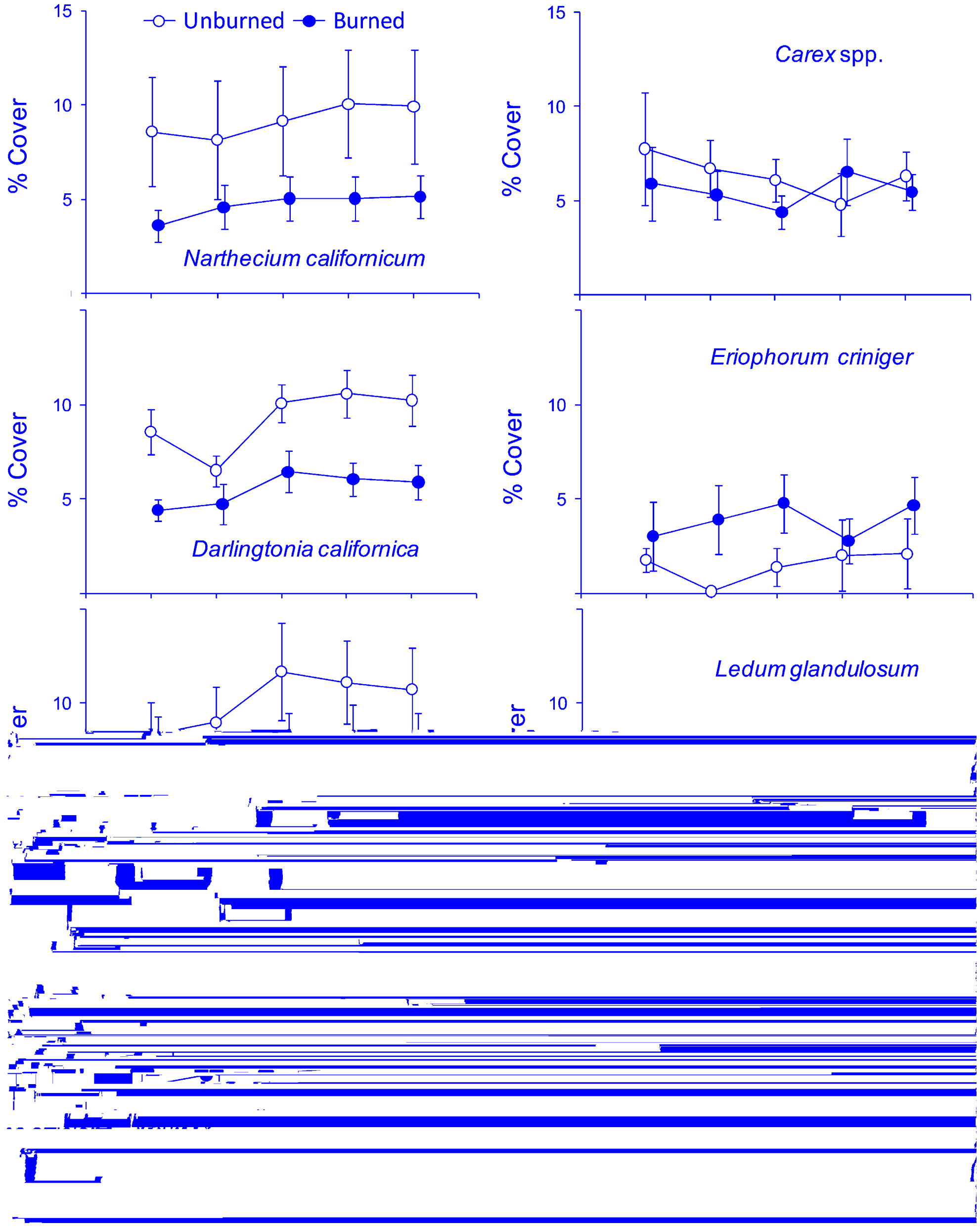

Fig. 3. Average percent cover of seven dominant species in unburned (n = 8) and burned (n = 8) *Darlingtonia* fens. Error bars show ±1.0 SE. Data are jittered to avoid overlap.

It is also worth noting that cover increased not only for burned fens but also for unburned fens during the 3 yr after the fire (Fig. 1). We consider two plausible explanations of the similar pattern seen in both habitat types. First, the dense smoke that covered much of the region from late July 2002 until well into the autumn could have temporarily reduced cover in the unburned fens. Smoke has been shown to have significant effects on plant productivity, even in areas outside of the immediate fire (Davies and Unam, 1999; Calder et al., 2010). Second, 2001–2003 included notably dry summers in the study region as measured by the Palmer Drought Severity Index (PDSI), an index of soil moisture, temperature, precipitation, and evapotranspiration, where higher PDSI indices indicate low moisture stress (Palmer, 1965). The summertime PDSI value (June–August) for the previous 10 yr (1991–2000) was always positive and averaged 2.36. In contrast, the indices for the years 2001, 2002, and 2003 were –2.56, –1.89, and –1.21, respectively. It is possible that throughout our study, all the fens were recovering from smoke or drought regardless of whether they had burned.

It is difficult to compare our results with those of other studies concerning the effects of fire on vegetation. The majority of fire-effects studies focus solely on dominant species (e.g., trees, shrubs), or they combine all species into large taxonomic groups such as graminoids, herbs, and shrubs (e.g., Menges et al., re on2( ) fi our resdiegctomiose otltsown becauseombineusucieynp thhetef-0.02 Tc0.09om smo fii

1.9 more species per 5 m^2 in burned serpentine habitat than in unburned serpentine habitat (Harrison et al., 2003), which is in agreement with the differences we found in *Darlingtonia* fens. Our work supports the prediction made by Safford and Harrison (2004) that fire would have relatively modest effects on serpentine floras. Taken together, the previous work on serpentine habitat and our own suggest that burning has relatively small yet positive influences on the number of species in local serpentine plant assemblages.

Safford and Harrison (2004) suggested that modest effects of fire on serpentine vegetation vs. adjacent sandstone vegetation were due to lower fertility of serpentine soils and the resulting open structure of serpentine vegetation. Because space and light are less likely to be limiting resources on serpentine than on sandstone soils, fire does not produce dramatic increases in the availability of these resources on serpentine. In our study, in which canopy cover is low and many species have well-developed rhizomatous networks, most species were able to quickly regenerate aboveground foliage after the fire. Extensive rhizomatous networks were visible in our burned fens in which fire had consumed much of the surrounding matrix of peat. Nitrogen availability had been assessed in nine of our 16 *Darlingtonia* fens and surrounding upland soils in a previous study (Franklin, 2009). That work, which was done 5 yr after the Biscuit Fire, found exceptionally low levels of available nitrogen (0.01–0.025 NH_4^+–N mg·g^{-1}and NO_{3-}N mg·g^{-1}). Differences in nitrogen between unburned and burned sites were not detected, nor were differences detected between fen and upland soils (Franklin, 2009). Although ephemeral changes due to burning may have been missed in that study, it is clear that *Darlingtonia* fens and their surrounding matrix are nutrient limiting. We suggest that vegetation in fens seems to be resilient to fire because of high moisture content, low productivity (and the resulting low fire intensity), as well as the dominance of perennials with large rhizomatous networks. Lastly, the lack of recruitment from seed banks may explain the small turnover of serpentine species (see also Safford and Harrison, 2004). Although little is known about seed banks in *Darlingtonia* fens, high soil moisture and the resulting low fire intensity may reduce postfire germination. Interestingly, *H. anagalloides*, the only plant we found that was not a perennial (i.e., it can be an annual or biennial) was found in six unburned fens but only one burned fen. Because it is short lived, *H. anagalloides* would be expected to have a well-developed seed bank, but it was either not present or was not stimulated by the fire.

Our study results indicate that few species show significant changes in abundance as a result of fire. Of the seven dominant plants, only *D. californica* appeared to have been significantly negatively affected, and this effect was still visible 5 yr after the fire (Fig. 3). In contrast, *E. criniger* showed strong positive effects of burning (Fig. 3). The effects on *D. californica* and *E. criniger* that we observed are in agreement with the findings of Cramer (2005). Both species have rhizomes, and it is unknown what factors control the differential responses to fire. Cramer (2005) found that *Danthonia californica* (California oatgrass) was less common in burned fens and suggested that belowground parts may be sensitive to fire. None of our burned fens contained *Danthonia californica*, though it was found in low abundance (average cover ~0.08%) in 2–4 unburned fens, depending on the year. *Rhododendron occidentale* showed a similar response; we found this shrub in five unburned fens (average cover ~0.9%) and in only two burned fens (average cover ~0.2%). Lastly, *Calamagrostis* spp. were found in 2–3 unburned fens (average cover ~0.2%) and in 6 burned fens (average cover ~1.6%). Our findings for *R. occidentale* and *Calamagrostis* spp. are in agreement with Cramer's (2005).

Several caveats should be taken into consideration when interpreting our results or using them to inform any management issues. First, because fires vary in their effects on vegetation, primarily on the basis of differences in their intensity, frequency, and size (Agee, 1993), little doubt exists that the burning that occurred in our 16 fens varied considerably. Although we tried to capture some of these differences by using a coarse measure of intensity and incorporating that into our site characterization, we were unable to predict how burn intensity influenced the response of fen vegetation. Second, because the study region has been an area of active fire suppression since the early to mid 1900s (Skinner, 2003a; Taylor and Skinner, 2003), *SeveraoR1Tres vbithe study rams*

Our results suggest that the effects of fire on plant assemblages in *Darlingtonia* fens were both slight and subtle. Importantly, some of these effects only manifested themselves several years after the fire. A single year of study would not have detected most of the differences we found between unburned and burned fens, supporting the great value of studies that use multiple years of observation for assessing vegetation responses to fire (e.g., Menges et al., 1993; Hutchinson et al., 2005; Webster and Halpern, 2010). The relatively high soil moisture levels coupled with the lack of an effect of fire on light availability and the well-developed underground rhizome of many plant species in *Darlingtonia* fens suggest these assemblages are moderately resilient to fire. More generally,

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