

The Effects of Fire on Serpentine Vegetation and Implications for Management¹

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Abstract

We summarize the results of two studies comparing fire effects on adjacent serpentine and non-serpentine soils in two vegetation types, grassland and chaparral. In both vegetation types, serpentine soils were less fertile and supported less biomass. Mean time-to-last-burn was longer, and fire severities lower, in serpentine vs. non-serpentine chaparral. Positive effects of fire on species richness, diversity, species turnover, and exotic invasion were most pronounced in the more productive non-serpentine vegetation. Management of unique, low productivity habitats like serpentine must take into account differing responses and lower resilience to fire that often characterize these environments.

Introduction

Ultramafic “serpentine” substrates underlie approximately 5,000 km² of the State of California. Although this amounts to less than 1.5 percent of California’s total area, fully 10 percent of the state’s endemic plant taxa are restricted to serpentine soils (Kruckeberg 1984). Two and a half percent of USDA-Forest Service managed lands in California are found on serpentine soils, and in the state’s northwestern corner, about 14 percent of the land area managed by the Klamath, Six Rivers, and Shasta-Trinity National Forests is underlain by serpentine substrates. Thirty percent of the rare plant species managed as “Sensitive” in these three forests are serpentine obligates, and a further 10 to 15 percent are primarily found on serpentine soils (J. Nelson and L. Hoover, pers. comm.). Further extensive occurrences of serpentine occur on the Mendocino, Plumas, Tahoe, and Los Padres National Forests. Because of the botanical and geological resources associated with ultramafic outcrops, a large number of Research Natural Areas (RNAs) and Special Interest Areas (SIAs) in California’s National Forests have been designated to protect serpentine habitats. The U.S. Bureau of Land Management and California State Parks also manage a number of conservation units composed primarily or entirely of serpentine vegetation.

Although the ecology of serpentine in California has been the subject of many dozens of scientific studies, the fire ecology of serpentine habitats has remained largely unexplored, and the role of fire in serpentine ecosystems is poorly understood. This fact is a serious impediment to management of serpentine habitats in California (McCarten and Rogers 1991, Six Rivers NF 1998). As McCarten and Rogers (1991) note, “predictions about the response of serpentine vegetation to fire must (presently) be based on studies in non-serpentine vegetation, but substantial differences between the two habitats may render such predictions false.”

¹An earlier version of this paper was presented at the 2002 Fire Conference: Managing Fire and Fuels in the Remaining Wildlands and Open Spaces of the Southwestern United States, December 2–5, 2002, San Diego, California.

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Differences in the ecology of serpentine and non-serpentine habitats are based fundamentally in the chemical idiosyncrasies of ultramafic rocks and the soils that develop on them. Ultramafic rocks are composed primarily of ferromagnesian minerals high in Mg- and Fe-oxides and heavy metals, and low in silica and oxides of Ca, K and P. Soils which develop on these substrates are thus critically low in most of the basic macronutrients essential to plant growth (Proctor and Woodell 1975). Compared to most other soil types, very low levels of soil fertility in serpentine soils lead to 1) low rates of plant growth and low levels of community productivity, 2) a very heterogeneous vegetation structure, often characterized by thin vegetative cover and large extents of bare ground, 3) high ratios of native to exotic species, and 4) a high number of stress-tolerating, edaphic-endemic taxa (Baker and others 1992). In addition, serpentine vegetation typically supports a much larger component of perennial herbs (grasses and forbs) than its non-serpentine counterparts.

Ecological theory predicts that the amount of resources available in an ecosystem should affect its response and sensitivity to disturbances like fire. Plant stature, biomass, rates of growth and fuel accumulation are all influenced by habitat productivity, and all of these factors play an important role in determining fire frequency and intensity (Pickett and White 1985, Bond and van Wilgen 1996). Site quality may also be related to rates of competitive displacement, with relatively unproductive (and therefore less competitive) environments less reliant on disturbance for diversity maintenance, on both spatial and temporal scales (Grime 1979, Huston 1994). Since the most significant direct effect of fire is to increase available amounts of space and light, the effects of fire in a given vegetation type should relate positively to productivity, since more productive plant communities are more strongly limited by above-ground competition (Tilman 1982).

Here, we summarize results of two independent studies carried out in California's northern Coast Range, comparing effects of an October, 1999 wildfire on serpentine and non-serpentine grassland and chaparral (Harrison and others 2003, Safford and Harrison 2004). Due to strong differences in soil fertility and community productivity between serpentine and non-serpentine habitats, our basic hypothesis in both studies was that the effects of fire (on, e.g., species richness, diversity, composition, exotic invasion) would be stronger on non-serpentine soils than the less productive serpentine soils. In the Discussion, we explore management implications of our results.

Methods

Study Site

Our study site was located at the junction of Napa, Lake, and Yolo Counties (38° 51' N, 123° 30' W), California, USA. 16,000 ha of this area were burned in the Sixteen Fire in mid-October, 1999. Field sampling was carried out on properties managed by the University of California (Donald and Sylvia McLaughlin University of California, Natural Reserve) and U.S. Bureau of Land Management. Elevations in the study area range from 370 to 945 m; climate is Mediterranean. Annual precipitation averages 725 mm, and mean annual temperature is approximately 18.1° (11.4° January, 27.8° July). Geology, flora and vegetation of the area are described in UCD-NRS (2000). Botanical nomenclature in this paper follows Hickman (1993).

Sampling Methods

In grassland, we took advantage of a series of long-term study plots which were partially burned by the Sixteen Fire (Harrison and others 2003). Species richness had been previously sampled at 80 sites in 1998 and 1999, using five 1 m² quadrats subsampled along a 40 m transect; 35 of these sites burned. After the fire, we added 10 burned serpentine sites, and 10 unburned sites (mostly non-serpentine) to more evenly balance the sampling design. Our final sample included 45 burned sites (18 serpentine, 27 non-serpentine) and 55 unburned sites (33 serpentine, 22 non-serpentine). We continued sampling for 2 yr after the fire (in 2000 and 2001). At each site we measured total, native, and exotic species richness and frequency; we collected soil samples, and (in 1998 and 2001) we clipped, dried and weighed aboveground biomass.

In chaparral we sampled from a design pairing burned sites with neighboring unburned controls (Safford and Harrison 2004). In spring and summer of 2000, 2001 and 2002, we sampled 40 pairs of burned and unburned sites, 20 in serpentine chaparral and 20 in non-serpentine chaparral. At each site we sampled one 250 m² macroplot, subsampling for percent cover of all species, numbers of shrub seedlings, and a suite of environmental variables. We estimated fire severity in burned quadrats by measuring carbonized stem termini on individuals of chamise (*Adenostoma fasciculatum*; in a few cases *Quercus durata* was substituted). We estimated time since last fire by counting growth rings from 3 to 5 fire-killed individuals of non-sprouting species of *Arctostaphylos*, *Ceanothus*, and *Cupressus*. In 2001 and 2002, we sampled woody and herbaceous biomass, and assessed regrowth of the vegetation by measuring the heights of the most common shrub species within each burned site. In some analyses, we used unburned sites as surrogates for “pre-fire” conditions; their paired burned sites represent “post-fire” conditions.

Analyses

In grassland, we used ANOVA and MANOVA to test the effects of year, soil, fire and their interactions on species richness and composition, and to compare bunchgrass frequency before and after fire on serpentine and non-serpentine sites. In chaparral, we used ANOVA/MANOVA to test for differences between soil types in 1) site and vegetation variables independent of fire; 2) fire severity and time since last fire; 3) post-fire changes in species richness, diversity and composition; and 4) rates of post-fire recovery in biomass, species richness, and seedling densities. For each soil type, we used regression to test the relationship between post-fire change in richness, diversity and composition and a suite of predictor variables, including fire severity, time since last fire, and variables related to productivity and soil fertility. Repeated-measures ANOVAs were used where appropriate (Proc Mixed; SAS 8.0).

Results

Grassland

Serpentine grasslands were significantly higher in soil Mg, and lower in soil N, P, and Ca than non-serpentine grasslands; biomass and cover were significantly higher in non-serpentine grasslands (Harrison 1999). Pre-fire, non-serpentine sites were less species rich on average than serpentine sites. Fire significantly increased the mean number of species in burned non-serpentine grassland, such that richness was comparable to that in serpentine sites, but this effect lasted only one year. On the average, non-serpentine richness dropped significantly between 2000 and 2001, but

there was no significant difference in mean serpentine richness between 2000 and 2001 (*fig. 1*). The relative proportions of native and exotic species in serpentine sites showed no significant effect of fire. The mean number of exotics in non-serpentine

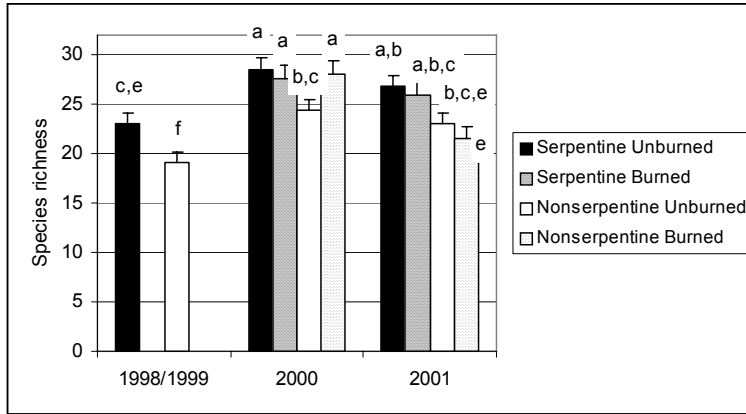


Figure 1—Mean species richness (+ standard error) of burned and unburned grassland sites, from 1998/1999 (two pre-fire years averaged) to 2001. Bars with different letters are significantly different at $P < 0.05$.

sites increased significantly after fire (9.7 to 13.2; $P < 0.005$), but there was no effect on mean native species richness. Neither species richness nor post-fire change in richness (i.e., post-fire minus pre-fire richness) were significantly related to biomass on either soil type. Species turnover between 1999 and 2000 did not differ significantly between burned and unburned sites in serpentine grassland (54 percent vs. 49 percent), but fire had a significant positive effect on turnover in non-serpentine grassland (63 percent burned vs. 56 percent unburned, $P = 0.01$).

Perennial grasses occurred in 7 to 14 percent of our non-serpentine quadrats (sub-samples), depending on the year, but there were no significant differences across years or between burned and unburned sites. Frequency of perennial grasses was much higher in serpentine grassland (4 yr mean=49 percent), with a marginally significant increase occurring in burned sites after fire (59 percent in 2000 vs. 45 percent in 1999, $P = 0.10$).

Chaparral

Serpentine chaparral was significantly higher in soil Mg and pH, and lower in soil P, K, and Ca than non-serpentine chaparral (Safford and Harrison 2004). Unburned (“pre-fire”) cover (81.4 percent vs. 69.6 percent) and post-fire biomass (woody species: 660 g m^{-2} vs. 84 g m^{-2} ; herbaceous species: 81.5 g m^{-2} vs. 25.3 g m^{-2}) were both significantly greater in non-serpentine than serpentine chaparral (all $P < 0.001$). Fire severity, measured as the mean diameter of carbonized stem termini, was significantly greater in non-serpentine than in serpentine chaparral (5.1 mm vs. 3.3 mm; $P < 0.005$). Mean time-to-last-burn was much greater in serpentine chaparral (73.7 ± 39 yr vs. 18.6 ± 3.1 ; $P < 0.001$).

Total species richness, diversity (measured as 1-Simpson’s Index), and exotic species richness were all significantly higher on burned than unburned sites in the year following fire (all $P < 0.001$). The positive effects of fire on richness were significantly greater in non-serpentine sites (mean=15 species unburned vs. 35.8 burned) than in serpentine sites (mean=21.5 unburned vs. 31.5 burned (*fig. 2*)). This same significant Fire X Soil interaction was found for species diversity and exotic richness as well (the latter increased from 1.2 to 6.9 species on non-serpentine soils,

and from 0.9 to 4 on serpentine soils). Species turnover due to fire was also significantly greater in non-serpentine than in serpentine chaparral (77 percent turnover vs. 55 percent; $P < 0.001$).

“Post-fire” change in diversity (i.e. burned minus unburned diversity) was positively related to “pre-fire” (unburned) cover on both soil types (serpentine: $r^2 = 0.382$, $P = 0.004$; non-serpentine: $r^2 = 0.149$, $P = 0.09$), while post-fire change in richness was positively related to soil total N in non-serpentine chaparral ($r^2 = 0.224$, $P = 0.04$), and to the soil Ca/Mg ratio (a reliable predictor of productivity in vegetation of ultramafic soils) in serpentine chaparral ($r^2 = 0.157$, $P = 0.08$). Mean time-to-last-fire was not significantly related to post-fire changes in richness or diversity on either soil type. Fire severity showed a negative relationship to post-fire change in diversity in nonserpentine chaparral ($r^2 = 0.397$, $P = 0.003$), and a unimodal relationship to change in diversity in serpentine chaparral ($r^2 = 0.367$, $P = 0.021$).

In burned plots, we found 11 species on each soil that are either documented as, or assumed to be, fire-dependent species (i.e., whose germination is stimulated by heat, charate, and etc.; Keeley 1991). These species contributed 40 percent of post-fire herb cover in non-serpentine chaparral, but only 4.4 percent in serpentine chaparral. Obligately seeding shrub species (species which do not regenerate by sprouting) contributed more than twice as much pre-fire cover in serpentine chaparral as in non-serpentine (57 percent vs. 26 percent).

In the 3 yr after fire, species richness in burned non-serpentine sites dropped rapidly in concert with a strong recovery of vegetative cover (and biomass). During the same period, post-fire growth in serpentine chaparral was much slower, and the decrease in species richness much less pronounced (fig. 2). Shrub seedling densities in 2000 were significantly higher in burned non-serpentine chaparral than in burned serpentine (122.8 m^{-2} vs. 62.7 m^{-2} $P < 0.001$). Seedling densities in burned sites dropped strongly in 2001 and 2002, but remained higher in non-serpentine than in serpentine chaparral ($P < 0.01$).

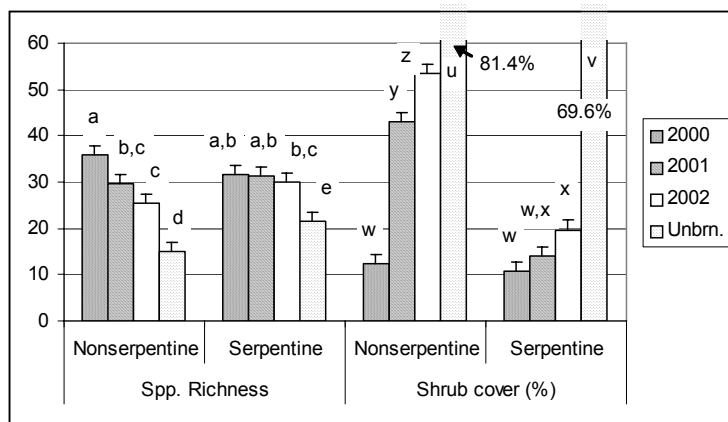


Figure 2—Means (+ standard error) of species richness and shrub cover in chaparral. Unbrn.=unburned controls in 2000. Bars with different letters are significantly different at $P < 0.05$.

Discussion

The two studies summarized in this paper are among the first to explicitly treat the fire ecology of serpentine vegetation. In both studies, serpentine vegetation was much less productive than non-serpentine vegetation, and—at least in chaparral-fires

were less severe and occurred less frequently on serpentine soils. Results of both studies showed strong effects of soil type on vegetation response to fire, but we were able to statistically link these effects to productivity only in chaparral. In general, the effects of fire appeared to be longer lasting in serpentine vegetation, with returns to pre-fire levels of richness and diversity, cover and biomass taking longer (in chaparral, much longer) than in similar vegetation types on non-serpentine soils.

In both chaparral and grassland, the richness of exotic species increased substantially after fire, and did so proportionately more on non-serpentine than on serpentine soils. These results are consistent with the prediction that invasibility should increase more in response to disturbance in productive than in unproductive environments (Grime 1979, Huston 1994). In grassland, although the effects of fire on species richness largely disappeared by the second year after fire, the number of exotics in non-serpentine grassland remained higher than before fire. At the same time, the post-fire increase in frequency of perennial grasses on serpentine soils was sustained for at least two years. Much evidence in the literature suggests that isolated fires, especially those occurring outside the growing season, have little long term impact on grassland ecosystems and are thus of little use in grassland restoration (Bond and van Wilgen 1996, Galley and Wilson 2001). However our results suggest that the thatch-removing effects of dormant-season fire can be at least ephemerally beneficial in low productivity grasslands already dominated by native perennials.

Lower fire severities and longer fire intervals in our serpentine chaparral sites are probably due primarily to the generally lower availability and continuity of woody fuels in these environments. However, dissimilarities in fire severity and time-to-last-fire were not the primary factors explaining differences in fire-induced changes in species diversity between the two soil types. Instead, it appears that the more open vegetation structure of serpentine chaparral allows for recruitment of opportunist/heliophilic herbs and shrubs in inter-fire years. Many of these same species occur in non-serpentine chaparral, but encounter opportunities to germinate and reproduce only after fire. In general, at the landscape-level, a disturbance-generated mosaic of early and late seral vegetation types seems less important to diversity maintenance in serpentine habitats than it is in most non-serpentine habitats.

Low fire frequencies in serpentine chaparral lead to the dominance of obligately seeding (non-sprouting) species in the shrub and tree layers (see also McCarten and Rogers 1991). These types of species require relatively long fire free intervals to reach reproductive maturity. Many rare “serpentine” species (and serotinous conifers like *Pinus attenuata* and *Cupressus spp.*) may be restricted to serpentine outcrops simply because of their intolerance to frequent and/or intense fire. Overall, it seems that although fire is inescapably an integral part of the ecology of any Mediterranean vegetation type, its importance to the functioning and persistence of low productivity habitats on substrates like serpentine is less pronounced than in habitats of higher productivity. Development of practical management strategies for vegetation of serpentine and other unusual soils demands that we take these fundamental ecological differences into account.

Acknowledgments

We thank the University of California Natural Reserve System, the Homestake Mining Company, and U.S. Bureau of Land Management for permission to conduct field sampling: Sydney Smith and three anonymous reviewers for constructive comments on the manuscript. Support was provided partially by NSF grant DEB-0072804 to SH.

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