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FIRE EFFECTS ON PLANT DIVERSITY IN SERPENTINE VS. SANDSTONE CHAPARRAL

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Abstract. Fire contributes to the maintenance of species diversity in many plant communities, but few studies have compared its impacts in similar communities that vary in such attributes as soils and productivity. We compared how a wildfire affected plant diversity in chaparral vegetation on serpentine and sandstone soils. We hypothesized that because biomass and cover are lower in serpentine chaparral, space and light are less limiting, and therefore postfire increases in plant species diversity would be lower than in sandstone chaparral. In 40 pairs of burned and unburned 250-m^2 plots, we measured changes in the plant community after a fire for three years. The diversity of native and exotic species increased more in response to fire in sandstone than serpentine chaparral, at both the local (plot) and regional (whole study) scales. In serpentine compared with sandstone chaparral, specialized fire-dependent species were less prevalent, mean fire severity was lower, mean time since last fire was longer, postfire shrub recruitment was lower, and regrowth of biomass was slower. Within each chaparral type, the responses of diversity to fire were positively correlated with prefire shrub cover and with a number of measures of soil fertility. Fire severity was negatively related to the postfire change in diversity in sandstone chaparral, and unimodally related to the postfire change in diversity in serpentine chaparral. Our results suggest that the effects of fire on less productive plant communities like serpentine chaparral may be less pronounced, although longer lasting, than the effects of fire on similar but more productive communities.

Key words: chaparral; California (USA); disturbance; fire; productivity; serpentine; species diversity; species richness.

INTRODUCTION

Disturbances such as fire, windstorms, floods, and grazing play a role in the maintenance of species diversity that has become well recognized in ecological theory (e.g., Pickett and White 1985, Petraitis et al. 1989, Huston 1994, Mackey and Currie 2000). By reducing or eliminating aboveground biomass, such disturbances make space, nutrients, and light available for species low in the competitive hierarchy. Species diversity at the local scale may be maximized by an intermediate frequency or severity of disturbance (Connell 1975, Grime 1979) or, alternatively, by a high variance in disturbance return intervals (Tozer and Bradstock 2002); regional diversity may depend upon the existence of a mosaic of areas in varying stages of recovery from disturbance (Pickett and White 1985, Forman and Godron 1986, Huston 1994). These ideas have been particularly well applied in the case of fire, where widespread attempts are being made to restore appropriate spatial and temporal regimes of burning to maintain plant diversity (Keeley and Scott 1995, Whelan 1995, Bond and Van Wilgen 1996).

Gaps exist, nonetheless, in our understanding of fire as an ecological process. Bond and van Wilgen (1996) note that fire may commonly consume 80% of aboveground net primary productivity, while herbivory seldom consumes more than 10%. Yet fire has been little integrated into theoretical concepts of population regulation and community structure in comparison with biotic interactions such as competition, herbivory, and predation. For example, there have been few attempts to predict the circumstances under which fire should be most significant as a community-structuring force, in contrast to the effort that has been devoted to making such predictions for herbivory and predation (e.g., Fretwell 1987, Oksanen 1988).

Productivity is one factor that may mediate the strength of the dependence of community structure upon disturbances such as fire. If the most significant effect of disturbance is to make space and light available, disturbance may enhance diversity more in productive plant communities where aboveground competition is more intense (Grime 1979, Huston 1994). There are both ecological and evolutionary components to this prediction. On ecological grounds, a disturbance of a given intensity will cause more change in space and light availability in dense vegetation than in open habitats where these resources are already more abundant. On evolutionary grounds, species are less likely

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to specialize on regenerating after disturbance in communities where space and light are less limiting (Grubb 1977, Bond and van Wilgen 1996).

The prediction that productivity should influence the effects of disturbance on diversity may apply even more to fire than other disturbances. A unique feature of fire as a disturbance is that, within a given vegetation type and climatic regime, its frequency and intensity increase with fuel availability and thus—at least broadly—with plant productivity (Pickett and White 1985, Whelan 1995, Bond and Van Wilgen 1996). Productivity may thus influence a wide range of fire-related phenomena. Assuming a constant rate of ignition, faster accumulation of biomass may lead to shorter intervals between fire, and slower accumulation to longer intervals. Modulations in fire frequency may have important effects on, among other things, postfire recruitment. For example, excessively long fire-free intervals in chaparral may lead to seed pool attrition and reduced postfire recruitment (Zammit and Zedler 1988). Variations in biomass accumulation may also alter fire intensities, which directly impact germination and survival rates in the dormant seed bank. Across its full range, fire intensity may be unimodally related to postfire recruitment, where initial increases in heat release induce progressively more germination of refractory seeds, but where the highest intensities heat-kill seeds (Moreno and Oechel 1991, Rice 1993, Odion and Davis 2000).

In this study we compared the effects of fire on plant diversity in chaparral vegetation on more productive sandstone and less productive serpentine soils. The fire ecology of nonserpentine chaparral in California has been extensively studied (see Hanes 1988 and Keeley 2000 and references therein). Fire in these shrublands is intense and nearly always stand replacing. Between fires, chaparral stands typically support a closed shrub canopy and a species-poor herb layer. Shrubs either survive fire by resprouting or are cued by fire to reproduce by seed; a few species, including the widespread dominant *Adenostoma fasciculatum* (chamise), use both strategies. Dormant seeds of chaparral shrubs and herbs may germinate in response to smoke, ash, heat, or increased light and solar warmth or some combination of these factors, resulting in varying degrees of dependence on fire for reproduction. Large numbers of herbs appear in the first several years after a fire; these include truly fire-dependent species that germinate in response to smoke, ash, or high heat, and many heliophilic species that increase in abundance after fire but may also recruit in other canopy openings (Zammit and Zedler 1988).

The fire ecology of plant communities on serpentine soils, especially the degree to which species diversity depends on or is affected by fire, has been almost completely uninvestigated. Serpentine (ultramafic) rocks are high in magnesium and iron, and are found in many parts of the world at the former margins of crustal plates. Soils derived from these rocks are typically shallow, rocky, and nutrient deficient; levels of Ca, N, and P are low, while levels of Mg and various metals are high. Vegetation on serpentine soils is typically slow growing, stunted, and xeromorphic (Whittaker 1954, Proctor and Woodell 1975, Kruckeberg 1984). Like other unusual soils (e.g., those formed on limestone, gabbro, or gypsum), serpentine soils often support a distinctive flora. In our study region in northwestern California, the dominant vegetation type is mixed serpentine chaparral; it is relatively diverse, with roughly 30 woody species and around 200 species of herbs, including at least 30 that are restricted (endemic) to serpentine (Kruckeberg 1984, Callizo 1992, Harrison 1999).

The extensive literature on the Californian serpentine flora does not document any species that are both restricted to this soil and dependent on fire for reproduction (e.g., Kruckeberg 1984). Whittaker (1960) concluded that, in the serpentine vegetation he examined, fire did not greatly alter woody species composition but only reduced stem densities. Parker (1990) observed that species growing on serpentine soils may suffer greater mortality and poorer recruitment after fire than conspecifics on adjacent sandstone-derived soils. McCarten and Rogers (1991) suggested that responses of serpentine chaparral to fire could not be reliably predicted from chaparral fire ecology in general.

We compared fire-induced changes in plant diversity in chaparral on adjacent serpentine and sandstone soils following a wildfire in autumn 1999, and monitored these changes for three growing seasons (2000–2002). Our general hypothesis was that the effects of fire on plant diversity would be weaker in the less productive serpentine vegetation than in the more productive sandstone vegetation. Specifically, we hypothesized that serpentine chaparral compared with nonserpentine chaparral would show: (1) lower soil fertility and plant productivity; (2) lower mean fire severity, higher spatial heterogeneity in fire severity, and longer mean time since last fire; (3) less postfire increase in plant species diversity, both locally (within plots) and regionally (in the whole study area); and (4) slower recovery to prefire levels of species diversity and woody cover.

METHODS

Study site

Our study site was the 3100-ha Donald and Sylvia McLaughlin University of California Natural Reserve, plus surrounding areas of public land administered by the U.S. Bureau of Land Management. An arson fire on 16, October 1999, burned 16 000 ha of this region, which lies at the junction of Napa, Lake, and Yolo Counties (38°51′ N, 123°30′ W), California, USA. Elevations in the area range from 370 to 945 m above sea level, and the climate is mediterranean. Serpentine chaparral occurs on shallow rocky soils underlain by serpentine and serpentinized peridotite. Dominant woody species are *Quercus durata*, *Arctostaphylos viscida*, *Cupressus macnabiana*, *Pinus sabiniana*, and *Adenostoma fasciculatum* (chamise). The understory in serpentine chaparral includes many species of geophytes, a high diversity of often endemic forbs (e.g., in the genera *Streptanthus* and *Hesperolinon*), and a large number of native bunchgrass species. Nonserpentine chaparral occurs largely on sandstone substrates, and is dominated by chamise on xeric exposures, and a mixture of shrub species (e.g., chamise, *Quercus berberidifolia*, *Ceanothus cuneatus*, *Heteromeles arbutifolia*, *Toxicodendron diversilobum*) in more mesic situations. In both chamise-dominated and mixed stands, canopy cover often exceeds 90%; understory herbs are sparse, and include *Zigadenus fremontii*, *Chlorogalum pomeridianum*, *Pedicularis densiflora*, and *Galium* spp. In mature serpentine and sandstone chaparral, there are very few exotic species (see University of California–Davis, Natural Reserve System 2000 for further study site information).

Sampling methods

We chose 40 pairs of burned and unburned sites, 20 in serpentine chaparral and 20 in sandstone chaparral. To identify prospective sites, we used 1:12 000 and 1:18 000 scale aerial photos taken in 1982, 1996, and on 31 October 1999 (15 days after the fire), as well as maps of geology, soil, and vegetation. We located pairs of sites where adjacent stands of burned and unburned vegetation occurred on slopes of approximately constant inclination and aspect. We examined prospective sites to ensure that they were not anthropogenically disturbed, and that burned and unburned members of each pair were characterized by the same soil, vegetation, and successional stage. We consulted the State of California fire history coverage (available online)[4] to further ensure that time since last fire was equal for each paired set of burned and unburned sites. We chose roughly equal numbers of north, south, east, and west-facing sites, ranging from 415 to 820 m in elevation. To test our assumption that burned and unburned sites did not differ significantly independently of the fire, we measured a suite of environmental covariates including slope, aspect, elevation, and soil chemistry.

At each of the 80 sites, we established one 50 × 5-m belt transect $\geq$5 m from the edge of the burn. We visited each site four times from late April to early July 2000 to sample both early and late flowering species. We repeated these visits in the springs of 2001 and 2002. At each site we searched the entire 250-m^2 transect to measure richness of all native and exotic vascular plant species. We measured cover of shrub species by line intercept along the 50-m center line. We sampled five 1-m^2 quadrats at 10-m intervals along the transect center line, measuring: percentage cover of all native and exotic species; numbers and heights of shrub seedlings; percentage cover of rock, bare soil, and litter; litter depth; and slope and aspect.

From the center of each quadrat, we collected 50 g of soil at 5–10 cm depth and combined these to create one sample for each site. Soil samples were air dried, ground, and analyzed by A & L Western Agricultural Laboratories, Modesto, California, and the Soil Analytic Laboratory of the Division of Agriculture and Natural Resources, University of California–Davis, for cation exchange capacity, organic matter, pH, exchangeable K, Mg, Ca and Na, total N, and Bray P.

We estimated fire severity in burned quadrats by measuring the stem diameter (1 cm from the stem terminus) of four stems from a randomly chosen individual of *Adenostoma fasciculatum* (and in a few cases *Quercus durata*) rooted in or adjacent to the quadrat (Pérez and Moreno 1998). At the belt-transect scale (250 m^2) we augmented these data by measuring stem termini from ten additional randomly chosen chamise individuals. We estimated shrub mortality by recording the fire response (killed or survived) of $>$25 shrubs whose canopy remnants intersected the transect center line. We identified these individuals to species and measured the diameter of their largest stem at the root collar. We estimated time since last fire by counting growth rings from 3–5 fire-killed individuals of nonsprouting species of *Arctostaphylos*, *Ceanothus*, and *Cupressus* within each burned site. We divided the mean radius of individuals of *A. fasciculatum* and *Q. durata* sampled along the transect center line by time since last burn to obtain a measure of annual growth.

We repeated the measurements of plant species richness and cover in 2001 (burned transects only) and 2002 (burned and unburned transects). In each year we also assessed regrowth of the vegetation by measuring the heights of 10–30 seedlings and resprouts of the most common shrub species within each burned transect. We sampled biomass by removing all of the previous year's growth from four 50 × 50 cm quadrats placed randomly within each burned transect. Biomass was split into herbaceous and woody components, dried, and weighed.

Analyses

We used species cover values to calculate the complement of Simpson's index for each quadrat, a measure of diversity that includes evenness as well as richness. Using pairs of transects as replicates, we calculated the ''postfire change in species richness'' by subtracting the unburned site value (''prefire'') from the burned site value (''postfire''), and likewise calculated the ''postfire change in species composition'' by using the number of unshared species divided by the total number of species for each pair of burned and unburned sites (i.e., 1-J, the complement of Jaccard's coefficient of similarity). We converted slope and aspect to a single

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[4] URL: ⟨frap.cdf.ca.gov⟩

TABLE 1. Comparison of environmental covariates and soil and vegetation characteristics between serpentine and sandstone chaparral in 2000.

Variable	Unburned transects			Burned transects		
	Sandstone	Serpentine	*P*	Sandstone	Serpentine	*P*
Annual shrub growth (mm)†	0.55 ± 0.20	0.26 ± 0.07	<0.0005			
Shrub cover (%)	81.4 ± 7.3	69.6 ± 11	<0.0001			
Heterogeneity in shrub cover (%)‡	15.5 ± 7.8	36.8 ± 22	<0.001			
Litter cover (%)	85.9 ± 9.4	69.2 ± 15	<0.0001			
Heterogeneity in litter cover (%)‡	13.0 ± 13	39.5 ± 26	<0.001			
Elevation (m)	647 ± 139	577 ± 83	NS	652 ± 140	577 ± 85	NS
Radiation (% of max. input)	76.7 ± 14	78.7 ± 12	NS	77.6 ± 12	78.9 ± 12	NS
Rock cover (%)	9.50 ± 9	26.8 ± 15	<0.0005	11.9 ± 8.8	40.4 ± 18	<0.0001
pH	6.05 ± 0.3	6.50 ± 0.3	<0.0005	6.18 ± 0.2	6.59 ± 0.4	<0.0005
Organic matter (%)	4.35 ± 0.9	5.44 ± 1.5	<0.01	4.27 ± 1.0	4.89 ± 1.5	NS
Soil total N (%)	0.17 ± 0.05	0.19 ± 0.04	NS	0.17 ± 0.04	0.17 ± 0.04	NS
Soil P (Bray) (ppm)§	6.70 ± 2.5	3.60 ± 1.9	<0.0005	7.4 ± 2.8	3.15 ± 1.6	<0.0001
Cation exchange cap. (meq/100 g)	22.3 ± 5.5	25.3 ± 4.3	NS	21.5 ± 4.2	23.4 ± 6.2	NS
Soil K (ppm)§	229 ± 44	113 ± 31	<0.0001	227 ± 78	144 ± 95	<0.005
Soil Ca (ppm)§	2152 ± 403	768 ± 249	<0.0001	2295 ± 335	895 ± 388	<0.0001
Soil Mg (ppm)§	910 ± 440	2342 ± 557	<0.0001	802 ± 370	2058 ± 733	<0.0001

Notes: Values given are means ± 1 SD. For statistics, all percentage data were arcsine-square-root transformed; soil P was ln-transformed. Bonferroni-adjusted *P* values are presented from MANOVA for effects of soil type on listed variables. Unburned transects: Wilks' lambda = 0.050, df = 1, 38, $P < 0.0001$; burned transects: Wilks' lambda = 0.092, df = 1, 38, $P < 0.0001$.

† Mean annual increment in shrub diameter for *Adenostoma fasciculatum* and *Quercus durata*.

‡ Calculated as the coefficient of variation for shrub and litter cover between the five 1-m^2 quadrats sampled along each transect.

§ For soil P, K, Ca, and Mg, ''ppm'' refers to parts nutrient per million parts soil by mass.

measure: percentage of maximum potential radiation (hereafter ''radiation input'').

All variables collected at the 1-m^2 scale were averaged to give a value for the whole 250 m^2 site. For several variables (e.g., shrub and litter cover and fire severity), a value of heterogeneity was calculated using the coefficient of variation for the five quadrats within a transect. All data were tested for univariate and bivariate normality. Percentage data (including Simpson diversity) were arcsine-square-root transformed; other transformations were applied where necessary. Collinearity diagnostics were run for multiple regressions. Statistical analyses were carried out in SPSS 9.0 (SPSS 1999).

We used multivariate analysis of variance (MANOVA) to test (1) whether burned and unburned sites differed overall with respect to physical environmental covariates (radiation input, elevation, and soil variables); (2) whether the two soils differed with respect to the above variables plus shrub and litter cover, heterogeneity in cover, shrub growth, fire severity, heterogeneity in fire severity, and time since last fire; and (3) how species richness, species diversity, exotic species richness, and seedling densities were affected by soil, fire, and the interaction between soil and fire.

With burned sites as replicates ($N = 40$), we used regression analysis to test the relationship between postfire change in richness, diversity, composition, and a suite of predictor variables, including fire severity, time since last fire, and a number of variables related to productivity and soil fertility. We carried out these analyses for all sites combined, and for each soil type individually. With burned sites as replicates ($N = 40$), we used analyses of variance to test for differences between serpentine and sandstone in the rate of postfire recovery, measured as herbaceous and woody biomass, species richness, and seedling densities.

RESULTS

Site attributes independent of fire

Sandstone and serpentine sites did not differ significantly in mean radiation input or elevation. Prefire shrub growth, shrub cover, and litter cover were all significantly higher in sandstone than serpentine chaparral, while spatial heterogeneity in shrub and litter cover within sites was significantly higher on serpentine. Sandstone soils showed higher levels of P, Ca, and K than serpentine soils, while soil pH and Mg were lower; soil total N and cation exchange capacity (CEC) did not differ significantly between soils (Table 1).

Burned and unburned sites within each soil type did not differ with respect to any of the environmental covariates we measured (see Table 1 for means), except for rock cover on serpentine ($P = 0.01$), which is an effect of removal of litter by fire.

Fire severity and time since last fire

Mean and maximum fire severity were greater in sandstone than in serpentine sites, while spatial heterogeneity in mean fire severity was higher in serpentine than sandstone sites. Mean time since the last stand-replacing fire was greater on serpentine (Table 2).

TABLE 2. Comparison of measures of fire severity and frequency between serpentine and sandstone chaparral.

	Sandstone	Serpentine	*t*	df	*P*
Mean fire severity (mm)†	5.10 ± 1.9	3.30 ± 1.3	3.9	38	<0.005
Heterogeneity in mean fire sev (%)‡	34.8 ± 15	50.4 ± 20	2.79	38	<0.05
Maximum fire severity (mm)†	5.77 ± 2.1	3.76 ± 1.5	3.81	38	<0.005
Heterogeneity in max. fire sev (%)‡	39.9 ± 21	51.2 ± 20	1.76	38	NS
Mean time to last burn (yr)	18.6 ± 3.1	73.7 ± 39	6.26	38	<0.0001

Notes: Values given are means ± 1 SD. For statistics, mean and maximum fire severity were ln-transformed, and heterogeneity measures were arcsine-square-root transformed. *P* values for *t* tests are based on Bonferroni adjustments.

† Fire severity determined by measurement of carbonized stem termini.

‡ Calculated as the coefficient of variation for fire severity between the five 1-m^2 quadrats sampled along each transect.

Postfire changes in diversity and composition at the local scale

In two-factor MANOVA, total species richness, species diversity, and exotic species richness were all significantly higher on burned than unburned sites in the year following the fire (all $P < 0.0001$; Wilks' lambda $= 0.124$). Overall species richness did not differ between soil types ($P = 0.578$), but species diversity was higher on serpentine soils ($P < 0.0001$) and exotic richness was higher on sandstone soils ($P = 0.014$; Wilks' lambda $= 0.695$, $P < 0.0001$). There was a significant interaction between soil and fire (Wilks' lambda $= 0.763$, $P < 0.0001$), such that the positive effects of fire on all three of these response variables were significantly greater in sandstone than serpentine chaparral (Fig. 1).

Within individual soils, postfire changes in diversity were positively associated with prefire (i.e., unburned) shrub cover (Fig. 2A). Postfire change in richness was positively associated with total soil N on sandstone soils only ($R^2 = 0.224$, $P = 0.04$); change in richness was positively associated with Ca:Mg ratio for serpentine soil only ($R^2 = 0.157$, $P = 0.08$); and change in composition was positively associated with Ca:Mg for serpentine only ($R^2 = 0.379$, $P = 0.004$). In sandstone chaparral, the postfire change in diversity was negatively related to mean fire severity, while in serpentine chaparral the relationship was unimodal (Fig. 2B). The postfire change in diversity in sandstone chaparral showed a tendency to decrease with time since last burn, but this relationship was not statistically significant (Fig. 2C). Postfire shrub seedling density was positively related to fire severity in serpentine chaparral ($R^2 = 0.301$, $P = 0.01$), and (marginally) negatively related to severity in sandstone chaparral ($R^2 = 0.148$, $P = 0.09$).

The greater postfire increase in richness (per 250-m^2 plot) in sandstone chaparral was due primarily to a stronger response in annual forbs. In 2000, sites in sandstone chaparral showed a mean postfire increase of 14.8 ± 7.6 (mean ± 1 SD) annual forb species, while serpentine sites showed an increase of 5.3 ± 4.9 ($P < 0.0001$). Although other lifeforms differed in their importance on the two soil types (on average, perennial forbs and perennial grasses were significantly more speciose in serpentine sites), increases in richness due to fire for these other lifeforms did not differ in magnitude between sandstone and serpentine sites.

Postfire changes in diversity and composition at the regional scale

In the year after fire (2000), we found 191 total species, including 158 natives and 33 exotics. The number of native species was lower in sandstone chaparral (unburned 55, burned 87) than in serpentine chaparral (unburned 80, burned 106), but in sandstone chaparral it increased relatively more in response to fire. On both soils, the regional number of exotic species roughly tripled after fire (serpentine: unburned 7, burned 22; sandstone: unburned 9, burned 30). Postfire changes in species composition at the regional level, as measured by the dissimilarity statistic (1-J), were greater for sandstone (56%) than serpentine (44%). Fire had a homogenizing effect between soils; the floras of serpentine and sandstone chaparral overlapped by 25% in unburned sites, while in burned areas this overlap increased to 66%.

By lifeform, the largest fire-mediated changes in regional species richness for both soil types occurred in the annual and perennial forbs. A 218% increase (from 17 to 54) occurred in the number of annual forbs in sandstone chaparral, dwarfing the 96% increase (from 27 to 53) in serpentine chaparral. Perennial forb species were much more numerous in serpentine chaparral both before (30 vs. 17) and after fire (40 vs. 25), but the magnitude of fire-caused change was greater in sandstone chaparral (47% increase vs. 33% increase on serpentine). Overall numbers of annual grass (serpentine vs. sandstone: 11 vs. 13 postfire, 6 vs. 7 prefire) and shrub species were very similar on the two soil types, as were the proportions by which richness changed postfire (annual grasses: ~45% on both soil types; shrubs: serpentine 0% change, sandstone 9% decrease).

Fire-dependent species

The year after fire, fifty-nine native forbs were either found only on burned sites, or showed >500× greater

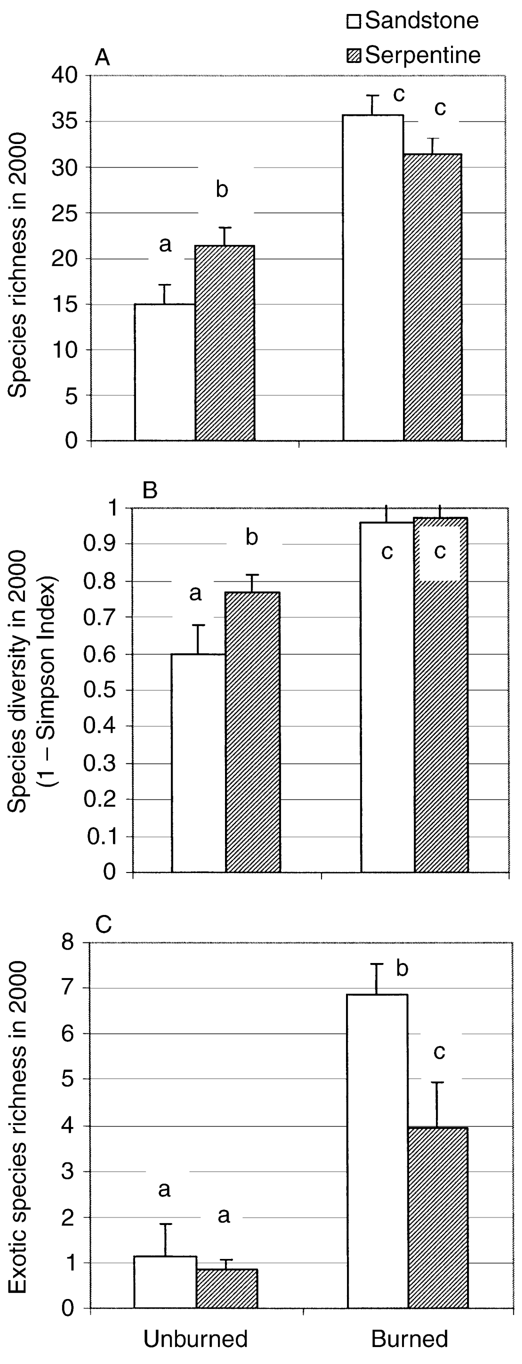

FIG. 1. Means (+1 SE) of (A) total species richness, (B) species diversity, and (C) exotic species richness for burned and unburned sites in sandstone and serpentine chaparral. Bars with different letters are significantly different at $P < 0.05$.

mean cover in burned than unburned sites. Of these, 50 were found in sandstone chaparral and 42 in serpentine chaparral, with 55% shared between soils. Ten of these are documented in the literature as being fire-dependent species with refractory seeds whose germination is stimulated by exposure to high heat, chemicals from charred wood, or both; four others are probably fire dependent, based on studies of congeners (e.g., Keeley 1991). Of these 14 species, 11 were found on each soil, with 8 (57%) found on both soils. However, these 14 species constituted 40% of postfire herb cover on sandstone, but only 4.4% of postfire herb cover on serpentine. The apparently fire-dependent species found only on serpentine were *Calystegia collina* ssp. *collina*, *Malacothrix floccifera*, and *Phacelia corymbosa*.

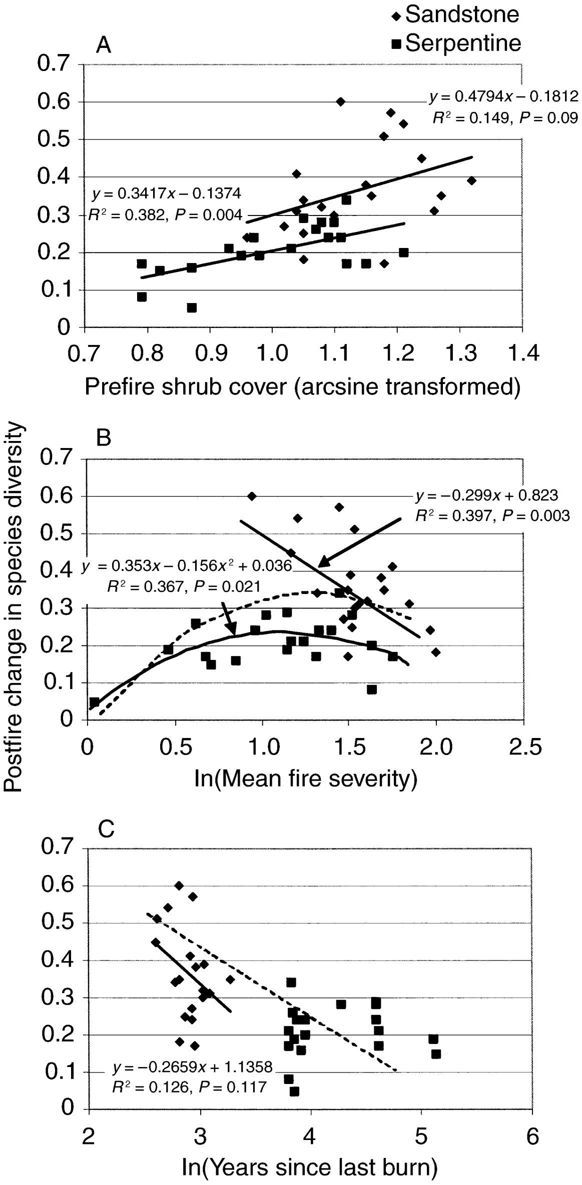

FIG. 2. Postfire changes in species diversity in the first year after fire, for each soil type, vs. (A) prefire shrub cover (arcsine transformed), (B) mean fire severity (ln transformed), and (C) time since last fire (ln transformed). The dotted regression line in panels (B) and (C) represents the overall relationship, with soil types pooled.

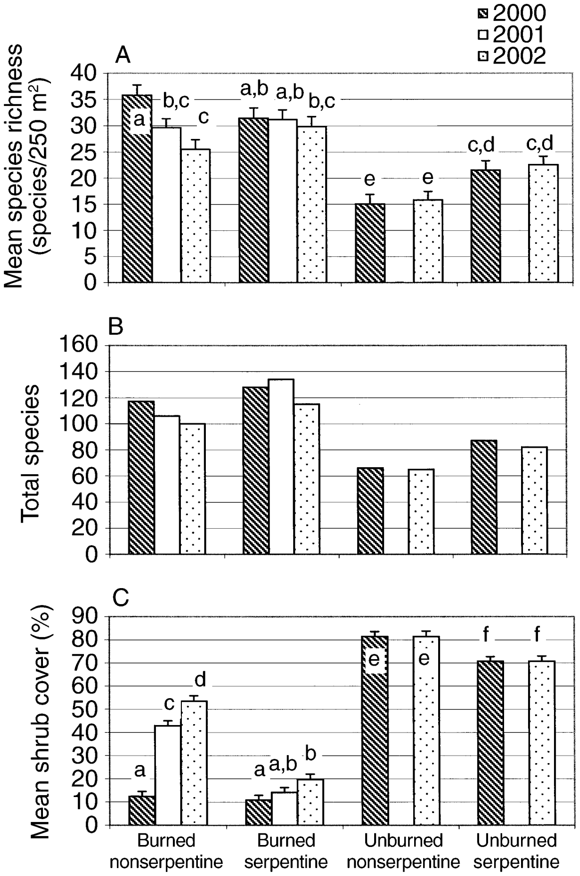

Fig. 3. Postfire recovery (+1 SE) of (A) local species richness, (B) regional species richness, and (C) woody cover on burned sites during 2000–2002, with values from unburned sites in 2000 and 2002 for comparison. Bars with different letters are significantly different at $P < 0.05$.

Postfire recovery

Species richness in burned sandstone sites dropped rapidly from 2000 to 2002 at both the local and regional scales. On serpentine, in contrast, species richness in burned sites dropped slightly at the regional scale and was virtually unchanged at the local scale (Fig. 3A, B). The opposite trend was seen in shrub cover, which increased by more than twice as much on sandstone as on serpentine during 2000–2002 (Fig. 3C). Biomass and height of the vegetation on burned sites, which we measured in 2001 and 2002, were likewise substantially greater on sandstone than serpentine (Fig. 4). Shrub seedling densities in 2000 were significantly higher on sandstone than serpentine, as well as on burned than unburned sites (two-factor ANOVA, $P < 0.0001$). Seedling densities in burned sites dropped strongly in 2001 and 2002, but remained higher in sandstone than in serpentine chaparral (Fig. 5).

Of 24 shrub species found in sandstone chaparral, 15 were either facultative or obligate resprouters and 9 were obligate seeding species (i.e., species which are generally killed by fire and do not resprout). Of 21 species found in serpentine chaparral, 12 were resprouters and 9 were obligate seeders. The contribution of postfire seeders to total prefire shrub cover was more than twice as high in serpentine as in sandstone chaparral (57 vs. 26%). Fire-caused mortality in resprouting species was generally low: 0% (0/56) in *Heteromeles arbutifolia*, 2% (2/99) in *Quercus durata*, and 3.4% (1/29) in *Garrya congdonii*. Mortality in the facultative species *Adenostoma fasciculatum*, which reproduces by both seed and resprouting after fire, was higher on serpentine soils than on sandstone (25.7 vs. 19.1% mortality).

Discussion

In summary, soil fertility, plant cover, biomass, and fire severity were all higher on sandstone than serpentine soil, while time since last fire and heterogeneity in fire severity were higher on serpentine. Fire stimulated increases in richness and diversity of native and exotic species on both soils at the local and regional scales. However, as predicted, these effects were sub-

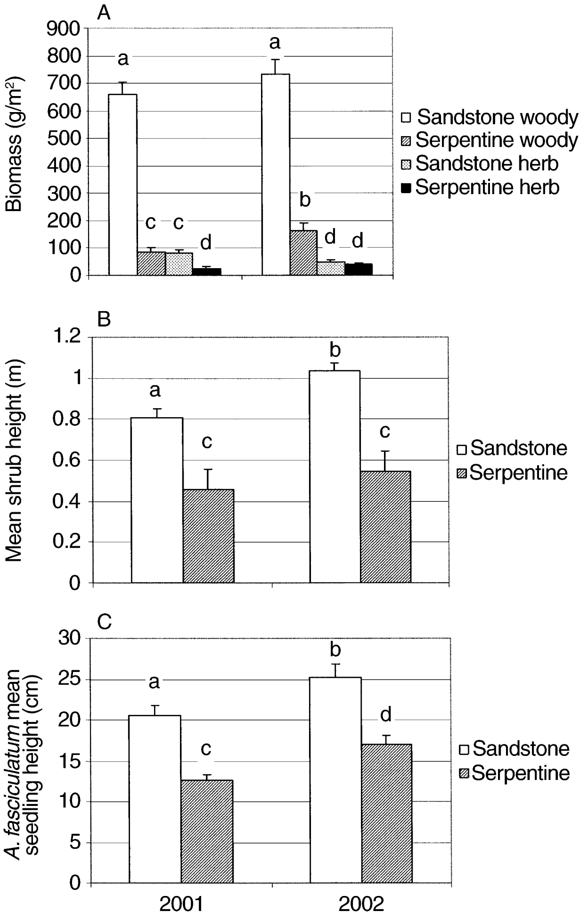

Fig. 4. Postfire values (+1 SE) of (A) woody and herbaceous biomass, (B) height of resprouting shrubs, and (C) height of chamise seedlings, in 2001 and 2002 on burned sites only. Bars with different letters are significantly different at $P < 0.001$.

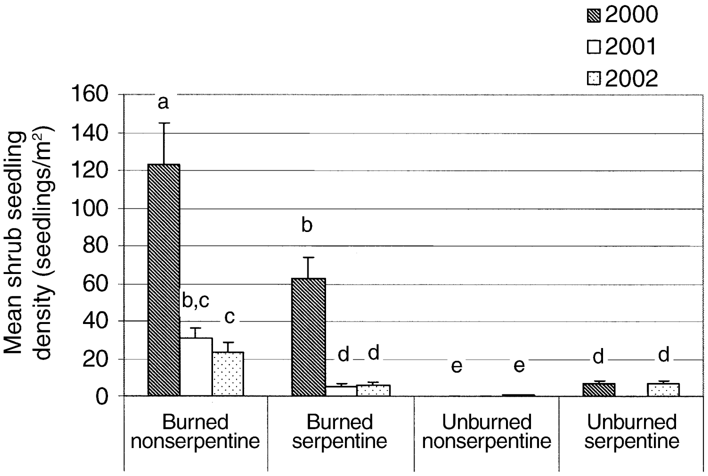

FIG. 5. Shrub seedling densities (+1 SE) on burned sites during 2000–2002, with values from unburned sites in 2000 and 2002 for comparison. Bars with different letters are significantly different at $P < 0.05$.

stantially weaker on serpentine soils, regardless of which measure of diversity was used. While serpentine chaparral was richer in native species at the local scale before the fire, sandstone chaparral attained nearly equal native species richness as well as higher exotic species richness in the first year after fire. At the scale of the study region, fire likewise increased species richness more in sandstone than serpentine chaparral (58 vs. 33%), although serpentine chaparral maintained substantially higher regional species richness than sandstone chaparral even after the fire.

One possible explanation for the difference in fire response between the two vegetation types is that serpentine and sandstone chaparral support different floras, with the number of fire-responsive species being much larger in the sandstone flora. While such floristic differences undoubtedly contributed to our results (in particular, the much higher number of perennial forb species in the serpentine flora), there is evidence to suggest that they are not the main factor involved. We found that fire increased the overlap between the floras of sandstone and serpentine chaparral from 25 to 66% after the fire, demonstrating that species that responded to fire (largely annual forbs) tended disproportionately to be species that occur on both soils. Corroborating this trend, the species that we identified as showing particularly strong recruitment responses to fire showed a relatively high level of overlap between the soils (57%).

Still another possibility is that for a given size of seed bank, fire is less likely to lead to successful postfire germination on serpentine: for example, the release of refractory seeds from dormancy might be less complete because of the lower fire intensities in serpentine chaparral. However, although we found a significant positive relationship between fire severity and shrub seedling density in serpentine chaparral, we did not find such a relationship for richness or diversity. Further possible explanations include differences in seed predation and seedling survival between the two chaparral types. Full evaluation of such mechanisms will require experimental studies in which the seed pool is measured and manipulated.

We believe the best general explanation for the difference in fire response between serpentine and sandstone chaparral is that the lower fertility of serpentine soil leads to more open vegetation, and thus to a lesser release from aboveground competition following fire. This is corroborated by several lines of evidence. First, serpentine chaparral supported more species than sandstone chaparral before the fire, but sandstone chaparral reached a virtually identical level of diversity immediately after the fire. This appears to be because many of the species responding positively to fire (mostly annual forbs) were present sparsely as adults in serpentine chaparral before the fire, but were absent from sandstone chaparral until it burned. Second, shrub species whose seeds required fire to germinate in sandstone chaparral (e.g., *Ceanothus* spp.) were able to manage low but constant levels of recruitment in the more insolated understory of serpentine stands. Third, in the three years after fire, sandstone chaparral reverted rapidly toward its prefire level of diversity in concert with the rapid regrowth of biomass. In the same period, serpentine chaparral recovered very slowly in biomass and retained its elevated diversity. Fourth, within each soil, postfire increases in diversity were positively correlated with prefire cover and with other measures of fertility (N on sandstone and Ca:Mg ratio on serpentine). Finally, studies in chaparral-like heathland in Australia (e.g., Specht and Specht 1989, Bond and Ladd 2001, Tozer and Bradstock 2002) have come to similar conclusions based on findings which include remarkably similar interactions between species diversity and overstory cover and growth rates.

Whichever of these nonexclusive explanations are true, our results are in good agreement with the general idea that the effects of disturbance on diversity should depend on productivity (Grime 1979, Huston 1994, Pickett and White 1985, Proulx and Mazumder 1998).

In fact, our results are strikingly consistent with the prediction that the regional diversities of communities characterized by low productivity and low frequency of disturbance should differ little from the regional diversities of more productive communities that are subject to more frequent disturbance (Huston 1994). Our results for exotic species are consistent with the prediction that the invasibility of productive environments should increase more in response to disturbance than the invasibility of less productive environments (Grime 1979, Huston 1994, Burke and Grime 1996).

Although the plant community changes caused by fire were much smaller in serpentine than sandstone chaparral, they appeared to be longer lasting. Postfire recovery of the woody vegetation on serpentine was extremely slow, with less than one-fourth the biomass accumulation shown by sandstone chaparral in the three years of our study. Paralleling this, plant species richness at the per-plot scale barely decreased on serpentine over the three years, in contrast to its rapid drop on sandstone. Extrapolating linearly from the trends seen in 2000–2002 (Fig. 2), sandstone chaparral might be expected to reattain its prefire values of species richness and woody cover in perhaps 4–5 years, while serpentine chaparral might take 12–15 years for a comparable recovery.

Our results have important implications for understanding the fire ecology of California serpentine chaparral. Fire is clearly important in this vegetation type, and we found a few herbs that appeared to be restricted to serpentine and dependent on fire for recruitment. Almost no seedlings of *Calystegia collina*, a long-lived clonal herb, were observed during a five-year study when no fires occurred (Wolf and Harrison 2001); in this study we found as many as 80 seedlings/m^2 in burned areas. However, our results suggest that fire frequencies may tend to be lower in serpentine vegetation. Further evidence for this is the greater prevalence of woody species that regenerate only by seed in serpentine than sandstone chaparral; similar patterns have been noted elsewhere in California (e.g., Vogl et al. 1988, McCarten and Rogers 1991, Jimerson et al. 1995). Most or all *Arctostaphylos* and *Ceanothus* species occurring on serpentine are obligate postfire seeders (McCarten and Rogers 1991), while about 30% of their congeners on more fertile soils are postfire sprouters. Serotinous conifers such as *Pinus attenuata* and *Cupressus* spp. are especially common on serpentine and other low-productivity soils (Vogl et al. 1988). These patterns suggest that fire-return intervals on serpentine may tend to be long but relatively predictable, conditions that are considered to favor seeders over sprouters in ecological and evolutionary time (Christensen 1985, Bellingham and Sparrow 2000).

Our results may have general implications for fire ecology and management in the wide range of harsh soils, including gabbro, limestone, gypsum, shale barrens, and relictual sand deposits as well as serpentine, that support unique native floras throughout the world (Anderson et al. 2000, Kruckeberg 2002). In some of these cases, such as the serpentine barrens of the eastern U.S., periodic fire may be essential to maintaining the characteristic open vegetation with its associated rare species (Tyndall and Hull 1999). But in others, such as the endemic-rich serpentines of Cuba, the vegetation may be so poorly adapted to fire that even a single fire can cause the loss of many species (Matos Mederos and Torres Bilbao 2000). Our results caution against assuming that fire plays the same role or produces the same resilient responses on the nutrient-poor soils that harbor edaphic endemic species as it does in the vegetation of more typical soils.

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