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Patch to landscape patterns in post fire recruitment of a serotinous conifer

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Abstract

Obligate seeding species are highly specialized to fire disturbance and many conifers such as cypress, which are adapted to high intensity stand-replacing fires, have canopy seed banks stored in serotinous cones. Resilience of these trees to fire disturbance is a function of disturbance frequency and one focus of this study was to determine the effect of patch age on postfire recruitment. A second focus was to determine the extent to which fire induced a landscape level change in the location of the forest boundary. Prior to a fire in 1994, a large *Cupressus sargentii* forest was a mosaic landscape of different aged patches of nearly pure cypress bordered by chaparral. Patches less than 60 years of age were relatively dense with roughly one tree every 1–2 m^2 but older patches had thinned to one tree every 3–15 m^2. Older trees had substantially greater canopy cone crops but the stand level seed bank size was not significantly correlated with stand age. Fire-dependent obligate seeding species are sensitive to fire return interval because of potential changes in the size of seed banks – facing both a potential 'immaturity risk' and a 'senescence risk'. At our site, *C. sargentii* regeneration was substantial in stands as young as 20 years, suggesting that fire return interval would need to be shorter than this to pose any significant risk. Reduced seedling recruitment in stands nearly 100 years of age may indicate risk from senescence is greater, however, even the lowest density seedling recruitment was many times greater than the density of mature forests – thus this cypress would appear to be resilient to a wide range of fire return intervals. Changes in landscape patterning of forest and chaparral are unlikely except after fire. Factors that inhibit tree establishment within the shrubland, as well as factors that affect shrub establishment within the forest border likely affect the 'permeability' of this ecotone. After the 1994 fire this boundary appeared to be stable in that cypress recruited best within the shadow of burned canopies and cypress were weak invaders of adjacent shrublands.

Introduction

Disturbance is widely viewed as an important factor determining the structure of many plant communities. A major disturbance factor is fire and it has played an important role in the life history evolution of many species (Keeley 1981; Trabaud 1987; Bond & Wilgen 1996). A substantial number of plants exploit postfire conditions for recruitment of offspring. This is accomplished by a dormant soil seedbank that is triggered to germinate by fire (Keeley 1991; 1995) or by a canopy seed bank of 'closed cones' that are triggered to disperse seeds after a wildfire. This latter adaptation is known as serotiny and is widespread in angiosperm genera in South African fynbos and Australian heath (Lamont et al. 1991), but in the Northern Hemisphere it is restricted to the coniferous genera *Pinus* (Vogel et al. 1977; Keeley & Zedler 1998) and *Cupressus* (Vogel et al. 1977; Zedler 1977; Schild 1986; Lev-Yadon 1995).

Most serotinous pines and cypress lack the ability to vegetatively resprout after fire and thus are obligate seeders. Such fire-dependency carries with it risks of localized extinction if fire-return intervals are too short or too long (Zedler 1995). While there is relatively little evidence of long fire-return intervals threatening a species, there are well-documented examples that short return intervals may threaten many obligate seeding species (Zedler et al. 1982; Haidinger & Keeley 1993; Keeley et al. 1999).

The dependency of obligate seeding species on successful postfire seedling recruitment makes such sites potentially vulnerable to invasion by other vegetation and thus landscape patterns may change after a single fire. Particularly critical are the recruitment patterns at the ecotone. Although stochastic effects, such as unpredictable weather patterns, may affect postfire recovery, prefire stand conditions likely play an important deterministic role. Prominent here is the level of the canopy seed bank. Another important factor is the demographic pattern, which affects fuel arrangement and subsequent fire intensity (Davis et al. 1989) and ash deposition (Moreno & Oechel 1991). Prefire stand conditions may also affect the heterogeneity of burn severity creating a wide range of local (Zammit & Zedler 1988; Rice 1993; Atkins and Hobbs 1995) and landscape effects (Turner & Romme 1994). Although there is no doubt that the prefire vegetation structure affects the postfire recovery process, limited effort has been invested to document it (Davis et al. 1989; St-Pierre et al. 1991; Izhaki et al. 1992; Ne'eman 1997; Ne'eman et al. 1992; Rice 1993; Filion & Morin 1996), and to understand its mechanism and ecological significance (Moreno & Oechel 1991; Ne'eman & Izhaki 1998).

Cupressus (cypress) is a widespread genus in the Northern Hemisphere and, particularly in the southwestern USA, a large proportion of the species is serotinous (Wolf 1948; Hickman 1993). On a landscape scale, most cypress are quite restricted, forming dense localized even-aged populations that are widely disjunct from one another (McMillan 1956; Vogel et al. 1977; Zedler 1977). Commonly they are juxtaposed with chaparral and coastal sage shrublands, often in a complex mosaic of cypress patches interspersed with shrublands. Stability of this mosaic is dependent in part upon fire frequency. For example, the southern Californian *Cupressus forbesii* Jepson, is sensitive to frequent fires and under the current 20–30 year interval, populations are being invaded by shrublands (Zedler 1977, 1995). The explanation appears to lie in relatively slow maturation rates and time required to accumulate sufficient canopy seed bank to ensure reproduction. In this species postfire recruitment success is tied to prefire stand age.

In the present paper we studied the age, density and size of *Cupressus sargentii* Jepson, restricted to the Coast Ranges of California (Hardham 1962). In the Santa Lucia Mountains of central California this species is generally restricted to serpentine substrates. One large population of this species was burned in the August 1994 'Highway 41' wildfire and we initiated a study of the prefire and postfire patterns at this site. Fire maps (USDA Forest Service) indicated that different patches of the cypress population, which burned in 1994, had burned at intervals ranging from 21 to 96 years previously. The fact that different aged stands burned together gave us the opportunity to study the effect of stand age on post-fire seedling recruitment. In addition, this population forms discrete forest patches and has sharp borders with chaparral vegetation. Some effort was focused on the success of seedling recruitment at this ecotone.

Methods

Study sites

In the Santa Lucia Mountains, west of Cuesta Pass in San Luis Obispo County, California, USA there is a very large, nearly mono-specific population of sargent cypress – *Cupressus sargentii* Jepson – that extends for hundreds of hectares. Here, as throughout its range *C. sargentii* is restricted to serpentine-derived soils (McMillan 1956). The cypress stand is bordered on all sides by mixed chaparral and all vegetation types are distributed on soils derived from the same serpentine substrate. Short and steep ravines, making for relatively rugged terrain fragment the mountain ridge. This population is approximately 10 km east of the Pacific Ocean at an average elevation of ca. 750 m. The climate is Mediterranean-type with annual precipitation between 1000–1500 mm (Hardham 1962). For the nearest climate station (Paso Robles, 250 m) mean winter and summer temperatures are 9 and 21 °C, respectively, and annual precipitation averages about 360 mm (NOAA 1993). The cypress groves receive substantially more moisture due to the orographic influence on precipitation patterns and from substantial condensation of fog (Hardham 1962).

At the end of the first postfire growing season, sixteen months after the fire, we selected 10 study sites on the north and south sides of the ridge line distributed over a distance of several km, all west of the Cuesta transmitting tower. Sites were selected to be homogeneous, with respect to cypress tree size. Our criteria for site selection was to pick a range of different aged subpopulations, which we inferred from obvious differences in tree size, in addition to picking sites that were easily accessible. All slope aspects were included in our samples and inclinations ranged from nearly level to 30°. USDA Forest Service maps showed many large fires (>15 ha) since early in this century. Since many of our sites were within homogenous sized forests less than 15 ha in size and possibly were not mapped, we aged our sites by counting growth rings. We found this species produces distinct growth rings but we did not use any techniques such as cross-dating (Stokes & Smiley 1968) to verify they were annual rings as the growing conditions often produced material not suitable for this technique. Slope inclination and aspect were measured at each site, and total annual solar insolation calculated from slope aspect, inclination and latitude (Frank & Lee 1966).

Sampling method

A 50 m transect (permanently marked at the top and bottom with reebar) was established down slope in each study site, with 5 10 × 10 m plots on either side, for a total of 10 plots. Within each plot the skeletons of all burned sargent cypress trees were censused. Height and basal trunk diameter of ten burned trees were measured and their cones counted. The percentage cover of vegetation, excluding that of cypress, was visually estimated. In the upper interior corner of each 10 × 10 m plot, a 5 × 5 m subplot was nested and number of young cypress seedlings recorded and 10 random individuals measured for height and basal stem diameter.

At each site an additional sampling procedure was directed towards recruitment differences under the canopy at the ecotone versus within the adjacent chaparral matrix. At the ecotone 10 individual standing burned trees were chosen and measured. From the trunk of each such a tree, a belt transect was laid, perpendicular to the fire border, beginning at the burned trunk until well outside of the vertical projection of the burned canopy, but still in the burned area. Along this transect, in three 1 × 1 m squares beginning at the burned trunk under the burned canopy, and in three 1 × 1 m squares outside the burned canopy, beginning at its edge, all cypress seedlings were counted, the

Table 1. Site parameters, prefire forest characteristics based on skeletal remains and postfire regeneration of *Cupressus sargentii*. Mean ± S.E. for 10 plots 10 m × 10 m in each stand.

Stand	Aspect		Per-fire Forest							Post-fire forest		
		Annual insolation (Kcal cm^{-2})	N	Estimated age (years)	Density (trees m^{-2})	Basal diameter (mm)	Height (per tree)	Cones (m^{-2})	Seed density	Seedling density (m^{-2})	# of seeds per seedling	Offspring per parent
1	N	172	40	20	0.68 ± 0.20	66 ± 5	4.8 ± 0.2	44 ± 7	1257	50.9 ± 11.6	25	75
2	S	294	47	95	0.32 ± 0.05	110 ± 10	6.1 ± 0.1	514 ± 257	5819	14.0 ± 3.6	416	44
3	E	262	17	95	0.07 ± 0.01	255 ± 27	8.9 ± 0.3	327 ± 124	1181	4.8 ± 1.4	246	69
4	E	262	14	95	0.06 ± 0.02	246 ± 41	9.4 ± 0.3	267 ± 43	708	6.2 ± 1.9	114	103
5	W	281	30	55	0.86 ± 0.11	22 ± 2	2.7 ± 0.1	14 ± 2	486	30.8 ± 4.2	16	36
6	N	198	47	55	0.86 ± 0.26	73 ± 6	5.2 ± 0.2	57 ± 17	2172	81.7 ± 10.2	27	95
7	S	296	44	80	0.37 ± 0.08	128 ± 10	8.6 ± 0.5	63 ± 13	989	12.3 ± 1.8	80	33
8	N	181	33	80	0.89 ± 0.75	138 ± 13	9.1 ± 0.5	160 ± 48	6477	28.4 ± 5.8	228	32
9	N	181	35	80	0.20 ± 0.04	143 ± 8	10.6 ± 0.3	40 ± 6	347	6.3 ± 0.8	55	32
10	S	294	50	55	0.69 ± 0.09	32 ± 2	2.8 ± 0.4	10 ± 1	301	37.6 ± 14.6	8	54

height and basal diameter of the five tallest ones were measured.

In the burned stand we estimated postfire seed rain by multiplying number of cones per tree × tree density × average number of seeds per cone (42±30 seeds per cone, $n = 20$). This latter parameter was determined from the following sampling. Unburned cypress trees of variable sizes, near each of the study sites, were cut down at their base ($n = 50$). Height and basal trunk diameter were measured, The number of cones per tree, seeds per cone, and number of growth rings were counted.

Statistical analysis

The means of density, height, basal diameter per stand were used for correlation analyses within and between the cypress cohorts. Comparisons among variable means of several plots were done by ANOVA using Tukey HSD multiple comparisons. We used paired t-test, to test the hypothesis that there was no difference in the measured parameters of cypress seedlings and vegetation cover outside the burned canopy and under the projection of cypress trees growing at the ecotone of the burned forest. Regression was used to examine the relationship between basal diameter of burned trees with the number of annual rings, and with seedling size. Log and semi-log models were used when they provided a better fit. All statistical analyses were carried out with Systat 6.0 For Windows (Wilkinson et al. 1992).

Results

Prefire landscape patterns

The burned cypress forest was a mosaic landscape of different aged patches prior to the fire, representing stands initiated after fires 21, 56, 81 and 96 years prior to the 1994 fire (Table 1). This was based upon USDA Forest Service fire maps and growth ring counts

Log_{10} transformed stem diameter was significantly correlated with the number of growth rings in tree skeletons (Figure 1). ANOVA showed significant differences ($F_{7,43} = 19.514$, $P < 0.001$) in average age of the sampled trees among stands, suggesting a mosaic landscape of stands having previously burned at different times. Although, stands were dominated by trees of similar diameter, trees substantially smaller, and with fewer growth rings, than the surrounding trees were present in most stands. It is unknown whether these had recruited in since the previous fire or were of comparable age as the last post-fire cohort, but with missing rings due to suppression of growth. Estimated stand age (Table 1) was based on the modal frequency counted for the largest stem sections.

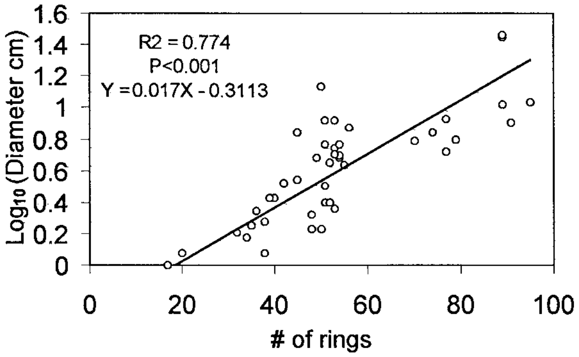

Figure 1. Regression of $\log_{10}$ transformed basal diameter (cm) of sampled *Cupressus Sargentii* trees. vs number of annual rings.

Another reason for believing that differences in pre-fire tree size and density were due to differences in stand age was the sharp borders between different sized stands that were not related to apparent soil differences or slope exposure. Also, there was no significant correlation between the calculated total annual solar insolation and prefire tree diameter ($P = 0.995$) or height ($P = 0.440$) or with tree density ($P = 0.437$). Rock cover varied between sites from 5 to 75% ground surface covered, but was not significantly correlated ($P > 0.420$) with size or density of trees.

The average height of the prefire cypress varied from less than 3 m to more than 10 m and basal diameter varied between stands by an order of magnitude (Table 1). Prefire stand age was negatively correlated with tree density (Figure 2A) and positively correlated with tree basal diameter (Figure 2B) and height ($P = 0.038$, $R^2 = 0.44$). The larger trees in older stands accumulated substantially greater numbers of cones than trees in younger stands (Figure 2C). Due, however, to stand thinning, seed density, which was estimated to range from 300 to nearly 6500 seeds m^{-2}, was not significantly correlated with age ($P = 0.42$).

Postfire landscape patterns

Fires killed all above ground biomass, but tree skeletons and attached cones were largely left intact. Fire intensity varied between stands, as suggested by patterns of fire severity. The number of trees burned to ground level varied from 0% to 17% and was related

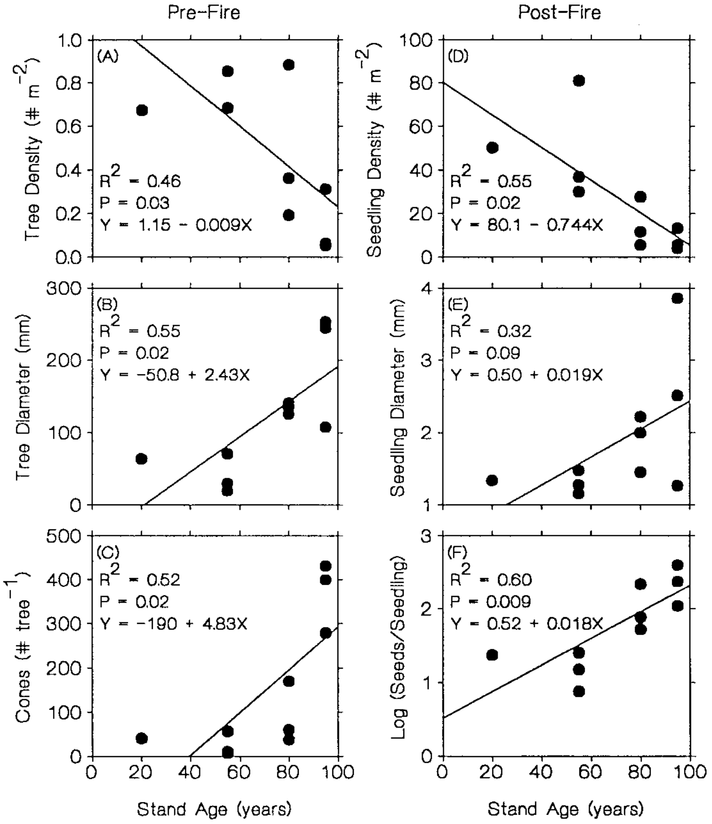

Figure 2. Regression of prefire tree density (A), Trunk diameter (B), # of cones per tree (C), postfire seedling density (D), seedling stem diameter (E) and seeds per seedling (F) as a function of stand age.

to age; stands 55 years or younger had no trees burned to ground level (data not shown).

Postfire patterns showed that seedling density was negatively correlated with stand age (Figure 2D) and there was a tendency for seedlings in stands with older prefire trees to have large stem diameters (Figure 2E). The ratio of seeds/seedlings was positively correlated with stand age, indicating that as stands aged, a larger number of seeds were required in order to produce the same number of seedlings (Figure 2F). Plant cover by other species was significantly correlated with the annual insolation calculated for the site ($P = 0.048$, $R^2 = 0.40$), but cover was not significantly correlated with seedling density ($P = 0.287$). Estimated rock cover was also not correlated with seedling density ($P = 0.917$).

Postfire ecotone patterns – the effect of the burned canopy

Illustrative of factors affecting seedling survivorship and growth is the demographic comparison of seedlings beneath the canopy of burned *Cupressus* skeletons with those immediately outside the canopy shadow along the border of the forest (Table 2). *Cupressus* seedling density, height and basal diameter were significantly greater (by 197%, 156% and 44% respectively) beneath the canopy of burned trees, relative to areas bordering chaparral vegetation, but other vegetation cover was significantly lower (by 82%) under the burned canopies (Table 2).

Discussion

Prior to the fire of 1994, the Cuesta Ridge cypress forest was a mosaic landscape of different aged patches of nearly pure *C. sargentii*, bordered by chaparral. Stands less than 60 years of age were relatively dense with roughly 1 tree every 1–2 m^2. As patches approached the century mark, trees were markedly larger (Figure 2B) and they had thinned to 1 tree every 3–15 m^2. Older trees had substantially greater canopy cone crops (Figure 2C), but due to stand-thinning

Table 2. Comparison of *Cupressus* seedling density and size, and vegetation cover (excluding *Cupressus*) under canopy of burned trees with immediately outside burned canopy projection (mean ± S.E.).

	Under	Outside	$T_{(\mathrm{df})}$	P
Cupressus seedlings:				
Density (m^{-2})	37.7 ± 15.6	12.7 ± 4.4	$3.34_{(33)}$	0.002
Height (mm)	12.2 ± 1.1	7.8 ± 0.7	$7.09_{(31)}$	0.000
Diameter (mm)	2.3 ± 0.3	1.6 ± 0.3	$2.41_{(31)}$	0.022
Vegetation cover				
(% ground surface)	19.7 ± 4.1	35.0 ± 4.5	$6.68_{(38)}$	0.000

(Figure 2A), patch level seed bank size was not significantly correlated with stand age.

In spite of the absence of differences in seed densities among stands, the density of seedling recruitment was lower following fire in old stands than in young stands (Figure 2D). Possible explanations include reduced seed viability with age and higher seed loss from more intense fires in older stands, both of which may account for the fact that it takes more seeds to produce a seedling in old stands (Figure 2F). Other factors accounting for lower seedling density in older stands could be lower seedling survivorship due to predation or abiotic factors such as ash cover (Wilman et al. 1993).

Studies on a more arid-adapted species, *C. forbesii*, have shown the importance of stand age in determining postfire reproductive success. That species requires several decades in order to generate significant canopy seed storage, and thus it is extremely vulnerable to short fire-return intervals – e.g., more frequent than once every 30 years (Zedler 1977, 1995). It is apparent that, at our site, fires at 20 year intervals pose little risk to successful regeneration in *C. sargentii*. The difference between these species likely results from higher growth rates under less drought-prone conditions – *C. sargentii* is distributed more than 300 km north of *C. forbesii* and on sites subjected to summer fog (Hardham 1962). Thus, the 'immaturity risk' risk appears to be greater for *C. forbesii* than for *C. sargentii*.

Obligate seeding species also face a 'senescence risk' if the fire return interval exceeds the lifespan of the seed bank. In many obligate seeding species the seed bank can outlive the population, but because cypress cones open when branches die, and the seeds are not deeply dormant, the longevity of the seedbank is limited by tree lifespan. Cypress are relatively long-lived and Zedler (1995) found no evidence that fires at intervals as infrequent as once a century posed any senescence risk for *C. forbesii*. However, there may be greater risk for *C. sargentii*, as there was a significant reduction in seedling recruitment with stand age (Figure 2D). However, we should be prudent in drawing such conclusions, since the 95 year old stands recruited 4–14 seedlings m^{-2} after fire, which may be sufficient to restock the stands at the same density as the parent populations. Indeed, the highest prefire tree densities were fewer than 1 m^{-2} (Table 1).

In order to conclude whether or not the decline in postfire seedling density observed in older stands will translate into differences in the subsequent demographic structure of the forest, we need to know what factors drive stand thinning. For example, if stand thinning were driven by density independent factors, such as solar insolation, then the higher postfire seedling densities in young stands may translate into higher-density mature forests. However, if stand thinning is driven by density dependent factors, then young and old stands may ultimately restock these sites at similar densities. Answering this question will require follow-up study in subsequent years.

Fire is important to obligate-seeding species, not just because forest rejuvenation is dependent upon it, but because fire is the prime opportunity for population expansion (Keeley 1995). In the mono-specific *C. sargentii* stands, population expansion of the forest border into the adjacent shrublands would alter landscape patterns. However, there is little evidence this will occur. At our sites, seedling recruitment was reduced immediately outside the forest border (Table 2). One of the potential factors limiting forest expansion may be the greater vegetative cover in the adjacent chaparral stands that is associated with diminished growth of cypress seedlings (Table 2). Studies with other serotinous conifers have also shown that postfire expansion of stands is inhibited immediately outside the forest border and enhanced within the shadow of the burned canopies (Ne'eman et al. 1992, 1995).

Thus, it would appear that forest boundaries of these mono-specific even-aged conifers are relatively stable and there is limited possibility of forest expansion, nor is there any significant risk of from invasion by shrubland. The 'permeability' of this ecotone is likely affected by factors that inhibit tree establishment within the shrubland, as well as factors that affect shrub establishment within the forest border.

One of the primary factors behind the stability of this boundary could be differences in storage of dormant seed banks. Brushland species have soil-borne seed banks and their limited establishment under the burned forest canopy may be tied to high intensity fires that essentially 'sterilize' the soil (Keeley and Zedler 1998). This would be driven by high fuel loads produced by these forests, coupled with the high flammability of the litter. Recruitment of serotinous conifers would be less inhibited because they disperse seeds after fire. Seedlings of these conifers would be enhanced under the canopy, not only because of reduced shrub cover (Table 2) but because combustion of high fuel loads leads to greatly enhanced nutrient conditions. Outside the canopy, in addition to potentially less cypress seed rain and higher shrub seed banks, lower fuel loads may contribute to greater shrub and herbaceous re-growth and more intense competition for cypress seedlings (e.g., Katz 1993).

Alternatively, the high fuel load under the pines generates extraordinarily deep ash layers, which can be inhibitory to germination (Ne'eman et al. 1993) due to the very high pH (Henig-Sever et al. 1996). If ash accounts for the stability of this boundary it would suggest that cypress seeds are less sensitive to these high pH conditions than shrub seeds, something that has not yet been investigated for these species.

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