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FIRE AND DEMOGRAPHY

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Fire frequency can have a profound effect on chaparral demography and community structure. It is imperative that we have a clear understanding of these effects since nearly all chaparral lands are under some form of land management plan and often this includes prescribed burning as well as allowing natural lightning fires to burn unchecked. Certain agencies are mandated to manage so as to preserve ecosystems in their natural state. Thus, this workshop focused on two points: 1) What is the nature fire regime for chaparral? and 2) What effects do different fire regimes have on demographic structure in chaparral?

The current paradigm is that the natural fire regime included a fire recurrence interval on the order of approximately 20 years. However, not everyone agrees with this.

In short, there are two schools of thought. One argues that fire frequency is a relatively deterministic process driven by fuel load. In general, chaparral fuel load is conducive to burning after a 15–20 year recovery period. Under this model, a natural fire frequency of 20 years is considered natural because fire ignition is not considered to be a limiting factor to fire frequency. Ignitions are considered to be sufficient in time and space, both now and in the past, to burn chaparral once the fuel load is sufficient to carry the conflagration (Model 1). The other school of thought argues that chaparral has evolved in an environment in which fire frequency has been affected by a number of stochastic components, in particular an unpredictable source of ignition (Model 2). Under this model, it is argued that chaparral is resilient to a wide range in fire frequencies.

The major problem with evaluating these models is that man has had a major impact on the fire regime. In aboriginal times humans increased fire

frequency by increasing ignition sources (Timbrook et al. 1982). Contemporary man has greatly accelerated the frequency of ignitions (Keeley 1982) but at the same time plays a major role in suppressing fires. The net effect is a matter of debate. It is very likely that humans, both modern and aboriginal, have affected the fire frequency in chaparral. However, the role humans have played is probably one of affecting species distributions more than species adaptations. Potentially, this is less true in the Old World (with much longer human presence) and where adaptations are under simple genetic control, e.g., serotiny in certain coniferous species (Teich 1970).

The question of the natural fire frequency in chaparral has been addressed in several studies. Byrne et al. (1977) examined sediment cores off the Santa Barbara Coast for abundance of charcoal. They concluded that major fires over the past 400 years had a recurrence interval of up to 40 years or more, and the interval between fires has been getting shorter in modern times. Some have criticized these studies on the grounds that it is unknown to what extent charcoal deposition accurately reflects wildfires.

Minnich (1983) maintains that due to human interference through fire suppression, the present fire frequency is lower than in the past. He suggests that the much higher fire frequency in Baja California, where fire suppression is not practiced, is similar to the natural burning cycle one would expect if man had not upset the system. This conclusion, however, assumes that ignitions by humans are irrelevant; in Baja there are three times more fires, nearly all of which are started by humans. In other words, Minnich assumes that fire frequency is determined by fuel load and ignitions in the absence of man would not be limiting (i.e., Model 1).

On the other hand, based on the observation that natural ignition sources, namely lightning, account for only a small fraction of the ignitions of wildfires each year (humans are responsible for the remaining), Keeley (1982) suggested that wildfires are more frequent today than under pre-human occupancy. Such an argument assumes that under natural conditions fire frequency is limited by ignition source (Model 2).

In support of the notion that fire ignitions are not limiting, Minnich (personal communication) argues that a little fire can go a long way. In the absence of fire suppression, ignitions can produce fires that smoulder for months and thus potentially initiate numerous fires. He cites newspaper accounts, prior to the modern fire suppression era, which illustrate that this can happen. Stohlgren (personal communication), however, points out that in Sequoia National Park there are large areas where no lightning strike has been detected in more than 60 years. Lightning strikes tend to be concentrated at the higher elevations and ridgetops (Vankat 1985). Under the right conditions fires can burn downslope and into areas with infrequent ignitions. The probability of this is not determined solely by fuel load but by the appropriate combination of lightning ignitions, weather variables, topography, and vegetation structure.

One approach to evaluating this problem is through modeling. If one takes into account lightning ignition distribution in time and space, fire behavior with respect to topography, weather conditions, and stand age, it is possible to predict burning patterns (and thus fire frequency) that will result from natural ignitions. In the central Coast Ranges Greenlee and Langenheim (1980) did such an analysis and concluded that the 'natural fire cycle' for the inland reaches of Santa Cruz County may have ranged upwards to 100 years and was probably far longer in the coastal and lower elevational areas.

Chaparral species differ in their response to different fire regimes. It is suggested that these responses may provide some clue as to the natural fire frequency (Keeley and Zedler 1978, Zedler 1981, 1982, Keeley 1987). One can distinguish two extremes in shrub response to fire: those species that are present after fire due to vigorous resprouting (these species seldom establish seedlings at this time), and those species in which seedling recruitment is not only successful in the first season after fire but is restricted to burn sites.

Species typical of the former group would be *Quercus dumosa*, *Heteromeles arbutifolia*, *Prunus ilicifolia*, *Cercocarpus betuloides*, and *Rhamnus* spp. Seedling recruitment by these species appears to be restricted to older mature chaparral stands (Keeley et al. 1986), but much more study is needed here. Interestingly, many of these species appear as occasional components of oak or walnut forests in southern California. These may be the species which Axelrod (this volume) contends were understory shrubs in early laurophyllous forests. Rather than

understory species, more than likely these were gap-phase species and thus the brightly colored (bird-dispersed) berries characteristic of several of these shrubs are consistent with fruit characteristics of gap-phase species in contemporary forests. By virtue of being vigorous resprouters (a trait so widespread it could not be considered selected solely in response to fire, see Zedler and Zammit this volume) these species were preadapted to tolerate burning but show no clear adaptation to it. Seedling recruitment in these species appears to depend upon long fire-free periods.

Adenostoma fasciculatum and species of *Ceanothus* and *Arctostaphylos* illustrate a reproductive cycle clearly adapted to fire. Under natural conditions seedling recruitment is dependent upon fire. These species however are threatened if the time between fires is too short, e.g., less than a decade. On the other hand they are resilient to very long intervals and successful seedling recruitment is observed after fires in stands which may exceed 100 years of age (Stohlgren et al. this volume).

Certainly one aspect of the demography of these fire-dependent species, which is critical to their survival, is the longevity of the seeds in the soil. Some information is available. Seed demography studies have shown that far more seeds may be produced in a single year than are present in the soil seed pool. Thus, annually there must be a tremendous loss of seeds following dispersal. Ants, rodents, and other small mammals play an important role here but quantitative data are lacking. Deterioration due to fungi and other microbes is a factor (Mavis Hasey personal communication) but little data are available. Because certain of these fire-type shrubs, e.g., *Ceanothus* species, may be outcompeted in older stands, the dynamics and longevity of soil seed pools is critical to evaluating the resilience of such species to varying fire frequencies.

Many herbaceous species in chaparral have polymorphic germination responses. Some seeds may germinate in the absence of fire and other seeds, under field conditions, may not germinate unless exposed to a fire-related cue such as heat or charred wood. These species would be resilient to a wide range in fire frequencies. Many other species seldom appear except after fire and germination appears to 'require' fire-type cues. Our knowledge of germination patterns and seed longevity of such species is poorly developed. Most studies have involved seeds that never have been exposed to field conditions. There is growing evidence that complicated physiological changes take place in seeds under field, as opposed to laboratory, conditions (Nancy Vivrette personal communication). This area requires much more study.

Many other paradigms require further examination but were not discussed in detail. Certainly a number of the speculations about the evolutionary role of fire and climate made in Axelrod's presentation will continue to be debated. With respect to fire it is clear that some species show little evi-

dence of evolutionary change due to fire (Zedler and Zammit this volume). However, it is incorrect to say there is no evidence of adaptation to fire. Consider the dependency of fire-type species discussed above; under natural conditions fire is absolutely required for completion of their life cycle. That the postfire herb flora, with many species that never appear except after fire, and under natural conditions, requires the presence of a highly specialized germination cue (viz., charred wood) is a further example of fire adaptation.

Contrary to Axelrod's suggestion, changes have occurred in response to the mediterranean climate. One notable example is suggested by the absence of postfire herb flora in summer-rain Arizona chaparral. This interior chaparral also lacks species that produce burls as a normal ontogenetic stage as in *Adenostoma fasciculatum*, or certain species of *Ceanothus* and *Arctostaphylos*. Concomitant with the rapid speciation of the latter two genera in the mediterranean climate are other traits potentially selected for by fire, e.g., the solid-stone fruits of several southern California *Arctostaphylos* taxa. Also serotinous-cone conifers associated with mediterranean-climate chaparral are absent from Arizona. Axelrod (this volume) contends that serotiny was initially a response to predation, not fire. It is difficult to imagine how such species would complete their reproductive cycle in the absence of fire. Although animal predators may select for thicker cones in serotinous species, it seems that retaining all seeds in one cone, rather than dispersing them early, would be an unreasonable predator avoidance mechanism. Serotiny is a conifer's means of maintaining a dormant seed pool until postfire conditions. In this respect it is functionally equivalent to maintaining a dormant soil seed pool, as in fire-type chaparral shrubs. Serotiny may be under simple genetic control (Teich 1970) and thus the more likely mode in conifers which are seldom hard-seeded and seldom maintain seed viability very long in the soil.

In conclusion, the current paradigm of a deterministic, fuel load driven, short-return interval fire regime model for chaparral is being challenged. The resiliency of chaparral to long periods (>50–100 years) without fire, longevity of herbaceous and shrub seeds, and the stochastic nature of lightning ignitions, suggest chaparral is adapted to a wider range of fire intervals than previously thought. The short- and long-term interval fire regime models presented here should not be viewed as mutually exclusive, but as complementary mechanisms responsible, in part, for the diversity and stability we see in chaparral ecosystems.

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