Nodvin, Stephen C.; Waldrop, Thomas A., eds.
1991. Fire and the environment: ecological and cultural perspectives: Proceedings of an international symposium; 1990 March 20-24; Knoxville, TN. Gen. Tech. Rep. SE-69. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station. 429 pp.

FIRE MANAGEMENT FOR MAXIMUM BIODIVERSITY OF CALIFORNIA CHAPARRAL

Jon E. Keeley[1]

Abstract—Two reproductive modes present in chaparral shrubs are affected very differently by fire. Some species, called "fire-recruiters," are dependent upon fire for seedling establishment. These species have contributed to the notion that the chaparral community is dependent upon fire for rejuvenation. In the absence of fire, chaparral is often described in pejorative terms which imply that long unburned conditions represent an unhealthy state. However, many shrub species, called "fire-persisters," do not establish seedlings after fire, rather they require long fire-free periods in order to establish seedlings. These species are vigorous resprouters, not only after fire, but throughout their lifespan. Older stands of chaparral are continually rejuvenated by recruitment of new resprouts and seedlings of these fire-resister species. It is suggested that the long-term stability and diversity of chaparral requires a mosaic of fire frequencies.

INTRODUCTION

California chaparral is considered a "fire-type" vegetation based on the fact that all species are resilient to the modern fire regime of fires every few decades (Keeley and Keeley 1988). Resilience of the vegetation is reflected in the relatively minor changes in community composition resulting from fire. Species present before fire return rapidly afterwards, either regenerating aboveground parts from basal resprouts or by seedling establishment.

In addition to being considered a fire-type vegetation, chaparral is also often described as a fire-dependent vegetation. This is based on both population and community level phenomenon. Certain species, Adenostoma fasciculatum (Rosaceae), Arctostaphylos spp. (Ericaceae) and Ceanothus spp. (Rhamnaceae) for instance, require fire for seedling establishment. Seeds are dispersed in a dormant state and accumulate in the soil until germination is triggered by fire, either from heat or a chemical leaching from charred wood (Keeley 1987). These species have specialized their reproductive biology to the extent that they are dependent upon fire for completion of their life cycle and may be referred to as "fire-recruiters". At the community level, fire-dependence is implied by the frequent suggestion that stands require fire for rejuvenation. Chaparral unburned for 60 years or more is often referred to as decadent, senescent, senile and trashy (Hanes 1977).

This fire-dependent paradigm of chaparral has guided fire management strategy in southern California, although it is perhaps generous to call the modern fire regime "a strategy," since most acreage in southern California burns by catastrophic wildfires. Nonetheless, federal, state and county agencies have prescribe burn programs for chaparral sites under their fire jurisdiction. Some areas that escape wildfires are burned under prescription at return intervals of approximately 15-25 years. Such a prescription follows logically from the commonly accepted dogma about the fire-dependence of chaparral. This, however, is not the whole story.

FIRE RESILIENCE VS. FIRE DEPENDENCE

While it is true that the chaparral community is highly resilient to fire, all species within the community are not fire-dependent. In fact, a large component of chaparral, while persisting in the face of recurrent fire, may actually decline after repeated fires. Included here are species such as Quercus dumosa (Fagaceae), Heteromeles arbutifolia Rosaceae), Prunus ilicifolia (Rosaceae), Cercocarpus betuloides (Rosaceae) and Rhamnus spp. (Rhamnaceae). These shrubs are resilient to fire by virtue of the fact that they are vigorous resprouters, yet they do not establish seedlings after fire. These species are "fire-persisters" but not "fire-recruiters." A management plan oriented towards long-term stability and maintenance of biodiversity needs to consider the conditions necessary for reproduction of these taxa.

The conditions under which these species recruit seedlings have not been well worked out. It is clear that these species do not establish seedlings after fire, and there are aspects of their seed germination physiology which account for this (Keeley 1987). On the other hand, studies of mature chaparral have consistently pointed out the lack of seedling reproduction under the closed canopy of this dense shrub vegetation (Sampson 1944; Horton and Kraebel 1955; Hanes 1971; Christensen and Muller 1975).

One clue to this mystery is an observation made in an early paper by Patric and Hanes (1964). These authors studied a stand of chaparral unburned for more than 60 years and noted seedlings of Quercus dumosa, Prunus ilicifolia, and Rhamnus crocea. Spurred in part by these early findings I have been investigating the fate of chaparral in the long absence of fire.

[1]Professor of Biology, Department of Biology, Occidental College, Los Angeles.

My focus has been on the demographic structure of stands free of fire for 100 years or more in some cases. This study has revealed large seedling populations in older stands of chaparral; from 1,000 to 40,000 seedlings per hectare for taxa such as Quercus, Rhamnus, Prunus, Cercocarpus and Heteromeles (Keeley unpublished data). It is apparent that long fire-free conditions are required for seedling establishment by these fire-persister shrub species.

In summary, chaparral is dominated by shrubs that are resilient to fire. Some are fire-dependent taxa that recruit seedlings only in the first season after fire, and these are called fire-recruiters. Other shrubs, however, are not fire-dependent. They persist after fire but these fire-persisters require long fire-free conditions for seedling establishment (figure 1).

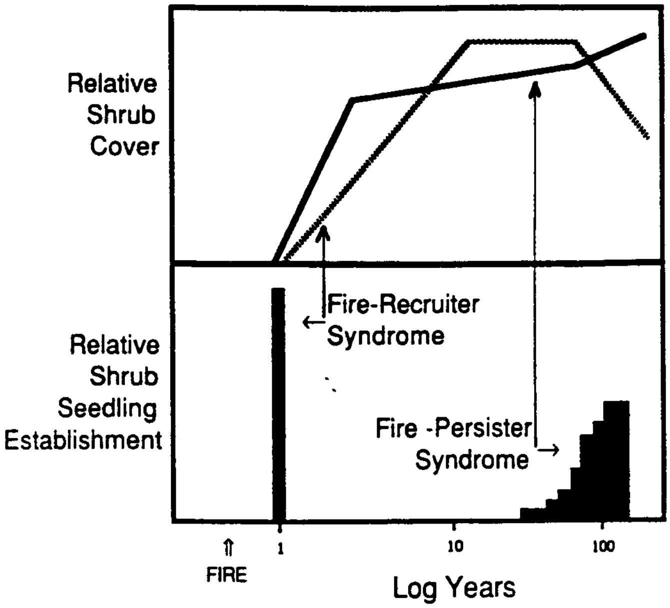


Figure 1.- Schematic illustration of the timing of seedling recruitment for chaparral shrubs described as fire-recruiters and as fire-persisters and longterm changes in relative shrub cover for fire-recruiters (dashed line) and fire persisters (solid line).

What is the best strategy for management of these systems. It appears that fire intervals on the order of every 20 years would potentially benefit fire-recruiters. Fire-persisters, while not obviously damaged by this fire return interval, over long periods of time will be threatened by the lack of opportunities for seedling establishment. I suggest the coexistence of these modes reflecs the natural stochastic fire regime. Under natural conditions, the eventuality of fire on any given site would have been nearly certain, however, the return interval over time would have been variable. Short return intervals would have provided opportunities for population expansion of fire-recruiters and long return intervals would have provided opportunities for population expansion of fire-persisters.

RESILIENCE TO LONG FIRE-FREE INTERVALS

Community stability is dependent on both fire-recruiters and fire-persisters being resilient to both short and long fire return intervals. The current fire regime of relatively short intervals of 20 years between fires does not pose an immediate threat to either group. I suggest that all chaparral shrubs are also resilient to long fire-free periods, although few chaparral sites remain unburned for more than a few decades.

This notion would seem to be contrary to much of the dogma about the decadence, senescence and senility of chaparral stands older than 60 years. These terms, however, are seldom defined; a former student once suggested that a senile chaparral shrub was one which forgot to close its stomates, and this definition is about as good as any proposed in the literature. Most certainly these terms derive from observations that, due to natural thinning of shrubs (e.g., Schlesinger and Gill 1978), dead wood accumulates. However, something that is seldom appreciated is that dead stems are continually replaced by basal sprouting in all sprouting shrubs (figure 2). Consequently, the age structure of sprouting shrub populations are not even-aged and exhibit continuous recruitment and turnover of stems (figure 3). In other words, resprouting, in addition to functioning to rejuvenate shrubs after fire, functions to rejuvenate the canopy throughout the life of the stand.

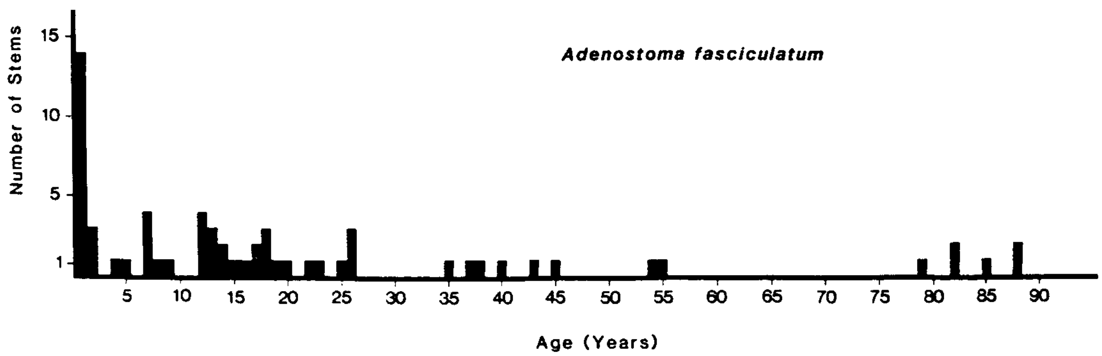


Figure 2.- Number of stems of different ages on a single resprouting shrub of Adenostoma fasciculatum in a stand of chaparral last burned 89 years ago (Keeley unpublished data).

How then did old stands of chaparral come to be described as senescent and unproductive? This idea is apparently derived from early studies which investigated browse production by different aged stands of chaparral (Biswell and others 1952; Hiehle 1964; Gibbens and Schultz 1963). These studies concluded that chaparral became very unproductive within several decades following fire. However, these studies were only concerned with production available of wildlife. Consequently they did not present valid measures of productivity, because production above 1.5 meters, which is unavailable for deer, was not included. Since most new growth in older stands occurs above 2 meters, it is not surprising that one would conclude that frequent fires were a necessity for maintaining productive chaparral communities. Since the concept of stand senescent seemed logically consistent with the fire-dependent nature of many chaparral species, this myth of low productivity in older stands of chaparral was not questioned by many chaparral ecologists and foresters. Modern studies, however, reveal that live biomass increases with age in chaparral (figure 4), and the terms decadence, senescence, and senility, while possibly true of some species, should not be used to describe chaparral communities.

In conclusion, chaparral is resilient to short and long fire-free intervals, and different fire-return intervals, favor different components of the vegetation. Longterm stability and biodiversity of chaparral communities may require a mosaic of fire regimes.

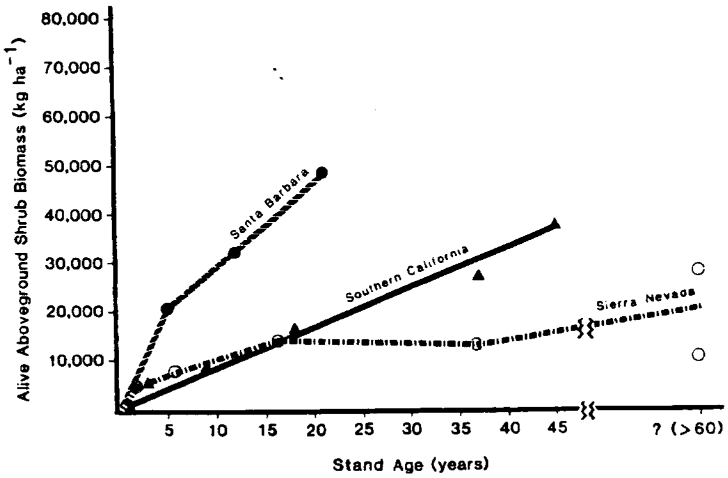
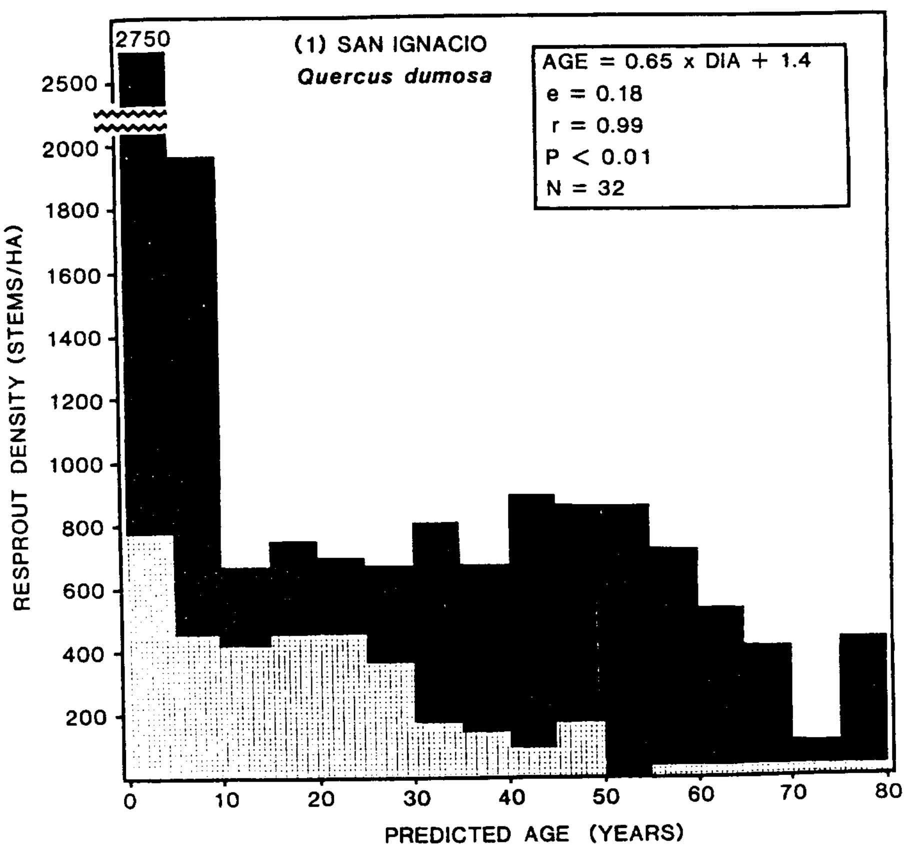


Figure 4.- Standing living biomass in chaparral stands as a function of age since last fire (from Keeley and Keeley 1988, with permission of Cambridge University Press, data from studies by Specht 1969, Conrad and DeBano 1974, Schlesinger & Gill 1980, Rundel and Parsons 1979, Stohlgren and others 1984, as cited in Keeley and Keeley 1988.)

Figure 3.- Predicted population age structure of Quercus dumosa stems sprouted from root crowns of mature shrubs in a stand of chaparral last burned 76 years ago (solid bars are living stems, vertical lines are dead stems). Stem diameters were measured in 36 4x4 m plots randomly placed in the stand. Age was predicted from the indicated regression line based on 32 stems aged by ring counts. In addition to the correlation coefficient, the estimate of relative error was calculated as the standard error divided by the mean value of y.



LITERATURE CITED

Biswell, H. H., R.D. Taber, D.W. Hedrick, and A.M. Schultz. 1952. Management of chamise brushlands for game in the north coast range of California. California Fish and Game 38:453-484.

Christensen, N. L. and C. H. Muller. 1975. Relative importance of factors controlling germination and seedling survival in Adenostoma chaparral. American Midland Naturalist 93:71-78.

Gibbens, R. P. and A.M. Schultz. 1963. Brush manipulation on a deer winter range. California Fish and Game 49:95-118.

Hanes, T.L. 1971. Succession after fire in the chaparral of southern California. Ecological Monographs 41:27-52.

Hanes, T. L. 1977. California chaparral, pp. 417-170. In: Barbour, M. G. and J. Major, eds. Terrestrial vegetation of California. John Wiley, New York.

Hiehle, J.L. 1964. Measurement of browse growth and utilization. California Fish and Game 50:148-151.

Horton, J.S. and C.J. Kraebel. 1955. Development of vegetation after fire in the chamise chaparral of southern California. Ecology 36:244-262.

Keeley, J. E. 1987. Role of fire in seed germination of woody taxa in California chaparral. Ecology 68:434-443.

Keeley, J. E. and S.C. Keeley. 1988. Chaparral, pp. 165-207. In: Barbour M.G. and W. D. Billings, eds. North American terrestrial vegetation. Cambridge University Press, New York.

Patric, J. H. and T. L. Hanes. 1964. Chaparral succession in a San Gabriel Mountain area of California. Ecology 45:353-360.

Sampson, A. W. 1944. Plant succession and burned chaparral lands in northern California. Agricultural Experiment Station, University of California, Berkeley, Bulletin 685.

Schlesinger, W.H. and D.S. Gill. 1978. Demographic studies of the chaparral shrub, Ceanothus megacarpus, in the Santa Ynez Mountains, California. Ecology 59:1256-1263.