

Successional Dynamics of Chamise Chaparral: The Interface of Basic Research and Management¹

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The subject of successional dynamics in chaparral has been a productive one for 60 years. Much of this past work, summarized in detail by Hanes (1977), has been descriptive, focusing on successional changes which may occur. There has been little attempt, however, oriented toward communicating the significance of these successional patterns for the development of informed resource management. In this paper, I will attempt to bridge this gap and provide a basis for the interface of basic research and management in studies of the successional dynamics of climax chaparral.

Intensive studies of chamise chaparral at Sequoia National Park have provided the large data base necessary to study the relationships between fire history and plant-soil interactions. These data, covering 43 0.1 ha plots with enumerations of species coverages, soil nutrients and structure, topographic patterns and fire history, has provided the basis for a quantitative model of the dynamics of successional change over a 90-year sequence following fire (Rundel and Lambert 1982).

SHORT-TERM SUCCESSIONAL PATTERNS

In this model (fig. 1) open stands following fire are rapidly recolonized by the same pre-fire dominants of older stands. *Adenostoma* reestablishes by both resprouting from underground root crowns and by post-fire seed germination. The two other important, long-lived shrubs; *Ceanothus cuneatus* and *Arctostaphylos viscida*, are obligate reseeder. In addition to these three shrubs, four other short-lived shrub species which are generally absent from mature chamise chaparral rapidly become established

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Abstract: Basic research on successional dynamics of chamise chaparral in the foothill zone of Sequoia National Park, California, can provide valuable data for assessing management alternatives for this zone. Fire seasonality and intensity strongly influence patterns of post-fire community development. An ecological understanding of both short-term and long-term successional dynamics is critically important to reach these management goals. Knowledge of flammability, fire behavior, plant demography and plant physiological ecology are all essential.

following fire and form the major shrub cover for the first ten years of succession. These are *Eriodictyon californicum*, *Malacothamnus fremontii*, *Dendromecon rigida* and *Lotus scoparius*.

Woody perennials are not the only important plant group in the early stages of succession. Mixed herb cover also becomes rapidly established and maintains dominance in direct response to the level of total shrub cover (Rundel and Lambert 1982). Fire is not a prerequisite for the establishment of dense herb cover, however. Manual cutting and removal of shrubs has a very similar effect in stimulating herb establishment, although the species composition of herbs may be quite different.

Fires play a very important ecosystem role in cycling limited nutrients back into the soil from litter and woody plant tissues. This role is particularly important in chamise chaparral where there is evidence that limited nutrient availability, particularly for nitrogen, may be a factor in bringing on senescence in mature

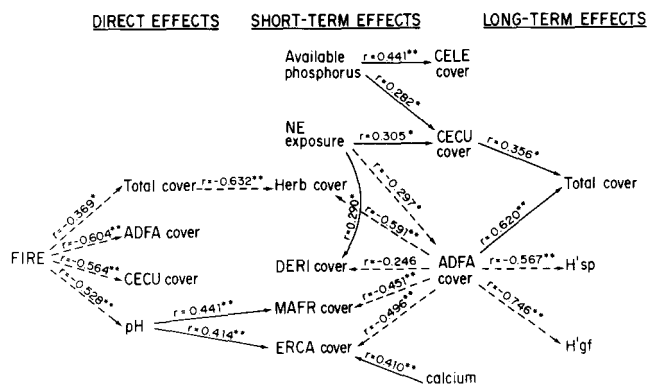


Figure 1. Dynamic model of significant interactions in succession of chamise chaparral at Sequoia National Park. Positive correlations are shown by solid lines and negative correlations by dashed lines. Statistical significance: **p < 0.01, *p < 0.05.

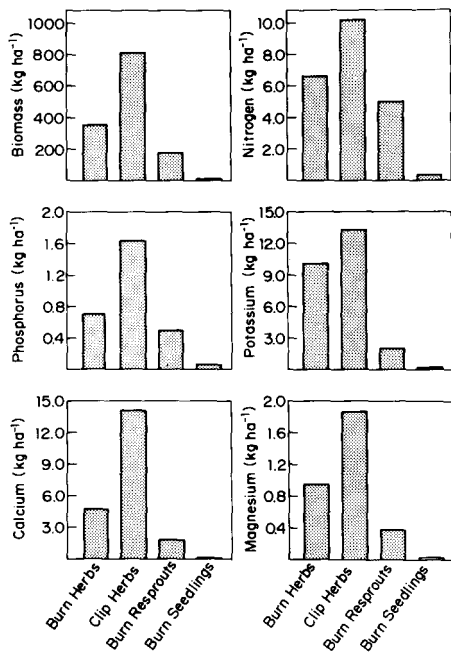


Figure 2. Above-ground biomass and nutrient pool in plant compartments after one year of growth following a fire in fall 1980. Resprout and seedling biomass of *Adenostoma fasciculatum* in clipped plots are comparable to those in burn plots.

stands (Rundel and Parsons 1980). Although total levels of soil nitrogen may be reduced by the heating effects of fire, inorganic forms of nitrogen available for plant uptake increase significantly (Rundel 1981).

Since litter and plant nutrients are initially recycled in the form of loosely consolidated ash, there has been considerable concern raised by resource managers in protecting this ash from erosion. While resprouts and seedlings of dominant shrub species take up relatively large concentrations of nutrients into their tissues, their total biomass is too small in the first year after fire to successfully tie up a significant percentage of the available nutrients deposited from ash. The dense post-fire herbaceous growth, however, does play a very important ecological role in immobilizing such nutrients and protecting them from loss from the ecosystem (fig. 2). At the end of the spring growing season following a fall 1979 experimental burn at Sequoia National Park, the total herb biomass was more than two times that of *Adenostoma* resprouts. *Adenostoma* seedlings were an insignificant part of the total biomass. A similar pattern of herb importance was found for all of the major nutrients as well, demonstrating the importance of herbaceous vegetation in sequestering nutrients. Herb biomass on clip plots was more than twice as great as on burn plots and sequestered considerably more nutrients.

As resprouts of *Adenostoma* continue to grow rapidly in the first decade of post-fire succession at Sequoia National Park, the importance of short-lived shrubs and herbs declines rapidly (fig. 1). Some species such as *Malacothamnus fremontii* appear to drop out largely due to a short life cycle and lack of reestablishments of seedlings. Other short-lived shrubs and herbaceous growth, however, appear to be shaded out since their decline in importance is inversely correlated with total shrub cover (Rundel and Lambert 1982). *Adenostoma* forms the major part of this shrub cover. Canopy closure by long-lived shrubs generally occurs by 20 years after a fire. By this stage short-lived shrubs and significant herb cover are absent from undisturbed stands of chamise chaparral.

Although most researchers suggest that 20-40 years may be a natural cycle for fire in chamise chaparral, many stands at Sequoia have reached considerably greater ages without burning under past policies of fire prevention (Parsons 1981). In such old growth chaparral, the increasing dominance of *Adenostoma* has very profound effects on the structure and diversity of the community. *Ceanothus cureatus*, the second most dominant shrub to *Adenostoma* and an important browse plant for deer and other animals, drops out before stands reach 60 years of age. *Arctostaphylos viscida* may reach 90 years of age before it dies out, but it is not a major browse plant. *Adenostoma* itself may live for considerably longer but old-growth chamise chaparral has an increasing level of dead branch tissues with age (Parsons 1976) and becomes less and less productive. Thus old growth chamise is not a productive source of wildlife browse. In addition, the accumulation of large amounts of dead fuels makes these stands highly flammable and subject to unnaturally high intensity fires.

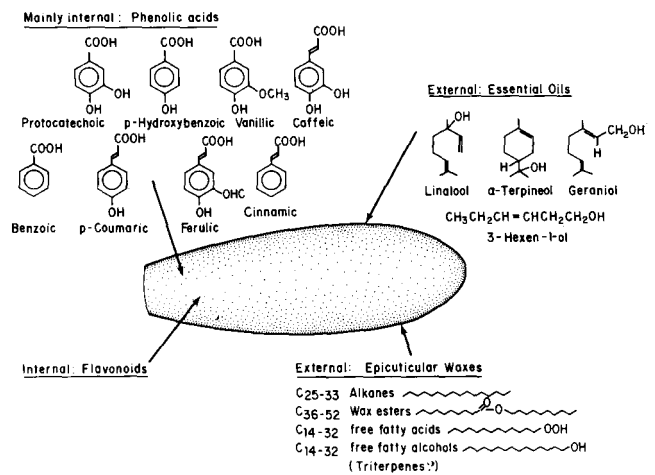


Figure 3. Secondary plant products present in leaves of *Adenostoma fasciculatum*.

From a management standpoint, therefore, a more natural cycle of chaparral fires would be beneficial.

SECONDARY CHEMISTRY OF ADENOSTOMA FASCICULATUM

The leaves of Adenostoma contain a diverse assemblage of secondary plant compounds and these chemical substances may play very important ecological roles (fig. 3). Phenolic acids in the internal leaf tissues have been associated with allelopathic effects of chamise on competing species. While the ecological significance of allelopathic constituents in Adenostoma have perhaps been overstated in the past (Muller and others 1968, McPherson and Muller 1969), the potential role of such compounds does deserve careful quantitative consideration. Such studies are now being carried out in conjunction with work on chamise chaparral at Sequoia National Park.

A second group of chemical compounds of ecological significance are the essential oils on the leaf surface of Adenostoma (Fig. 3). These volatile, high-energy compounds are a very important indicator of relative flammability of chamise. They are the most critical aspects of the ether extractive components of leaf tissues which have frequently been linked to flammability (see review by Rundel 1980). As succession proceeds through time there is a significant in-

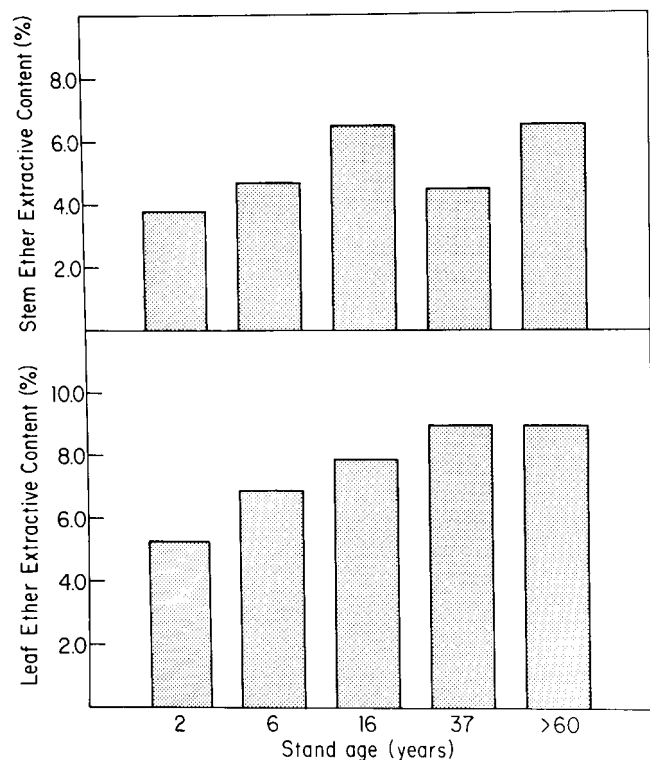


Figure 4. Concentration of ether extractives (percent of dry weight) in 1-2 year leaf and stem tissues of Adenostoma fasciculatum along a gradient of stand age.

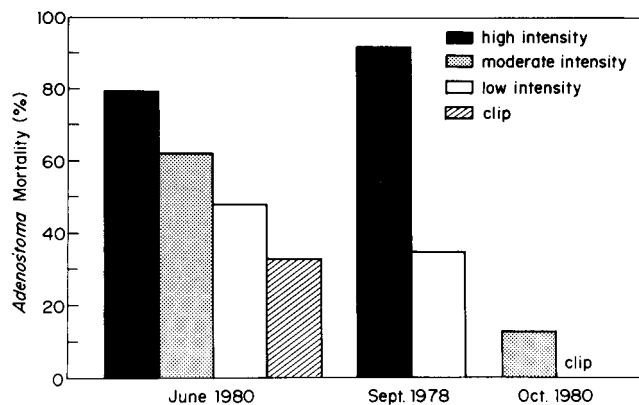


Figure 5. Mortality of root crowns of Adenostoma fasciculatum following fire or clipping treatments.

crease in the ether extractive contents of 1-2 year old leaf and stem tissues in Adenostoma (Fig. 4). This increase has been associated with the increased flammability of older stands.

EFFECTS OF FIRE SEASONALITY AND INTENSITY ON SUCCESSION

Although Adenostoma fasciculatum recolonizes following fires primarily through resprouts, the seasonality and intensity of fire have a great effect on the level of shrub mortality which may occur. Data demonstrating this impact at Sequoia National Park are summarized in figure 5. High intensity experimental fires in June 1980 resulted in nearly 80 percent dead root crowns, while a modest and low intensity fire resulted in 64 and 46 percent mortality, respectively. Only 36 percent mortality resulted following clipping in an adjacent unburned plot. Although a small percentage of dead individuals were present in the stands before the fire, the treatments are the cause of the majority of the mortality. Studies of post-fire recovery from a man-caused chaparral fire in September 1978 at Sequoia found a similar pattern. A very high intensity portion of the fire resulted in 92 percent mortality of root crowns, while only 35 percent mortality was present in a low intensity portion of the burn. The pattern of mortality associated with burns later in the fall is totally different. A moderately intense experimental burn in October 1980 had only 14% mortality. There was no mortality associated with a clipping treatment at this same time.

The seasonal effect of fire on root crown mortality can be readily explained by physiological data on root sprouting collected at the Hopland Field Station of the University of California more than 20 years ago (Jones and Laude 1960, Laude and others 1961). During a "typical" rainfall year such as 1956-57, high levels of starch present in root tissues in the early spring are metabolized and translocated

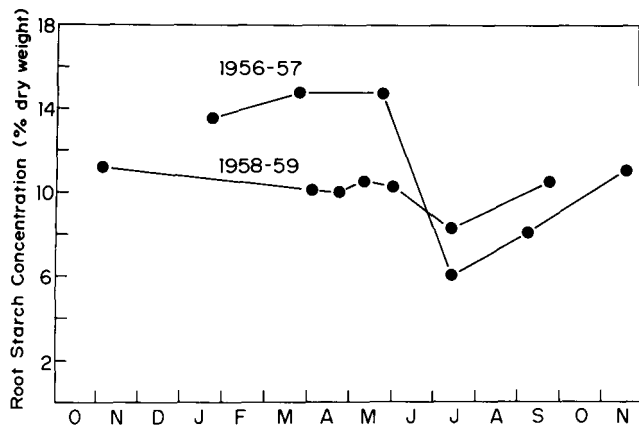


Figure 6. Seasonal pattern of concentration of starches in root tissue of *Adenostoma fasciculatum* during 1956-57 ("typical" year) and 1958-59 (a dry year). Data from Laude and others (1961).

out as shoot growth occurs (Fig. 6). These root stores of carbohydrate begin to slowly return in late summer and are reconstituted by late fall.

Chamise fires in late spring or early summer burn above-ground tissues at a time when there are few carbohydrate reserves in root systems to allow successful resprouting to occur. At these times of the year fire-or clipping-induced mortality of root crowns is high, particularly in smaller shrubs with less buffering capacity in their root crowns. By mid-fall when root carbohydrate stores have been reconstituted there is little mortality caused by removing above-ground tissues through burning or clipping. In dry years such as 1958-59, large starch reserves are not formed and major mobilization does not take place (Fig. 6). Under these conditions spring or summer fires might produce lower level mortality than in wetter years.

Fire intensity is clearly an important aspect of fire-induced mortality of *Adenostoma* root crowns. Intense fires, which burn away the major part of above-ground tissues, provide sufficient heat to cause the highest levels of mortality. As intensity declines down to zero (clip treatment), there is a resulting drop in mortality (fig. 5). Such an effect is caused by the depth of the heating front, a function of fire intensity, as it affects root crowns. Small shrubs have the shallowest root crowns with the lowest biomass and are thus most impacted.

MANAGEMENT IMPLICATIONS OF SUCCESSIONAL STUDIES

Basic research on patterns of successional dynamics provides an important framework for understanding the implications of management practices in chamise chaparral. In the first few years following fire, for example, herbaceous vegetation plays a very important role in sequestering nutrients that might otherwise be lost in erosion or runoff. Chaparral managers

should be cognizant of this importance and protect this herb growth from livestock grazing or other destructive impacts.

As chamise chaparral matures, the diversity of associated species declines steadily, and the wildlife use also drops correspondingly. Old growth chamise chaparral provides very low productivity with little wildlife value, while producing highly flammable stand structures with the potential for high intensity fires. A return to more natural chaparral fire frequencies, through either controlled burning or allowing natural fires to burn under appropriate conditions, would provide the maintenance of greater stand species diversity and greater availability of wildlife browse. Lower intensity fires would reduce the potential for significant ecosystem damage or property destruction. Similar management recommendations to optimize wildlife values have been described in detail by Biswell and others (1952).

If controlled burning is utilized in chaparral, resource managers should give careful consideration to the implications of fire seasonality and intensity. Intense fires cause significantly more root crown mortality than do light fires. Late spring and summer fires cause far greater mortality than do fall fires. If the management goal is to restore natural fire conditions, as with the National Park Service, then late summer and fall fires should be utilized (see Parsons 1981). Type conversions of chamise chaparral to other vegetation covers, at the other management extreme, would be facilitated by intense early summer fires.

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