Chaparral Succession[1]

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Abstract: Vegetation changes following fire usually result in a rapid return to the predisturbance species composition and structure. Regrowth takes place by root-crown sprouting and seed reproduction. Succession is cyclic except in ecotones and favorable sites where it is linear. Fire serves as a growth stimulus to the persisting plants, contributes to seed germination, and is a plant waste remover and ecosystem renewer. Other factors that affect succession are mountain building, landslides, erosion, soil development, climatic variability, and environmental stress.

A complete discussion of chaparral succession and a thorough review of the literature on the subject is presented by Hanes (1977). As a result, a review of the literature on chaparral succession will not be attempted in this manuscript. Rather, certain highlights of plant succession will be again presented and re-emphasized. In addition, a conceptual model of chaparral succession is advanced that is intended to help explain the controlling factors and dynamics of succession.

Chaparral vs. Classical Succession

Classical plant succession (Vogl 1970, Horn 1974, 1976) is largely nonexistent in California chaparral, except possibly in transitional areas where chaparral intergrades with other vegetation types. Missing in chaparral is the usual replacement series of various plants or seral stages, with each species modifying the site until it becomes unfavorable for that species and thereby available for invasion by another (Horton and Kraebel 1955, Sweeney 1956, Patric and Hanes 1964, Hanes and Jones 1967, Hanes 1971, Vogl and Schorr 1972, Biswell 1974, Keeley 1977, Keeley andLedler 1978). In most instances there is no species replacement that progresses until a stable or climax vegetation is established (Hedrick 1951). Even on virgin sites, the colonizing plants are also components of the mature vegetation. Virgin sites that are sometimes invaded by such species as annual grasses, <u>Selaginella</u> mosses, coffee fern (<u>Pellaea andromedaefolia</u>), and perennial herbs do not appear to be particularly modified or enhanced to encourage successional replacement with subshrubs followed by woody plants. Growth that resembles the early stages of classical primary succession does not necessarily lead to chaparral development, and primary succession is most often accomplished by the direct invasion of a site by climax chaparral elements. New sites in chaparral ecosystems are continuously produced by landslides which are triggered by rain or when slopes are undercut by runoff, or produced by instability as a result of tectonic activities.

With few exceptions, fire is the initiator of secondary succession in chaparral. Secondary succession following fire is also without seral stages (Hanes 1977). The temporary cover of annual fire-followers (Armstrong 1977) and short-lived perennial herbs (Keeley and Johnson 1977) and subshrubs does not modify the site to encourage a species invasion or replacement. In about 2 to 5 years after a fire almost all of these species cease growth (Vogl and Schorr 1972), and the spaces they occupied are usually taken by the expanding canopies of the resprouting or regrowing chaparral shrubs (Ammirati 1967); the same species that dominated the preburn vegetation. The seeds of these herbaceous plants apparently persist in place until their growth is again initiated by fire (Sweeney 1956). The rapidity and magnitude of the responses of these fire-followers, along with the usual large sizes of the burned areas, preclude that the seeds of most of these species invade the burned sites from adjacent unburned areas (Westman 1979).

Successional replacement is apparently hampered by the strong vegetative habits of many chaparral shrubs. Once a shrub occupies a site, it physically dominates that site. Perennial plants with the ability to recover after top damage or removal of stems have the potential to extend this dominance for long periods, perhaps for hundreds of years. Anything short of the destruction of the basal crown of the root system results in the persistence of these chaparral shrubs. Removal of the aerial portions of these perennials by fire is not just an adversity that these plants must overcome, but it also prevents-plant senescence by physiological rejuvenation and growth stimulation (Vogl 1980). Factors that help to initially determine the chaparral species that will become established on a given site are exposure of site, steepness of slope, soil moisture, elevation (Hanes 1977), and possibly the ash bed present after fire (Vogl and Schorr 1972).

Most chaparral shrubs also produce chemicals that inhibit competing invaders which contribute to site dominance (McPherson and Muller 1969, Hanes 1977). The allelopathic chemicals produced by nonsprouting shrubs may extend chemical suppression of other species after the nonsprouting shrubs have died, thus helping to ensure the re-establishment of the same species on that site. It has been noted that after the short-lived bush poppy (<u>Dendromecon</u> <u>rigida</u>) or certain species of <u>Ceanothus</u> die some 20 to 40 years or more after a fire (Quick 1959, Hanes 1971,

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Keeley 1975), the spaces they occupied remain open and unvegetated, or are only filled by the aerial portions of adjacent shrubs.

It has been generally assumed that among shrub species that possess the ability to regrow vegetatively after fire, plants established from seeds seldom contribute substantial numbers of individuals that become components of the mature vegetation (Hanes 1977). Usually little seedling growth occurs on sites dominated by shrubs capable of vegetative reproduction (Keeley 1977). It has been hypothesized that when seedlings do become established, they provide a temporary plant cover that is preferentially browsed by herbivores until the resprouting shrubs again regain dominance (Vogl and Schorr 1972). It appears that seed reproduction is only important as a replacement for shrubs that fail to recover vegetatively, or in places where the shrubs have been eliminated by such things as a landslide or a very hot fire.

An alternate explanation is that seed reproduction is commonplace among resprouting perennials and contributes substantially to the mature vegetational cover (Howe and Carothers 1980). If this assumption which contradicts most other studies is correct, then it appears that chaparral shrubs are shorter lived and have higher replacement rates than suspected, since the typical high densities of chaparral shrubs tend to otherwise physically saturate any given site with little or no space for successful seedling establishment (Hanes 1977). Further research is needed on this subject, particularly since shrub seedlings might often be misidentified as resprouts and vice versa (Howe and Carothers 1980).

Chaparral succession is also simplified by the absence of an understory vegetation (Hanes 1971, 1977). The mature chaparral usually consists of a single, although sometimes irregular, layer or stratum of dense shrub growth with canopies that are continuous and contiguous with each other. The general absence of an understory is considered to be a product of this dense growth, closed canopies, insufficient surface soil moisture, and allelopathic effects. Christensen and Muller (1975) and Ron Quinn (personal communication, Jan. 1980) have found that the establishment of an understory is also prevented by the activities of herbage and seed-eating small mammals. At any rate, the vegetational development does not usually progress beyond a single-layered formation.

Coastal Sage Scrub or Degraded Chaparral

Chaparral that has been severely disturbed or degraded is often dominated by different plant species than those found in undisturbed chaparral. Some of the more common of these are Eriogonum fasciculatum, Eriodictyon spp., Lotus scoparius, Salvia spp., Eriophyllum confertiflorum, Heleanthemum scoparium, and Artemisia californica. These subshrubs or half-shrubs usually produce open stands as they mix with introduced grass species and ubiquitous weeds. Such chaparral disclimaxes are often produced by long-term overgrazing and radical changes in fire frequencies (Vogl 1977). Much of what is presently classified as coastal sage scrub may have been either chaparral (Hanes 1977) or perennial grassland prior to its degradation. Grazing impacts usually extend well beyond the areas being directly used by livestock as rodent and other wild herbivore populations are displaced and reconcentrated. Ranching operations also often reduce the predators of an area thereby allowing prey populations to reach abnormal numbers that negatively impact the surrounding vegetation.

Coastal sage scrub appears to be relatively stable, in that in many areas it is not undergoing rapid vegetational changes and quickly reverting to chaparral (Mooney 1977). It may be that these areas are in a state of shock stagnation, whereby the degraded vegetation persists or is self perpetuating for an indefinite period with no evidence of species replacement. Degraded California grasslands and many desert plant communities also do not show signs of recovery indicating that the relative stability of these disclimax stages is commonplace among degraded ecosystems. Unless coastal sage scrub is not a product of degradation or the disturbances have not caused irreversible changes, such areas would be expected to be eventually replaced by chaparral.

The same floristic elements that characterize coastal sage scrub also occur on small, localized sites within undisturbed chaparral. They usually respond to minor soil disturbances caused by ground squirrels, pocket gophers, rock slides, erosion, and the like. Under such disturbance conditions, these species act like pioneer or weedy species responding to the open and unstable conditions. These species are replaced by the more stable chaparral species when the disturbances are eliminated. This type of successional replacement is similar to that found in perennial grasslands where short-lived opportunistic pioneers coexist with long-lived perennials. A natural grassland is constantly being turned over, a little at a time by various localized disturbances, with the result that "pioneer" species occur adjacent to and mixed with "climax" species (Vogl 1974). Apparently similar events happen in localized areas, but as in perennial grasslands, the pioneer species do not necessarily modify the site so that it can be invaded by the more stable species. Rather, small-scale disturbances favor opportunistic invader species and their absence favors the establishment of components of the stable vegetation.

Chaparral Ecotones

Chaparral succession involving a step-wise replacement of species occurs more commonly along ecotones where chaparral intergrades with other vegetation types. These transitional areas occur within and at the peripheral edges of chaparral distribution. Chaparral and the other vegetation types that it is juxtaposed upon usually form a mosaic of mutually-exclusive plant communities (Wells 1962).

This patchwork pattern is most pronounced at the lower elevational occurrences of chaparral where it impinges on grassland, oak savanna, oak woodland, and riparian forest. Chaparral and these other vegetation types appear to be distributed primarily by soil differences, including differences in pH, texture, ;water-retaining capacity, and nutrients, and the presence of ground water or soil moisture.

At the upper elevational and northern limits of chaparral distributions, angle and exposure of slope appear to be more effective than soil in determining vegetation patterns. Along these edges chaparral intergrades less distinctly with oak or with pine forest, principally _Pinus coulteri_, P. _sabiniana_, _P. jeffreyi_, and _P. ponderosa_.

Occasionally, sites dominated by grassland are invaded by chaparral shrubs, particularly on marginal grassland sites. Such replacement is probably most often facilitated by fire, with the time of the year of the fire perhaps being most critical (Biswell 1952, 1956). Replacement of chaparral by oaks or pines is a more common event along forest-chaparral ecotones (Wilson and Vogl 1965). This appears to occur often as a result of changes in fire frequencies and intensities. It appears that these transitional areas are in a continuous state of change, shifting from one vegetation type to another as subtle, but critical changes in environmental factors occur. In these transitional areas, forest cannot be considered the more mature or climax vegetation type, because over the long run forest is probably replaced by chaparral as often as chaparral is replaced by forest (Wilken 1967). Because of long-standing efforts of fire suppression in southern California, there is evidence that chaparral has replaced forest in numerous locations (Minnich 1977).

A Conceptual Model of Chaparral Succession

Vegetational changes in chaparral are best expressed as a series of simple, repetitive cycles Vogl 1970, Hanes 1977). If these changes are visualized linearly through time, perturbations are seen to cause pulsations or ocillations in growth and productivity (fig. 1). Disturbances in many other vegetation types act retrogressively to set back vegetational development to some earlier or more pioneer successional stage, and the vegetation slowly returns in a series of steps to the predisturbance composition. Fire in chaparral causes stimulating spurts of growth, vigor, productivity, and species diversity (Vogl 1980, Force 1981). These stimulating effects decline almost as rapidly as they increase, until I renewed by another perturbation. Maximum species I diversity, productivity, and energy capture are reached shortly after fire in chaparral, in contrast to classical plant succession where a considerable length of time is required as the vegetation progresses through various plant stages before maximum productivity is attained.

In many vegetation types the burned vegetation is often considered abnormal and a stressed environment, whereas the preburn vegetation is assumed to be normal and healthy. Many fire studies are concerned with the length of time that it takes for a burned site to recover or return to its preburn composition. When chaparral succession is considered a cycle and fire islconsidered a pulse stimulator, burned and unburned vegetational compositions and conditions become equally important. When postburn declines in productivity, species diversity, and community senescence occur, then the length of time until the next fire becomes more important, perhaps, than the recovery rates after a fire. The concern in chaparral is not so much if chaparral will recover after fire and how long it will take, but rather how rapidly the system will decline without fire. In other words, what fire frequencies or fire periodicity will maintain maximum chaparral productivity?

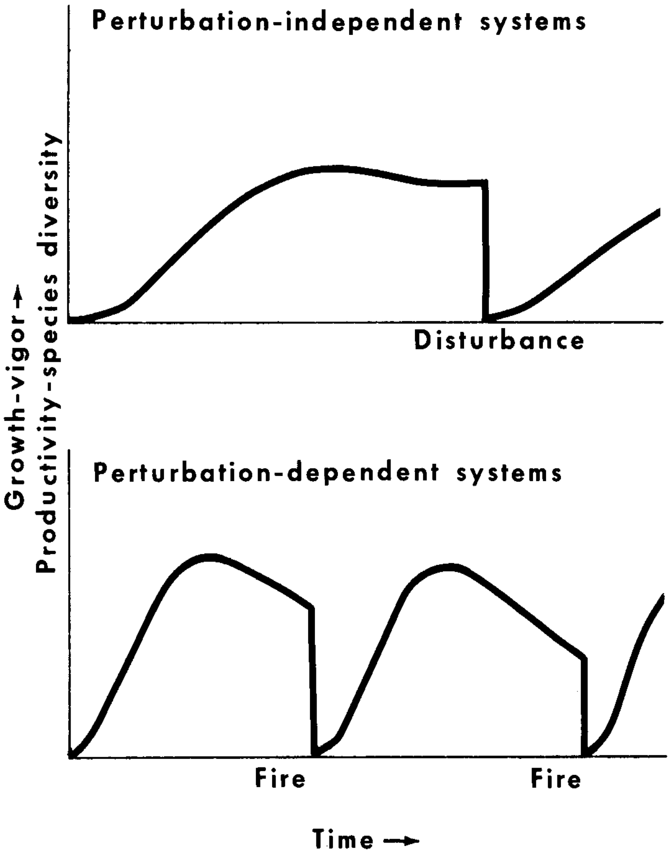

Figure 1--Disturbances in perturbation-independent ecosystems create vegetational setbacks and recovery is slow, whereas disturbances in perturbation-dependent systems such as chaparral stimulate pulses of growth which quickly decline unless disturbed again.

Pulse stimulation is common among perturbation-dependent systems (Vogl 1980), but the magnitude of response of chaparral following fire is exceptional. The short response time after disturbance and the rapid growth are particularly remarkable since chaparral exists under semi-arid conditions, being subject to drought stress during each growing season. Chaparral growth rates following fire stimulation may be unique among woody plants in dry environments.

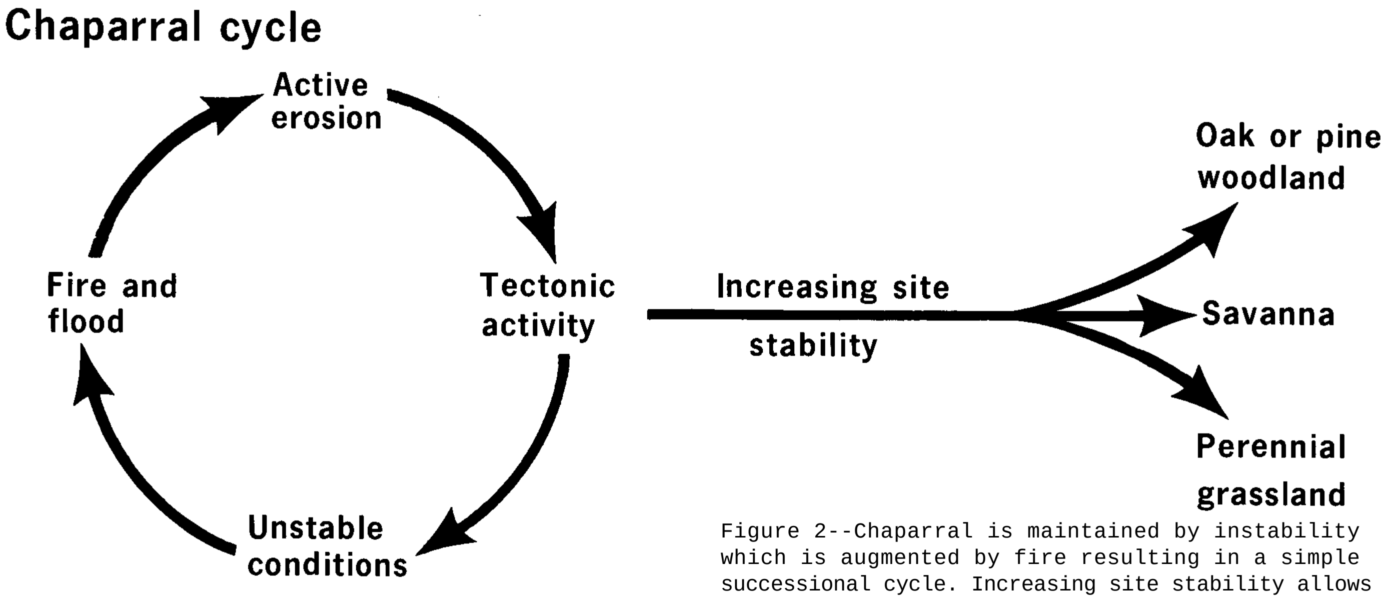

Figure 2--Chaparral is maintained by instability which is augmented by fire resulting in a simple successional cycle. Increasing site stability allows chaparral to be replaced by oak or pine woodland, savanna, or perennial grassland depending upon the degree of stability, fire frequencies, and location.

Nutrient flow through chaparral systems is largely open-ended, with most photosynthesis products moving down into adjacent communities such as valley grassland, riparian forest, and marshland where they remain or are temporarily trapped or detained before finally moving out to sea or on to desert playas. Chaparral fires also remove large quantities of materials off site in smoke plumes carrying particulates and volatilized products. Fire appears to act more as a waste remover than a nutrient recycler in chaparral (DeBano and Conrad 1978).

Continuance of this open-ended system is assured by the normal chemical and physical decomposition of bedrock by roots as well as by mountain building, uplifting, geological fracturing, fires, and floods which promote general instability and active erosion. This results in a continuous supply of new or raw nutrients which are readily extracted and utilized by the unique and extensive chaparral rhizosphere (Kummerow et al. 1977, Miller and Ng 1977).

A diagramatic model suggesting how instability contributes to a continuing chaparral cycle is presented in figure 2. Decreased erosion as a result of slopes wearing down without geological uplift and renewal leads to increased site stability. This new equilibrium allows chaparral to be replaced successionally by grassland or oak savanna or woodland at lower elevations and by pine or oak forest at higher elevations. The replacement of chaparral by these other types probably takes place slowly, an invasion which is undoubtedly augmented by changes in the fire frequencies that originally favored chaparral maintenance. In this model (fig. 2) fire not only serves as a pulse stimulator of growth and renewal, but also acts as a catalytic contributor to instability by encouraging erosion. This is accomplished by fire removing most of the above-ground growth and growth accumulations thereby allowing erosional materials to respond to the pull of gravity in an unimpeded manner. Fires followed by heavy rains create the notorious fire-flood sequences that perpetuate steep slopes and expose new substrates ((Munn 1920, Coleman 1953). Chaparral is able to replace chaparral as long as site instability prevails. The super-hot fires are just one of the key factors that contribute to the maintenance and continuance of chaparral (Hanes 1977). Other important factors include tectonic activities, the usual unstable and friable bedrock and soils (Krammes 1960), the typical heavy rains, and the fact that the steep slopes and substrates are not very receptive to water, particularly after fire (DeBano et al. 1979). The unreceptive soils result in rapid and heavy run off. These and other factors working together and in sequence help to ensure the continuance of steep and rugged topography; prime sites for optimum chaparral development. Successional replacement of chaparral with forest or grassland is prevented on most sites by controlling physical factors— various climatic and geologic features that help to perpetuate instability.

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