

Plant Demography and Chaparral Management in Southern California¹

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From the population point of view ecosystem behavior is the result of change in populations that is describable in terms of establishment, growth, and death. One example of the rigorous application of these ideas is the review of S. Levin (1976) which is sufficiently general to serve as a model for this discussion.

A landscape may be viewed as a mosaic of patches. The state of the ecosystem can be defined by the abundance of species measured in some appropriate way. Within each patch the species populations change as the result of mortality and establishment. Through time, species populations are disappearing in some patches and dispersing to and becoming established in others where they are absent; the general case of "island biogeography".

This simplification focuses attention on the processes which cause local extinction (disappearance from a patch) and which control local invasion (dispersal from outside the patch.) Extinction can result from biotically induced changes (competition, interference, parasitism, and predation); and from environmental extremes, including human disturbance.

Invasion into unoccupied patches by definition depends on dispersal ability, and the number of propagules of a particular species that will arrive in a patch during a period of time cannot be predicted unless the spatial distribution of the species is known. Predicting long-term change at the landscape level requires consideration of species distributions.

The disappearance of a species from a patch occurs when the local population is overwhelmed by biotic pressures or by environmental extremes. By causing mortality, competition generally acts to destabilize ecosystems. Predation and parasitism can be stabilizing forces, but interaction with variable factors of the physical environment means that often they are not. The expected situation is that species populations observed at any particular time will be undergoing change. True equilibrium or steady state probably does not

Abstract: Vegetation consists of interacting populations, with gap-formation and invasion having important short and long term consequences. Plant species differ in their requirements for establishment, and this must be considered in predicting their response to management.

exist in real ecosystems, and quasi-equilibrium (i.e. climax) can only be expected at large spatial scales which average the effect of local changes. The traditional emphasis on a hypothetical climax endpoint is now thoroughly discredited (White 1979).

Species differ markedly with respect to their liability to local extinction and capacity for invasion. Within a very large area, say 10,000 hectares, dominant species will have effectively a zero probability of extinction over a short period of time. The capacity to persist may be achieved by a short life span but high dispersal, or by living longer but perhaps sacrificing seed production or dispersal. Because of these kinds of life history differences, the rate of change of different species given a change in ecological circumstances can be different by orders of magnitude.

GAP REGENERATION

Despite the fact that ecosystems, especially those of arid regions, are expected to be continually reeling from the latest environmental extreme, it does not follow that there is an abundant supply of unoccupied space. Environments change, but not in a completely random way. At least before the unprecedented increase of the human population, ecosystems were formed of accumulations of species able to cope with the more-or-less recurrent patterns of environmental change superimposed on generally slowing changing averages. Assemblages of species in natural communities are able to survive and rebound from recurrent extremes, and large reservoirs of exploitable resources do not lie untapped for long. It seems reasonable to assume that if such instances of resource excess occurred, evolution would lead to the formation of genotypes capable of exploiting them. As a result, ecosystems, even as they are changing, tend to be close to fully occupied, with competitive interactions important, and conditions very unfavorable for the survival of immature individuals.

A consequence of the full occupancy of habitats is that a major factor limiting most plant populations is a suitable place in which to establish new individuals. Propagules of many, perhaps most species of plant require some kind of "gap" in which to become successfully established. Very few plants are capable of dispersing to a fully occupied habitat and maturing without relief, at some stage, from the competition of

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surrounding established individuals. Grime (1979) has elucidated some of the reasons for this pattern.

Because situations in which excess resources become available can be dramatically different, plant species have tended to specialize for establishment in particular circumstances. Grubb (1977) has discussed the importance of what he terms the "regeneration niche" of species, arguing that plant species diversity can only be understood by considering the critical importance of the establishment phase of plant life histories.

One measure of "regeneration niche" is the abundance of resource that must be available in order for a species to become established. A simple measure of the resource available at a particular point is whether or not another plant already occupies the space, and if it does not, how much unoccupied space lies around the point; that is, is a gap present, and what is its size. The concept of gap-dependent regeneration traces at least to A.S. Watt's classic 1947 paper, but it has recently been successfully applied to tropical rainforest, and it is clear that the concept can be generalized to provide useful insights into ecosystem change anywhere (Denslow 1980).

Plant species can be characterized by the properties of the gaps into which they are capable of invading. Some species appear to require large gaps in which the effect of competition is minimal, while others are capable of establishment in small gaps in which only limited growth is possible before competition with established individuals becomes significant. But capacity to invade depends not only on physiologically based stress-tolerance and competitive ability (Grime 1979), but also on dispersal characteristics which determine the ability of a species to find all of the available habitat.

GAP REGENERATION IN THE CHAPARRAL

The prevalence of fire in the chaparral obscures the fact that as in other vegetation types, chaparral species tend to be limited by the lack of suitable situations in which to become established. This has led to this hypothesis of vegetation change in the chaparral: For most of the interval between fires establishment of new individuals is unimportant because of competition and the accumulation of metabolic poisons in the soil. Exploitable gaps occur only when fire kills existing plants or portions of plants and stimulates germination. Dispersal is of limited importance. This hypothesis appears to have ample confirmation from the numerous studies that show that mortality of established shrubs results mainly from fire and that seedlings are common only after fire.

This model undoubtedly is correct for some species, such as the obligate seeders, but there is considerable variation among species with regard to features that determine ability to exploit gaps--dispersal, dormancy of propagules, dormancy breaking requirements, and seedling physiology. An alternative hypothesis is: What constitutes an exploitable gap differs among species. The recurrent nature of fire has resulted in many species developing an apparent dependence on fire for the creation of suitable gaps, but others may exploit gaps which arise without fire from the death of individuals from stress, predation, competition, or some combination of these. Dispersal, observed over lengths of time equivalent to the particular species generation time, will be significant.

EVIDENCE FOR THE GENERALIZED GAP HYPOTHESIS

It is well known that many species of the California shrublands do not require fire to establish seedlings. Less widely commented on are those species that do not seem to utilize the ideal conditions after fires to establish new individuals, such as Heteromeles arbutifolia, and Xylococcus bicolor in San Diego County (Zedler 1977, 1981). These species do not require fire-created gaps for establishment, and therefore projections of future stand composition based on knowledge of fire frequency without information on size, frequency, and distribution of gaps arising from other causes could lead to highly inaccurate predictions.

Heteromeles arbutifolia produces berries containing relatively small seeds which are bird dispersed. In studies conducted in chaparral in San Diego County, seedlings have not been observed in the first year after fire, but have been noted in both burned and unburned chaparral in a very wet year (Zedler 1980). H. arbutifolia is a vigorous sprouter which appears to suffer little mortality from fire. If the observed pattern of seedling establishment is typical, population change in this species is little affected by fire. The occurrence of gaps suitable for the survival of the seedlings to a stage where they can resprout after fire could be critical. Such gaps may occur independently of fire. It is possible that historically H. arbutifolia populations depended upon the senescence of shorter lived species for the creation of gaps suitable for establishment.

Heteromeles arbutifolia illustrates a general complication which arises in ecosystems of arid regions. During runs of dry years death or decline of individuals can produce gaps, but these gaps may not be exploitable because of insufficient moisture for germination and early survival, even though the supply is sufficient for the growth of established individuals. When a wet year or period occurs, the accumulation of unoccupied space may be available for colonization by species which have dispersed seeds into the

gaps. What constitutes a "gap" varies from year to year, even when the biotic occupancy does not.

FIRE FREQUENCY AND GAP FORMATION

In the chaparral fire, frequency clearly is a major determinant of the kinds of gaps that will occur. As the interval between fires increases, gaps formed by the death of individuals from other causes become more prevalent. In the limit, as in some ecosystems of moist regions, the establishment of species would become dependent on dispersal to relatively small gaps which appear from a variety of causes, and which therefore appear asynchronously.

The obvious accommodations of species to fire is clear evidence that chaparral in southern California burned frequently. However, the frequency of fire in the past is a matter of debate, and it is appearing increasingly likely that at least some portions of the southern California chaparral had fire frequencies much lower than has been previously thought (J. Keeley, this symposium).

If it is true that many areas in the chaparral remained unburned for 50 years or more, it may be that gaps created by the death of senescent individuals were a major feature of the landscape. This would explain the seemingly anomalous behavior of species such as H. arbutifolia. Also, with increasing interval between fires, the average size of dominant individuals would increase, so that the longer the interval between fires, the larger will be the average size of gaps created by the death of individuals. Increasing fire frequency would have the effect of decreasing the frequency of gaps formed by species senescence, and decreasing their average size. The diversity of gap types would therefore be reduced, and composition would gradually shift toward those species that are best adapted to exploit fire-created gaps.

The exploitation of fire-created gaps requires either an ability to build up a seed reserve between fires or dispersal from outside the area burned. Most species which are important fire-gap exploiters are of the first type, and dispersal plays only a limited role in post-fire recovery (Hanes 1971). But as fire frequency increases, species which depend on a local seed source run the risk of being burned before they have accumulated enough seed to regenerate. This has been documented for obligate-seeding species (e.g. Zedler 1977), but the same effect at a less drastic level might be expected for sprouting species. If a fire occurred after post-fire germination of seed reserves, but before the age of first reproduction of resprouts and seedlings, a drop in population abundance would result. Fire-gap exploiters with limited dispersal, even those that resprout, could suffer from very short intervals between fires. In such cases either the site would remain open until the next fire, or it

would be gradually filled by species which produce seeds which germinate without fire. Dispersal from outside the area is certain to be more important in instances where local seed banks are depleted.

FIRE-CREATED GAPS: AN EXTREME CASE

An opportunity to observe the effect of a short fire-free interval in mixed chaparral and coastal sage scrub was provided by a combination of circumstances on Otay Mountain in southwest San Diego County, California. In August of 1979 a wildfire burned a large area of shrubland, the greater part of which had not been burned since 1943. A portion of this burn was aerially seeded with annual ryegrass (Lolium multiflorum) as an erosion control measure. Rainfall was above normal in the 1979-80 growing season, and the ryegrass cover was dense over most of the seeded area. In the summer of 1980, an arsonist set fire to the grass, reburning a several-hundred-acre area within the 1979 burn. Although the fire burned in a somewhat irregular pattern, within the burned patches nearly all above-ground biomass was either consumed or badly charred. A study was designed to determine the effect of the grass fire on the regenerating shrubs. Five study sites were selected in which paired plots, one burned only in 1979 the other also burned in 1980 were established. Data were obtained on the frequency, density, and condition of shrubs and herbs in both areas, preliminary summaries of which are presented here. For simplicity, data from the twice-burned plots (1979 and 1980) are used with seedling densities for 1979-80 estimated from paired plot burned only in 1979 to produce a single merged set of data to show the population effects of the fire.

The changes in shrub densities and frequencies are the data most relevant to the the present discussion. Density (number of individuals per square meter) was measured for all species for which genus could reasonably be determined. Frequency was measured for all species.

The mortality of mature shrubs caused by the 1979 fire, which could be estimated by examination of the burned remains, followed patterns commonly observed (Table 1.) Ceanothus oliganthus, an obligate seeder, suffered complete mortality, as did Artemisia californica, a species which is sometimes capable of resprouting. Adenostoma fasciculatum suffered a little less than 50% mortality. Xylococcus bicolor is the most important species for which individuals could not be satisfactorily determined, and the change in frequency in 1/4 square meter plots is used as measure of fire effect. The species was considered present if at least one stem arose within the quadrat. The data (Table 2) show that in stand F, Xylococcus reappeared in 1980 in all quadrats in which it was present in 1979, showing that there was little if any mortality in this vigorous resprouter.

Table 1. Changes in density of selected species of shrubs after fire.

	Individuals (no./square meter ± SE)		
	Before 1979 Fire	After 1979 Fire	After 1980 Fire
<u>Adenostoma fasciculatum</u>			
mature (or sprouts)	1.5 ± 0.3	0.8 ± 0.2	0.2 ± 0.1
seedlings	nil	22.2 ± 6.1	0.6 ± 0.8
<u>Artemisia californica</u>			
mature (or sprouts)	0.3 ± 0.1	nil	0
seedlings	?	2.6 ± 0.6	0.4 ± 0.2
<u>Ceanothus oliganthus</u>			
mature (or sprouts)	0.2 ± 0.1	0	0
seedlings		6.0 ± 3.0	0

Table 2. Change in frequency (% occurrence in 1/4 meter square plots) of two species.

	Before 1979 Fire	After 1979 Fire	After 1980 Fire
<u>Adenostoma fasciculatum</u>			
mature (or sprouts)	.27	.15	.07
seedlings	nil	.75	.04
<u>Xylococcus bicolor</u>			
mature (or sprouts)	.13	.13	.04
seedlings	nil?	0	0

The 1980 grass fire caused severe to moderate mortality in both seedlings and resprouts which emerged after the 1979 fire (Tables 1 and 2). Ceanothus oliganthus seedlings were eliminated, Adenostoma fasciculatum seedlings were reduced by over 95%, and those of Artemisia californica by 85%. Surprisingly, the mortality from the grass fire was also substantial for the resprouts, with a 75% reduction in the number of individuals for Adenostoma fasciculatum, and almost a 70% reduction in frequency for Xylococcus bicolor.

Change in frequency of occurrence is a simple index of the creation of gaps by fire. The grass fire substantially decreased the occurrence of all four species, as is made clear by these data which give the percent change in frequency of occurrence of the species in 1/4 meter square plots resulting from the 1980 fire:

<u>Artemisia californica</u>	-15
<u>Xylococcus bicolor</u>	-66
<u>Adenostoma fasciculatum</u>	-84
<u>Ceanothus oliganthus</u>	-100

For Ceanothus oliganthus, this amounts to local extinction within the area of the 1980 burn. Adenostoma fasciculatum and Xylococcus bicolor also suffered substantially, while Artemisia californica, present at lower elevation sites, was much less affected, primarily because unlike most other species, a high proportion of burned seedlings resprouted after the 1980 fire.

It is clear that the 1980 fire has produced a disequilibrium, at least locally, in the vegetation on Otay Mountain. The gaps created may remain gaps, or as seems more likely, they will eventually be closed. If the interval between fire is long, the remaining individuals may become large enough to utilize all available space, with annual herbs and sub-shrubs occupying the space in the interim. However, there could also be establishment of shrub species that do not require fire for germination. It is possible that some of the chaparral species discussed above that do not establish seedlings after fire and that have animal-dispersed seeds could invade. More likely, however, is the expansion of coastal sage scrub species such as Eriogonum fasciculatum and Artemisia californica which produce large amounts of seeds and are common on disturbed sites. The changes to be expected will certainly vary locally and will be dependent on the local seed rain.

Elsewhere on Otay Mountain there are sharp boundaries between chaparral and coastal sage scrub that do not seem to correlate with soil type or topographic position. It seems possible that these boundaries are the margins of areas which might have been burned with one or more very short intervals, causing local extinction of chaparral species.

MANAGEMENT IMPLICATIONS

Whether planned or inadvertent, man's activities exert a strong influence on the many aspects of the environment which play a role in the formation and colonization of gaps. We have created novel ecological situations which have set in motion readjustments of species abundances in shrubland vegetation. The sharp changes observed in the grass fire of 1980 on Otay Mountain no doubt had natural analogs, but human influences have greatly increased the frequency of unique and rare episodes of gap formation.

Practical constraints make it unlikely that shrubland management in southern California can mimic the natural patterns of gap formation, assuming that these can ever be known. Although land managers speak of "restoring fire to its natural role"; this is probably impossible. Many natural fires must have been large and intense, and there is good reason to suppose that one large intense fire cannot be simulated by two smaller, cooler ones. Burning often enough to eliminate the possibility of wildfire may mean eliminating the distinctive micro-habitats needed for the germination and survival of some species. It seems certain that comprehensive management, no matter how carefully planned, will cause shifts in species abundances and distribution. These shifts may be readily observable, or they may take place slowly over many decades. Predicting what changes will occur will require much more knowledge of the population ecology of shrubland species, including native and introduced herbaceous plants.

It doesn't follow that all management must grind to a halt until research scientists certify that our knowledge is sufficient to make predictions within appropriate error bounds. However, skepticism about prevailing ideas and caution in implementing large-scale programs based on them are necessary. Research and evaluation by scientists from many disciplines and all sectors should be made an integral part of any management scheme.

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