Ecology of Some "Fire Type" Vegetation in Northern California

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CALIFORNIA is considered to have a "fire type" climate. Such climates are characterized by the coincidence of low temperatures with high moisture and, conversely, high temperatures with low moisture. By the end of May the rainy season is generally over and the hot dry season begins. As soil and fuel moisture become depleted the fire hazard increases and fires become commonplace during late summer and fall. In areas where fires are frequent and periodically destroy the plant cover these fires must be considered as an important aspect of the environmental complex. Such a consideration is based on the fact that fires produce rapid and, in most instances, marked changes in local environmental conditions as compared to the conditions which existed prior to the occurrence of the fire. The extent and degree of these changes are conditioned by the type and density of the plant cover, topography, temperature, wind, humidity, fuel moisture, etc.

Fire areas provide good examples where extreme conditions are imposed on plants and where adaptive mechanisms have been selected over long periods of time. These mechanisms can be directly

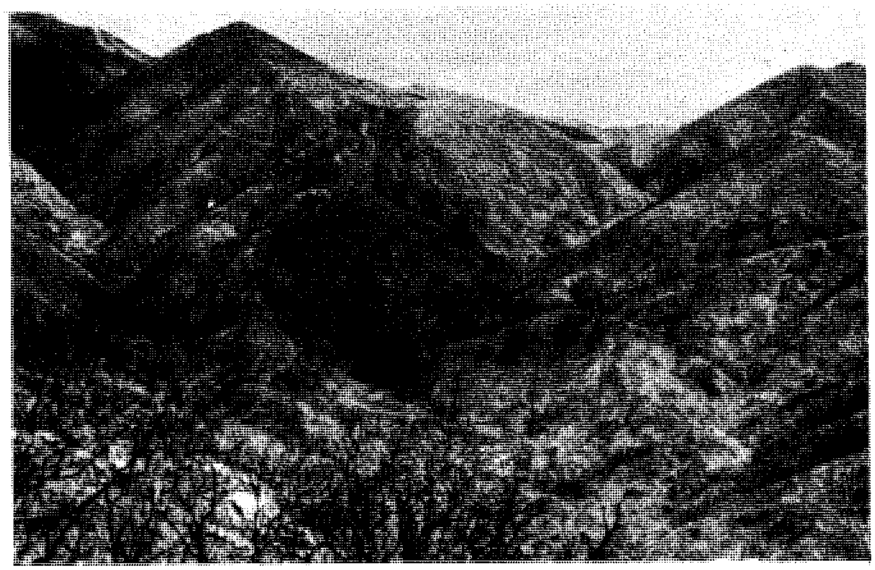

FIG. 3. Burned chaparral area (Santa Barbara fire).

related to the survival and perpetuation of populations, physiological races, and/or species in these areas.

VEGETATION FREQUENTLY SUBJECTED TO FIRES

The vegetation types often frequented by fire are: Scrub, Coniferous Forests, Mixed Evergreen Forests, Woodland Savanna, Chaparral, and Grassland (nomenclature from Munz and Keck, 1949). Chaparral and Coniferous Forests are considered here in detail owing to the fact that these types cover extensive areas in California and are burned frequently (Figs. 1 and 2). For example, the Donner Ridge Fire (August, 1960) burned in excess of 39,000 acres. The same year the Volcano Fire burned 42,000 acres. These fires burned both brush and conifer forest. In 1964, the Santa Barbara Fire consumed some 70,000 acres of chaparral (Fig. 3). In the fall of 1967, a single fire in southern California burned in excess of 100,000 acres of brush, timber, and grass. In California every summer and fall the fire cycle is repeated over and over. The vegetations that are frequently burned reproduce in abundance and prosper. The relations between environment and the adaptive mechanisms which provide for the perpetuation of the floristic elements of these vegetative types are the prime concern of this paper.

NATURE OF ADAPTATIONS

When considering adaptations one must constantly remind himself that whatever adaptive mechanisms exist in the "fire type" vegetations, they do not transcend the level of the individual organisms. It is not the vegetation but the individuals that make up the plant cover that respond to the environmental conditions imposed upon them. A second important fact: Vegetations are made up of species whose members are generally unable to exchange genes with members of other species. This means that similar adaptations have most likely evolved independently in the various floristic elements constituting the vegetation types mentioned earlier. It is also possible that these adaptations may have evolved very early and persisted, even though present genetic relationships are obscure. Whatever their genetic history, all have been rigorously selected by fire.

The kinds of adaptations that are most apparent among the members of many species which grow in areas frequented by fire are: 1) the ability to sprout and 2) increased reproduction from seed.

Sprouting and Bud Dormancy

In all the vegetation types listed earlier, some of the constituent species possess the ability to sprout. Two factors are involved here. First, some parts of the plant must survive the destructive effects of the fire and second, the apical meristems must be injured or destroyed so that their auxin production no longer inhibits the development of lateral buds and shoots. In other words, fire destroys the apical regions of the plant and the plant sprouts from roots, underground stems or lignotubers. Sprouting provides a rejuvenation of young vigorous growth on many plants that were formerly old, dry, and relatively useless. The new growth from sprouts provides a source of food for the browsing animals as well as a new "lease on life" for the plants. Sprouting results in a fairly rapid recovery of the vegetation where sprouting forms are common, such as chaparral and the brush understory in many forest areas (Fig. 4). Many tree forms also have the ability to sprout. Widely diverse groups such as oaks (*Quercus* sp.), manzanitas (*Arctostaphylos* sp.), coast redwood (*Sequoia sempervirens*), chamise (*Adenostoma fasciculatum*), and bunchgrass (*Stipa* sp.) exhibit these characteristics. The independent evolution of sprouting ability in many species that occur in "fire type" vegetations has very likely been an advantage to their survival. Furthermore, the selective pressure of fire has been an important factor in the development of these and perhaps, other types of vegetation. The positive influence of fire in the development of vegetations has been posed by Sweeney (1956), Ahlgren and Ahlgren (1960), and Cooper (1961).

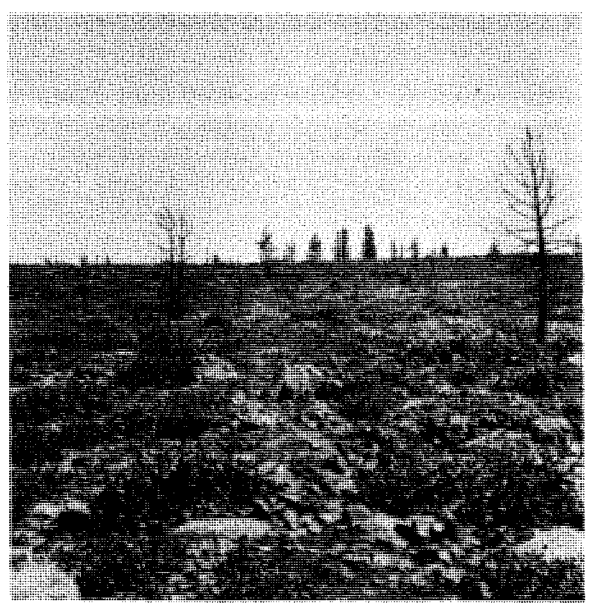

FIG. 4. Brush reproduction third year after fire in mixed conifer forest (Donner Ridge fire).

Reproduction from Seed

The vast majority of plants occurring on burns are from seed. In chaparral areas it has been shown that the seedlings are from viable seeds present in the soil before the occurrence of fire. The dispersal of seeds onto burns from plants present on adjacent sites does not contribute materially to the herbaceous cover of chaparral burns (Sweeney 1956). The limited herbaceous flora of burned areas within coniferous forests has no characteristic differences from that of the adjacent unburned areas and this flora is likely the result of a combination of the presence of viable seeds in the soil prior to the fire and, following fire, dispersal of seed onto the burn from plants of the adjacent unburned area. The factors governing seed production, germination and seedling survival are among the critical phenomena that pertain to vegetational history following fire.

Studies of burned areas in California, which include chaparral and coniferous forest types, indicate that the various elements of the flora of these areas are able to tolerate the conditions created by frequent burning owing to the evolution of different kinds of adaptive mechanisms which aid in their survival. Some of these adaptations are known, many are still unknown, or in the process of investigation.

One of the important adaptations that appears to be common is the tolerance of seeds to relatively high temperatures for short periods of time. These tolerance ranges, when correlated with time of exposure and heat penetration of the soil, become highly significant in explanations of the appearance of great numbers of seedlings following a burn. The tolerances of seeds to high temperatures is also conditioned by the amount of moisture present in the seed at the time of exposure. Generally, when the moisture level of the seed exceeds 30% as compared with the moisture content of the seeds in the air-dry condition, the seeds are killed at 80° C. This is in marked contrast to the survival of some air-dry seeds at temperatures in excess of 160° C. Measurements of heat penetration of soils and duration during burning indicate the heat levels during fires are often well within the tolerance ranges of the seeds (Sweeney 1956).

Another response of plants that is characteristic in burned areas is the marked increase in flowering (Stone 1951; Stocking 1966; Ammirati 1967). Stone (1951) points out that this is due to the increase in light intensity. The significance of marked increases in flowering and seed production relates to the continuation of these plants by periodically replenishing the supply of viable seeds in the soil.

Germination Behavior

Marked changes in the floristic composition of the vegetation the first, second and subsequent years following the occurrence of fire has led several investigators to study germination behavior of seeds of plants which characteristically appear in abundance following fires (Stone and Juhren, 1951, Sweeney 1956, Hadley 1961, Stocking 1966, Ammirati 1967).

The most striking correlation between germination behavior and species occurrence is with the "sudden" appearance and equally "sudden" disappearance of some herbaceous annuals. Experiments on germination behavior have shown these plants to have dormancy mechanisms that are inactivated by the action of fire. Most common of these is "seed coat" dormancy where the simple action of breaking the seed coats results in high percentages of germination. Conversely, without scarification, germination does not occur. Laboratory experiments using fire and/or heat has shown that these factors will break "seed coat" dormancy. More recently, Stocking (1966) has pointed out seed polymorphism in *Astragalus congdonii* and *Trifolium ciliolatum*. He found that these plants produce two types of seeds, some which germinated readily and some which required scarification. He further pointed out that those requiring scarification were the more abundant. Such seed polymorphism has also been reported in *Chenopodium album* (Williams 1962). The production of two types of seeds by these plants makes it possible for the occurrence of these plants during the interim between fires and accounts for their great abundance following fires. Further careful studies of the germination behavior of seeds may reveal that many more plant species may exhibit seed polymorphism.

Many species which occur on burned areas the first year after fire, are also normal to sites adjacent to the burns. The seeds of these same species generally fail to germinate under well established brush cover. This raises the question of the possible presence of inhibitors to germination and growth in the accumulated organic debris in addition to the effects of light and soil temperatures on germination behavior. Although the evidence is far from conclusive there are a number of interesting investigations on inhibitors. (Sweeney, 1956; Naveh, 1960; Liacos and Nord, 1961; Muller and del Moral, 1966).

Successional Patterns in Chaparral and Coniferous Forests

The chaparral vegetation type as described by Munz and Keck (1949) is a broad-leaved sclerophyll type of vegetation up to ten feet tall, dense and often nearly impenetrable. This plant cover is subject to fire. The physiognomy of the plant cover is much the same throughout its range, however, there is considerable floristic diversity. Sampson (1944) states that the chaparral of California covers approximately 8,000,000 acres. The range of distribution is in the coast ranges from Shasta County in the north to the mountains of southern California and the lower elevation on the west slopes of the Sierra Nevada. This vegetation is generally below the Yellow Pine Forest but the zones of overlap are considerable in many areas.

In the north, chaparral is generally restricted to the drier slopes of the inner ranges, while in the south, it occurs commonly on the west slopes of the outer ranges facing the ocean. The floristic differences between northern and southern distributions are also quite evident.

The similarities in the ecology of chaparral is remarkable throughout its range. With few exceptions the principal woody species are xerophyllous, fire tolerant and fire stimulated in terms of reproduction. Many show rapid regeneration by sprouting and seed germination is stimulated by fire. Herbaceous perennials show much the same response. Annuals reproduce primarily from seeds which were present prior to the fire. The tolerance of seeds of these plants to relative high temperatures has been demonstrated experimentally (Sweeney 1956). In addition to high temperature tolerance of seeds, there are numerous "fire type" herbaceous species which have evolved types of seed coat dormancy which is broken by the action of fire and/or heat. Members of these species are generally rare or absent except for the first season following a fire.

Studies of the fire responses of plants following the Napa-Sonoma fire in 1964 (Ammirati 1967) suggest that the east-west distribution of "fire type" annuals is closely associated with the moisture gradient. These species drop out of the herbaceous cover as moisture increases toward the west. Many of the perennials persist into the more mesic vegetations of the middle and outer coast ranges in the north.

Secondary successions are fairly rapid on chaparral burns where a large number of the brush species sprout vigorously following fire. Generally within a short period (6 to 8 years) the brush species again cover most of the burned over areas. The rate of recovery in southern California seems to be somewhat slower. In addition to sprouting, many seedlings appear as a result of fire stimulated germination of those exhibiting dormancy. (Fig. 5). Although there is a high mortality rate among seedlings the first year, there are numerous survivors that become part of the brush cover. After fire has temporarily removed the overstory, the burns are dominated by herbaceous plants which appear the first season (Fig. 6). These herbaceous forms dominate the burned areas the first, second, and third years. During the fourth and fifth years the broad-leaved herbs give way to grasses. The succession observed on chaparral burns follow somewhat similar patterns reported by Cooper (1922) and Sampson (1944). However, an analysis of population changes for different species shows that different species dominate the herbaceous cover during each of the first, second, third and fourth years. The "sudden" appearance of such species as *Antirrhinum vexillo-calyculatum*, *Emmenanthe penduliflora*, *Phacelia suaveolens*, *P. grandiflora*, *P. brachyloba*, and *Mimulus rattanii* the first season after fires and their scarcity or absence thereafter is correlated with their germination behavior. The seeds of these species are dormant and laboratory experiments have shown that scarification will induce germination. Germination is also induced by burning a light fire over the planted seeds. In the absence of fire or other means of scarification, the seeds of these plants fail to germinate. The populations of species which have no dormancy continue to increase until the environmental conditions change to the point where light, chemical inhibitors, or seedbed conditions become limiting. When the brush overstory has

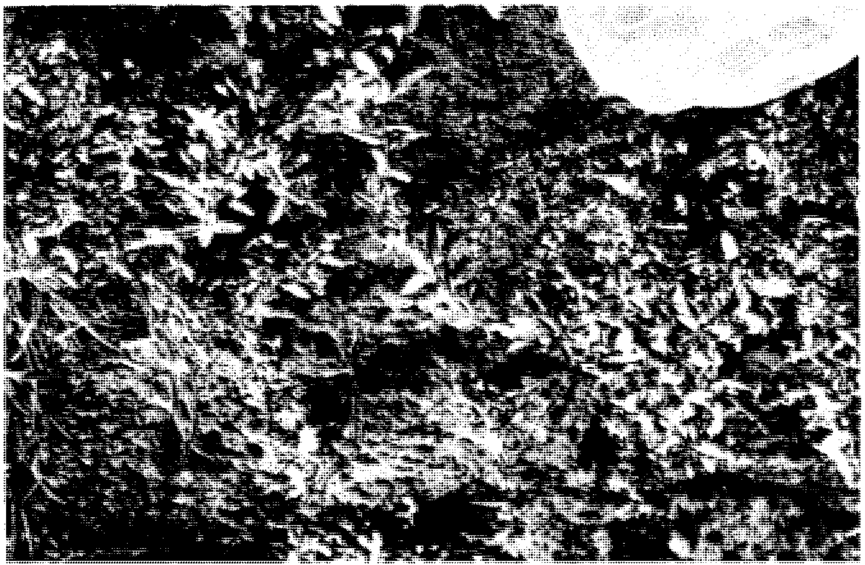

FIG. 5. Seedlings of *Ceanothus megacarpus* the first season after fire (Santa Barbara fire).

FIG. 6. Herbaceous vegetation the first season following fire (Santa Barbara fire).

FIG. 7. Herbaceous vegetation in mixed conifer forest after fire (Donner Ridge fire).

fully developed the herbaceous flora becomes rare or absent. With the advent of fire the whole cycle is repeated.

In some of the coniferous forest regions of California the successional sequence is somewhat similar. Studies of fire areas on the east side of the Sierra Nevada in mixed conifer forests of pine (*Pinus Jeffreyi*, *P. muxrayana*, *P. Lambertiana*) and fir (*Abies concolor*, *A. magnifica*) showed that fire was an important factor in maintaining the mixed conifer vegetation type. The plant succession was: mixed conifer → fire → herbs → shrubs → pine → fir.

A major difference in the herbaceous flora in the mixed conifer types and those of the chaparral is that there is no "fire type" herbaceous flora as such. The herbaceous cover on the burns is essentially like that of the surrounding areas, whereas on chaparral burns, many of the herbs occur only on the burned areas. Also there are fewer species than on the chaparral burns (Fig. 7). Brush shows a marked increase in the forest areas following fires. This is a result of the

FIG. 8. Development of brushfield on burned and degraded forest, Lassen County, California.

effect of fire on breaking the seed coat dormancy particularly in *Arctostaphylos patula* and *Ceanothus velutinus*, the two dominant shrubs in the understory. When the overstory of the forest is destroyed and/or burned, dense brushfields are established (Fig. 8). If and when the conifers overtop the brush, the brush dies and provides a good fuel source for the next fire. The inability of these shrubs to live under the conifers is probably owing to their inability to tolerate the reduced light intensities in the forest understory (Fig. 9). When fire is excluded from these forests, the conditions which are conducive to pine reproduction are changed. This results in marked changes in population densities of pine and fir. One might say that the pine forest reproduces fir, and following fire or other disturbance factors, the forest again reproduces pine. Fire thus becomes an important element in the continuation of the mixed conifer vegetation type in California (Fig. 10).

Experimental studies of germination behavior of seeds of pine and

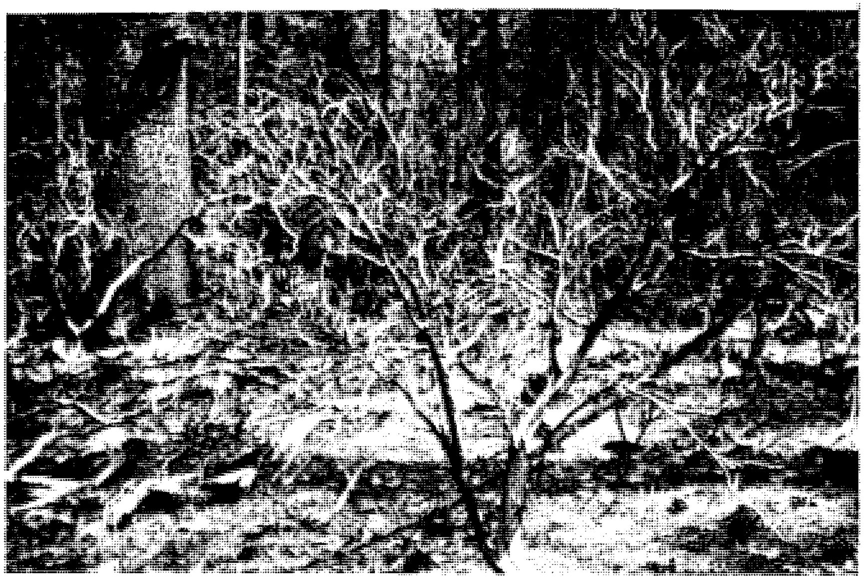

FIG. 9. Mortality in brush understory in mixed conifer forest, Lake County, California.

fir failed to reveal any dormancy mechanisms that were similar to those of "fire type" species mentioned earlier. Light and dark treatments also were not effective in stimulating or reducing the numbers of seeds germinating in laboratory tests. Field studies carried out at the Sagehen Field Station of the University of California establishes the action of fire in reversing the reproduction cycle of pine and fir. Population counts were made following the Donner Ridge fire which burned in August 1960 (Table 1).

Laboratory and field experiments have not as yet revealed any precise factor-function relationships between fire and pine reproduction other than pine seeds tend to germinate more readily on disturbed sites and there is a higher rate of seedling survival on mineral soils. Initial tests for the presence of organic inhibitors which may affect germination and/or seedling development has been negative.

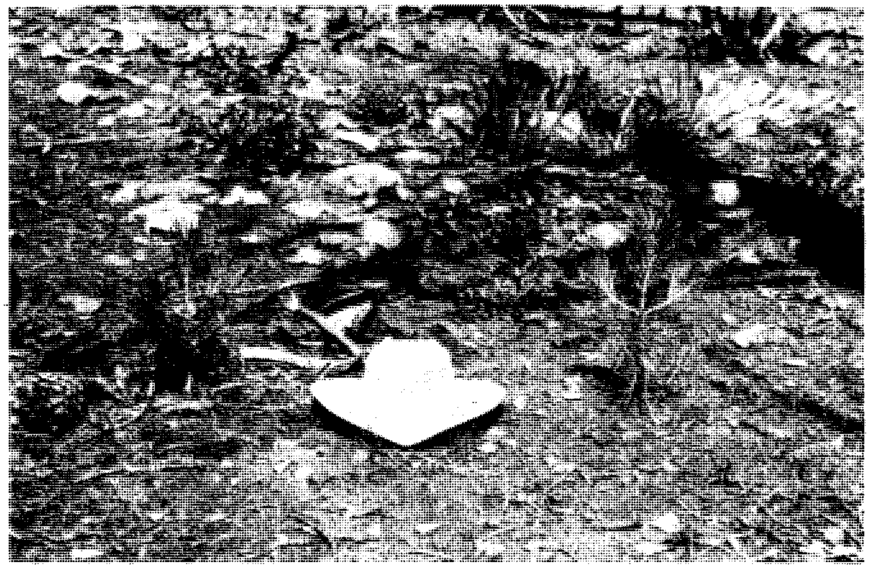

FIG. 10. Young pine trees in the understory in mixed conifer forest after fire, Nevada County, California.

Similar reproductive cycles are known for the redwoods. Both the giant sequoia (*Sequoiadendron giganteum*) and the coast redwood (*Sequoia sempervirens*) reproduce in abundance from seed following fire or other disturbance factors. The ecology of the giant sequoia has been admirably covered in an earlier paper at this conference. The seeds of both these trees show no dormancy characteristics in laboratory tests. We are now in the process of testing the effects of volatile substances being emitted by the fresh foliage of coast redwoods which tend to inhibit the development of seedlings of several test species including redwood seedlings.

The self-limiting aspects of these forests, where the tree overstory so changes the environment that proper conditions for reproduction no longer exists, further emphasized the importance of biotic factors in plant succession and further confuses the concept of climax vegetations.

TABLE 1

Pine and fir reproduction on burned and unburned areas in mixed conifer forest, Nevada County, California (data from Carl and Jane Bock, personal communication).

	Trees[1]		*Seedlings*[1]		
UNBURNED					
Pinus sp.	*Range*	*Total for all Plots*[2]	*Range*	*Total for all Plots*	*Total for Genus*
P. Jeffreyi	0–100	280	0–2	2	
P. contorta var. *Murrayana*	0–3	6	0–0	0	*3*
P. Lambertiana	0–9	18	0–1	1	
Abies sp.					
A. concolor	43–242	880	7–52	89	
A. magnifica	1–39	82	0–39	87	*563*
A. (unidentified)[3]			4–117	387	
BURNED					
Pinus sp.					
P. Jeffreyi	0–2	4	2–84	295	
P. contorta var. *murrayana*	0–0	0	0–19	44	*339*
P. Lambertiana	0–0	0	0–0	0	
Abies sp.					
A. concolor	0–1	1	0–0	0	
A. magnifica	0–1	1	0–0	0	*40*
A. (unidentified)[3]			0–21	40	

[1] Trees = over 5 years old. Seedlings = 5 years or less.
[2] Counts taken from 7 unburned and 10 burned 100 × 100 foot plots.
[3] Seeding of *Abies* which could not be identified with certainty as to whether they were *A. magnifica* or *A. concolor.*

CONCLUSIONS

Experimental studies of the ecology of these "fire type" vegetations points clearly to the fact that the aggregations of species and changes in population densities are the result of many different kinds of adaptations. It further emphasizes the danger of broad generalizations on reasons for the existence of vegetation types and successional changes in vegetation until investigations have been made in the field and laboratory of the ecological life histories of the plants making up the vegetation.

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