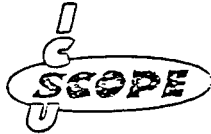


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## REPRODUCTIVE CYCLES AND FIRE REGIMES

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### ABSTRACT

An understanding of the evolutionary role of fire in ecosystem development requires knowledge of life history characteristics. Fire frequency plays an important role in determining the specific reproductive modes possible for a given environment. Since natural fires are randomly distributed in space and time, often a more important focal point than response to the modal fire frequency will be species' resilience to the range in fire frequencies encountered. Failure to appreciate species-specific differences in resilience in managing natural ecosystems can spell extinction for some species. A component of the fire regime particularly important to the evolution of reproductive strategies is the pattern of burning, i.e., patchy vs. extensive. Oftentimes a whole suite of characteristics will be associated with one pattern or the other. In some instances, a suite of characteristics may be common across all growth forms. More often, different growth forms carry with them a unique set of potentialities and limitations with respect to resilience to fire.

KEYWORDS: life histories, r and K selection, resilience

### INTRODUCTION

Emergent properties of ecosystems cannot be explained mechanistically without a clear understanding of population level phenomena. Thus, understanding fire's role in ecosystem development requires knowledge of the component species' life history attributes.

#### Life Histories and Growth Forms

A generalized life history of a plant population resembles that in figure 1a. We can distinguish an r-phase where the population is growing at or close to the maximum

possible (close to intrinsic rate of increase  $r$ ) and a K-phase where population growth is zero (close to carrying capacity  $K$ ). Not all populations have a senescence phase and in fact we can distinguish extremes in this respect (compare curves 1 and 2, fig. 1b). Different environments produce conditions which tend to favor a No. 1 or No. 2 type life history. The important environmental parameter is disturbance; No. 1 life history being favored in frequently disturbed environments, No. 2 in infrequently disturbed environments.

McArthur and Wilson (1967) described these respective environmental types as imposing r-selection (No. 1) or K-selection (No. 2), though as pointed out by Gadgil and Solbrig (1972) these are purely relative terms and no species is entirely r- or K-selected. Pianka (1970) attempted to define life history attributes of r-selected vs. K-selected species. According to Pianka, the former should have rapid development, small body size, early reproduction, and a high intrinsic rate of increase relative to K-selected species. Although this has provided a useful framework for life-history studies, there is abundant evidence that one must be cognizant of the particular ecology in order to predict attributes of organisms subjected to r- or K-selection (Wilbur, Tinkle, and Collins 1974).

One generalization concerning plant responses would be that growth form could be aligned along an r-K gradient with herbs at the r-end and trees at the K-end. While herbs could be favored for reasons other than r-selection, e.g., high winds could select for a low-growth habit, in the main this is probably a valid generalization. Thus, the frequency of a disturbance, e.g., fire, can select for different life histories and, as a consequence, different growth forms. It follows that the reproductive mode, i.e., those life cycle parameters which are immediately responsible for the continuance of the population through time, should be greatly influenced by differing fire frequencies.

#### Reproductive Cycles

It has recently been suggested (Harper 1977) that the term "reproduction" be restructured in usage to mean production of a new individual from a single cell, usually a zygote. Harper argues that what is termed "vegetative reproduction" is merely growth in a horizontal plane. However, the outcome of such "growth" may be identical to (apomictic) seed "reproduction," and unlike growth in a vertical plane, viz, production of new individuals distinct from the original plant. Janzen (1977) has perhaps suggested one solution to this problem by arguing that apomictic seed production be viewed as lateral growth. The purpose in making such a distinction

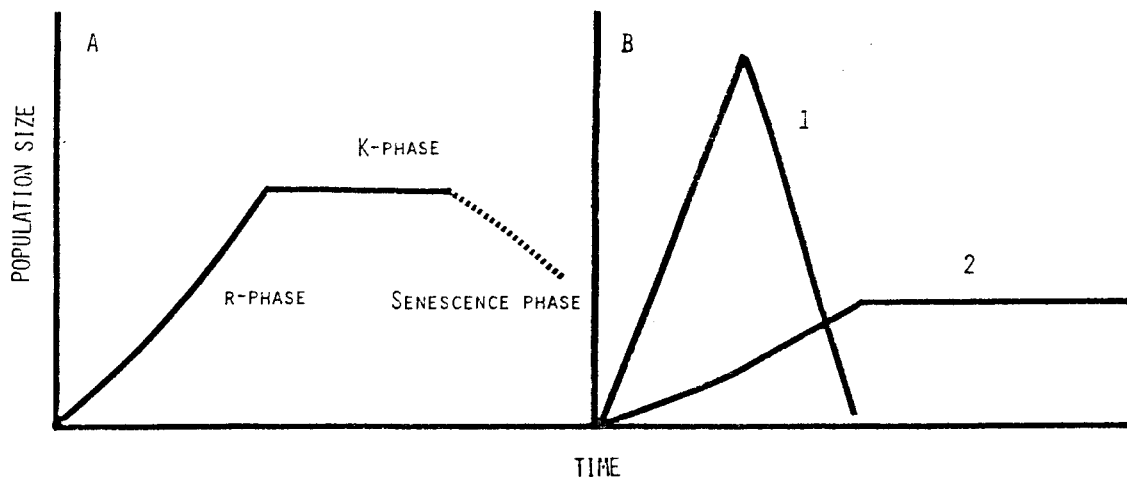


Figure 1.--(a) Generalized life history of a plant population, (b) life histories representing extremes with respect to population senescence.

is to emphasize the genetic identity of these offspring. The importance of such a distinction, in terms of r- or K-selection, is at least questionable in light of recent discoveries of abundant genetic diversity in many asexually reproducing populations.

In this discussion I will use reproduction in a more conventional sense and perhaps more broadly as "to produce again" (first definition, Webster's Collegiate Dictionary 1969). Thus, in the present discussion, the components of a reproductive cycle are those adaptations directly responsible for population recovery following destruction by fire. I will distinguish between "reproduction" and "regeneration." The former includes any lateral spread with the potential for producing "new individuals," either seed or vegetative reproduction. Regeneration will refer to the production of an individual in situ once it has been largely destroyed (e.g., resprouts from the stem or underground parts), see table 1.

The particular reproductive strategy (where strategy is the predetermined genetic component of the life cycle, after Harper and Ogden 1970) will include, to differing extents, both "reproduction" and "regeneration." It should be recognized that the basic genotypic program, or strategy, may include a range of possible developmental pathways dependent upon environmental conditions.

TABLE 1.--Reproductive and regenerative options in the reproductive cycle of plants

Reproduction		Regeneration	
Seed <sup>1/</sup>	Vegetative	From below-ground parts	From aboveground parts
Disperse	"Runners" above and below ground	Resprouts from stem or roots	Resprouts from epicormic buds
Remain <u>in situ</u> in the soil	Layering		
Remain <u>in situ</u> on the plant	Gradual spread by repeated resprouting from basal parts		

<sup>1/</sup>Sexual and asexual.

#### GROWTH FORM, REPRODUCTIVE MODE, AND FIRE REGIME

Particular growth forms and reproductive modes have evidently evolved in response to fire in many parts of the world, thus a wide array of plant communities have been labeled "fire adapted." In order to understand the evolution of these features we must consider the influence of fire per se, but also the components of a fire regime. Gill (1973) distinguishes three components: fire frequency, fire intensity, and season. Fire frequency plays a dominant role in determining vegetation structure and vegetation structure largely determines fire intensity.

In addition to being an important determinant of growth form, fire frequency may play an important role in determining reproductive strategies. The objective here is to evaluate the effect of fire frequency on reproductive strategies. The focus of this paper will not be to document the effect of fire on reproductive strategies of plants from all ecosystems; rather, selected systems will be emphasized. My approach will be to compare major vegetation types in which a particular growth-form dominates, viz, herbs, shrubs, trees, across the range of fire frequencies represented.

Several difficulties will be evident throughout. One, we have very incomplete knowledge of natural fire frequencies for most regions. As a consequence, the basis for ranking communities by fire frequency will be rough estimates based in large part on considerations discussed in the next section.

A second problem is that the preponderance of fire-ecology studies have been community level and thus there is a dearth of information on the population biology of most fire-type species. It is hoped that this report will illustrate the dynamics of postfire recovery and how little community-level indices tell about these processes.

A third difficulty is that fire is a natural disturbance with effects similar to other disturbances, e.g., frost, drought, blowdowns, tornadoes, heavy snowpacks, animal grazing, etc. Thus an underground stem may allow a woody plant to recover after a tornado or a fire. Likewise, thick bark may act as a barrier to dessication as well as fire damage. To evaluate the evolutionary effect of fire frequency on reproductive strategies, one must separate the selective influence of other environmental parameters. This, however, is not always possible.

Finally, one must distinguish between fire regimes which have a selective effect on plants, and those that do not. Harper (1977) distinguishes disasters from catastrophes; the latter being disturbances that do not occur frequently enough to be of any selective influence on the life cycle, e.g., to make a case that fire has played an evolutionary role in the Hawaiian flora, one must do more than demonstrate that wildfires can occur on occasion (cf. Vogl 1970).

#### Fire Frequency

Simplistically, fire frequency is determined by the frequency of ignitions concomitant with a "low" moisture content of the vegetation. A "natural" fire frequency is determined by the frequency of lightning and degree of aridity in a given environment. Since both of these parameters vary seasonally, the degree to which they coincide is important. Given "adequate" burning conditions, "natural" fire frequency should be a monotonic function of lightning frequency. On the other hand, fire frequency increases with aridity only to the point where increasing aridity results in insufficient biomass to carry a fire.

At present man plays a dominant role in determining fire frequency. On one hand he provides ignition for many wildfires (frequently during the driest season); on the other hand he puts out many "natural" as well as manmade wildfires. Whether the net effect is to increase or decrease the "natural" fire frequency is debatable and probably varies with the ecosystem.

Before proceeding, a word about the distinction between "natural" and "manmade" fire frequency is in order. "Natural" must be considered in context. To a sociologist, a natural fire frequency source may include modern man. To the U.S. Park Service (largely committed to the preservation of resources as they were at the time they came under its jurisdiction) natural fire frequency sources include aboriginal but not modern man. In the present discussion, "natural" is being used in an evolutionary context, i.e., the environment which has selected for reproductive strategies. It is assumed that relatively recent changes in fire frequency, e.g., due to aboriginal burning in North America, have tended to affect species distributions more than species adaptations. Potentially, this is less true in the Old World (with longer human influence) and where adaptations are under simple genetic control, e.g., serotiny in jack pine (Teich 1970).

Fire frequency has been defined in various ways. I suggest that the mean (arithmetic average) is not as relevant as the modal (most common) fire-free interval. Certainly, in many environments the variance and range is of more selective importance

than any measure of central tendency. Thus a species' resilience (i.e., ability to recover) to minimum and maximum fire-free intervals may be critical to its survival.

#### HERBACEOUS VEGETATION TYPES

The major herbaceous vegetation types representing a spectrum of fire frequencies are listed in table 2. Indicated also is a rough estimate of the modal fire frequency for each, based on interpretation of the available literature and evaluation of the fire climate and lightning frequency. Additionally, a suggested value for the minimum and maximum interval to which they could adjust (i.e., a measure of their resilience) is included.

TABLE 2.--Principal herbaceous vegetation types, with an estimate of their natural fire frequency and a rough estimate of the minimum and maximum fire-free interval to which they are resilient

Vegetation type	Modal fire frequency	Minimum fire-free interval	Maximum fire-free interval
----- Years -----			
Perennial grassland	5 - 25	0	10 - 50 (?)
Annual grassland	5 - 25	0	100 (?)
Fire floras	20 - 50	10	100 (200?)
Miscellaneous fire-tolerant species	?	1 - 2	?
Marshes	30 - 100	5	∞
Wet meadow and tundra	50 - 100	5	∞

#### Perennial Grasslands

Perennial grassland describes a number of plant communities in both temperate and tropical regions of the world. As the name implies, these areas are dominated by perennial grasses, though usually in association with a variety of annual grasses and herbaceous dicot species. In North America, there is an array of grassland associations (Kucera, this volume) and one can distinguish similar patterns in tropical regions (Phillips 1965). Grasslands generally have an annual period of drought coinciding with lightning storms, and occur on broad level plains or rolling hills that lend themselves well to the spread of surface fires (Daubenmire 1968, Vogl 1974). Fire plays a major role in the maintenance of many grasslands. A striking example of this is the experimental plots set up by P. V. Wells (University of Kansas) in eastern Kansas. Areas burned annually are vigorous grasslands whereas adjacent land unburnt for 15 years is largely second-growth hardwoods (personal observation, see also Bragg and Hilbert 1976). In light of this, it is not surprising that many tall grass prairie species play a dominant role in secondary succession in the East (Swan 1970). However, not all grasslands are fire dependent. Those on deep soils in regions subjected to occasional severe drought are generally not invaded by woody plants, even in the absence of fire (Weaver and Albertson 1956).

The dominant grassland species in both temperate and tropical regions are hemicryptophytes; the aboveground portion dies back at least once a year (Vogl 1974, West 1971). In most species the culms are tufted or caespitose with short rhizomes. Dormant buds occur at or just below ground level and commonly are protected by closely packed persistent dead leaves and leaf sheaths (Daubenmire 1968). Root systems are extensive and deep, commonly reaching depths of 2 meters (Weaver 1958). All these characteristics contribute to the ability of temperate and tropical grassland species to withstand intense grazing, frosts, and annual dry periods as well as severe periodic droughts (Albertson and others 1957, Weaver and Albertson 1956). Longevity of grass species varies widely; even among species of similar growth form, e.g., some tussock-forming grasses are reported to reach a maximum age of 10 years (Canfield 1957) whereas other species are thought to survive over 100 years (Crampton 1974).

The seed of some species is widely dispersed. The relatively small caryopsis, large awn, and persistent pappus-like hairs in some species (e.g., Andropogon) contribute to their ability to invade recently burned areas. Other species (e.g., Sporobolus), with different caryopsis characteristics, are seldom invasive into recent burns (Hodgkins 1958). Seed storage in the soil by perennial grass species is generally low to nonexistent (Lippert and Hopkins 1950, Major and Pyott 1966). This probably stems from a lack of soil carryover from year to year as well as erratic annual seed production. Apparently seedling establishment is an uncommon event (Hanson 1950).

Vegetative reproduction in perennial grasses is generally limited to production of small clumps or tussocks. This can, over long periods of time, lead to the formation of widely separated tussocks (Harberd 1967). Vigorous vegetative reproduction, through either stolons or rhizomes, is generally lacking. Under a frequent fire regime, such structures may be a liability since their proximity to the soil surface would mean greater losses to the plant (McLean 1969). There are, however, a variety of cost-benefit arguments for the presence or absence of stolons and runners.

Regeneration from basal buds following destruction of aboveground parts is well developed in most perennial grassland species. Commonly accompanying regeneration is an increase in seed production (Hadley and Kieckhefer 1963, West 1971, Vogl 1974). This probably results in seed production at a time of enhanced seedbed conditions. Undoubtedly, such a scenario would be affected by the season of the fire, particularly in temperate grasslands composed of mixtures of late-spring flowering C<sub>3</sub> grasses and late-summer flowering C<sub>4</sub> grasses. In North America lightning fires are concentrated between spring and summer (Komarek 1967, Barden and Woods 1973) with burning conditions beginning in the spring in the more southerly localities and later, northward. Cool season C<sub>3</sub> plants in southerly locations may have a higher probability of flowering as well as being in a more vulnerable phenological state at time of burning than late-flowering species. Warm season C<sub>4</sub> plants in southerly localities would be most resistant to spring fires since growth would be beginning, and afterwards they would be safe from fire for at least a year. Northward, fires would be later in the summer, after C<sub>3</sub> grasses had dispersed their seeds and at the time of C<sub>4</sub> grass flowering. There is some evidence to support this (Daubenmire 1968, Zedler and Loucks 1969, Rice and Parenti 1978).

Several factors affect the extent of postfire regeneration. Under annual burning, annual grasses and herbs commonly increase at the expense of perennial grasses (Pickford 1932, Kennan 1971, Smith and Owensby 1972). This is most marked under a natural regime of summer fires (Bragg 1978) since the perennial rootstocks suffer greater destruction (Garren 1943, Daubenmire 1968). Increased numbers of annuals also occur after severe drought (Weaver and Albertson 1956) and in both cases are probably related to increased open space for seedling establishment. In the absence of disturbance such species often are restricted to refugia created by extreme edaphic conditions.

Herbaceous dicot species common to grassland communities represent a variety of families and life histories, although mainly geophytes and hemicryptophytes. Seed production is annually more consistent among these broad-leaved herbs than in perennial grasses. Seed dispersal is via wind or animals. There is apparently little seed carryover from year to year except during prolonged droughts (Weaver and Albertson 1956). A few legume species, from frequently burned areas in the southeastern U.S., have seeds which demonstrate enhanced germination when exposed briefly to high temperatures ( $80^{\circ}$  -  $90^{\circ}$ C), though there is considerable germination without any heat treatment (Martin and others 1975). Some species spread both by seed and stolons or rhizomes, proportions varying with fire frequency. For example, wild strawberry (*Fragaria* sp.) invades recently disturbed sites via seeds, and once established spreads locally by stolons as well as producing seeds for more distal establishment. As the community becomes crowded, and probability of fire increases, stolons (which survive fires very poorly, McLean 1969) are produced less frequently (Holler and Abrahamson 1977).

Many herbaceous dicots can survive fires via underground parts which regenerate. The extent to which an individual can survive fire is closely tied to the depth of underground parts and thus one finds inter- and intraspecific variability in regeneration. A good example of prairie forbs capable of regenerating after fire is species of *Liatris* found throughout the midwestern and eastern portions of the U.S. Some can live perhaps 40 years (Levin 1973), and it is the older individuals with larger, deeper corms which are the most resistant to fire. Schall (1978) examined the age-structure of a population of *L. acidola* 2 years after fire in a mature prairie of southeast Texas. Her results (fig. 2A) suggest that many of the plants 1 to 3 years of age at the time of fire were killed, and following fire there was a flush of new seedlings. Thus, the population cost of fire for *L. acidola* is a loss of juveniles but the benefit is a surge of new seedlings. Benefits may outweigh costs in the life history of *Liatris* since Kerster (1968) has found that older midwestern populations of *L. aspera*, in the absence of disturbance, stop recruiting new individuals into the population (fig. 2B). Periodic fires may rejuvenate older populations. It is apparent from figure 2A that too frequent fires would be detrimental to *Liatris* populations as is true for other perennial forbs (Pickford 1932).

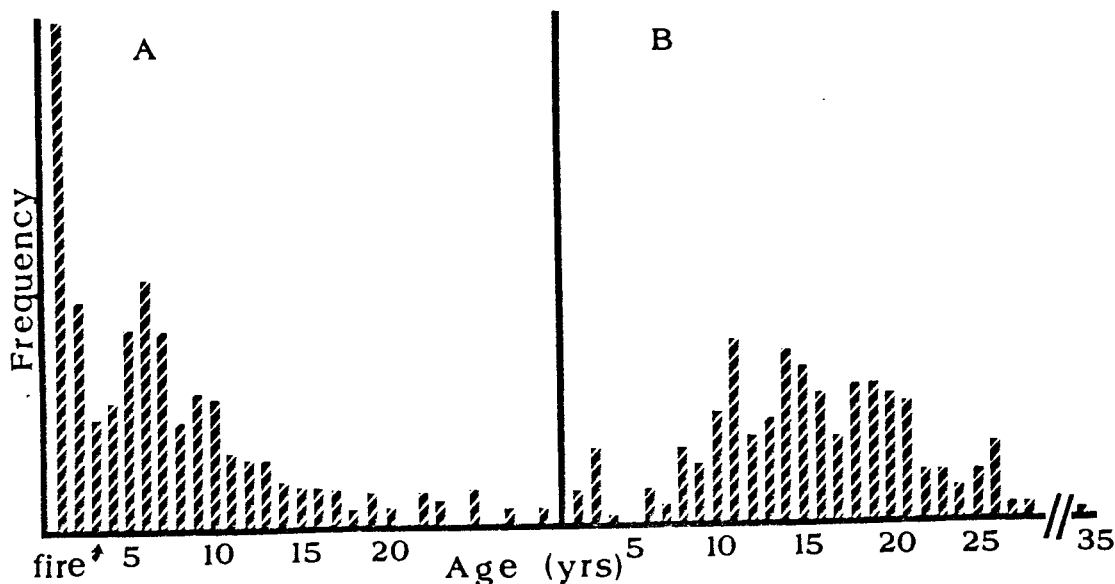


Figure 2.--(A) Age structure of a *Liatris acidola* population of 2 years after fire (redrawn from Schall 1978). (B) Age-structure of *Liatris aspera* population in the absence of disturbance (redrawn from Kerster 1968). Werner (1978) has demonstrated that there is a great deal of error associated with assigning ages in *Liatris*, though Levin and Kerster (1978) claim the ages are certain for plants under 5 years.



## Annual Grassland

Extensive annual grasslands are found mainly in Mediterranean climatic regions and are the result of disturbance (too frequent fires, severe drought, intensive grazing; any one or all). In California they occupy extensive portions of the Central Valley and Coast Ranges, having developed during the last 150 years from nonnative annual grasses and forbs. Clements (1920) proposed that the annual grassland replaced a pristine bunchgrass community after intensive grazing, coupled with drought. This view was based on the presence of small isolated populations of native bunchgrass assumed to be "relicts" and is considered by some to be true "beyond all doubt" (Heady 1977). However, Cooper (1922) argued that woody vegetation is climax in coastal valleys of California but has been replaced by grasslands due to repeated fires by man. Naveh (1967) invokes a similar scenario to explain the origin of annual grasslands in Israel (the origin of California's annual grass species). This theory is based on assumed "relicts" of chaparral within grasslands as well as historical documentation of chaparral replacement by grassland. In all likelihood, annual grasslands were derived both from perennial grasslands, particularly on deep clay soils, and (extensively) from woody vegetation on shallow rocky soils (Wells 1962). Increased fire frequency due to human exploitation is thought by Wells (1962) to be a major factor in their origin in the Coast Ranges of California.

Present fire frequency in annual grassland probably varies from annual fires to 50 or more years between fires. Despite the likelihood that annual grasslands in many situations owe their origin to frequent fires, there is little evidence that annual grasslands require frequent fire for maintenance. Perennial bunchgrasses invade annual grasslands very slowly (White 1966b), and the low vagility of chaparral seeds makes invasion of grassland by chaparral a threat only along narrow ecotones between the two vegetations (Schultz and others 1955, Biswell and Street 1948). Coastal sage species on the other hand have well-developed colonizing ability (Wells 1962) and when juxtaposed with grassland they can replace it in less than 15 years without fire (Westman 1976). Considering the broad expanse of many of these grasslands (and thus lack of an invading seed source) they are probably stable for long periods without fire. White (1966a) describes an oak-grassland area in the coast ranges which has remained stable more than 25 years without fire.

The dominant plants are annual grasses and forbs; most are natives of the Mediterranean region. Seed germination occurs late in fall following the first rains, with much of the growth occurring in winter and early spring. Flowering and fruiting are completed by early summer. Like other annual "weeds" these species are quite plastic in growth and phenology; in wet years they reach much greater sizes with larger seed production. Most species are highly r-selected for rapid germination and growth rates, small stature, and a large proportion of energy allocated to reproduction. Additionally, most possess typical colonizer attributes (viz, large numbers of small, widely dispersed seeds) and thus are ruderals in other than Mediterranean-climatic regions.

All species can tolerate frequent fires, largely because of sizable seed pools in the soil (Major and Pyott 1966), efficient means of burying seeds, e.g., hygroscopic awns (Naveh 1974), and the comparatively low temperatures of grass fires, which result in high seed survival (Daubenmire 1968). Annual grass species, however, are not well suited to annual fires. Smith (1970) found a 70 to 80 percent reduction in grass density the first year after fire and found that it took 3 years to reach prefire levels. In general, annual fires tend to favor forbs over grasses (Hervey 1949, Smith 1970). In some cases this may derive from slightly later flowering and fruiting by the grasses, which translates into a greater chance of seeds being attached to culms at the time of the fire, where temperatures are higher than at ground level (Daubenmire 1968). Also, the rosette growth form of the dominant forbs may enforce a greater spacing of individuals and thus lower burning temperatures in the seed-rain shadow. Additionally, since grasses are favored by a different set of growing conditions (Pitt and Heady 1978), fire may change the following season's growing conditions to favor forbs.

## Fire Floras

In some Mediterranean-climate regions of the world there are herb floras which have a life cycle closely linked to fire. Mainly the herbs exist only as dormant seeds in the mature scrub which is "climax" for the entire region. Except in isolated openings, no seeds germinate until fire removes the shrub cover, at which time there is a proliferation of many herbaceous monocot and dicot species. Among the Mediterranean areas of the world there are regional differences, e.g., in California the postfire herb flora is predominantly annuals, whereas in South Africa it is mostly geophytes, and in Chile there is no such flora (Keeley and Johnson 1977). Of the Mediterranean fire floras, California's is best understood, thus I will focus on this region.

Germination of the postfire herbs begins after the first winter rains following a chaparral fire. Flowering begins in early spring and fruitification is completed by late spring. The majority of species are annual dicots and will not be present the second year after fire.<sup>1/</sup> In order to germinate, the seeds require seed coat scarification, which comes in the next fire, presumably as intense heat, although this has not been convincingly demonstrated for many "fire-type" annuals (cf. Sampson 1944, Went and others 1952, Sweeny 1956, Christensen and Muller 1975) and other mechanisms have been proposed (Wicklowsky 1977).

The seeds appear to be quite long-lived, as evidenced by the proliferation of "fire-type" annuals after fires in very old (ca. 90-year) chaparral (personal observation). Undoubtedly, seed viability does decline in stands unburned for long periods of time; however, there is no information on the maximum fire-free interval they can withstand. On the other hand, the fire flora is sensitive to too frequent fires. Chaparral stands burned at several-year intervals are readily converted to annual grassland with elimination of native fire annual species. This is probably because the annual fire flora species do not compete well against aggressive annual grass species (Corbett and Green 1965). This is not surprising in light of the observation that the density of the fire-type annual vegetation is at least an order of magnitude less than the density of annual grasslands (cf. Sampson 1944, Horton and Kraebel 1955, Heady 1958, Smith 1970).

### Miscellaneous Fire-Tolerant Species

There are a number of herbaceous species not easily classified into any single community but which proliferate after fire. Epilobium angustifolium is a common fire follower in a variety of habitats throughout the higher latitudes of the Northern Hemisphere. It is a perennial which produces an abundance of small, widely dispersed comose seeds that quickly invade clearings caused by fire or other disturbances. Once established, an individual can spread over an area through vigorous rhizome production. It is eventually crowded out by later successional species and thus is dependent upon dispersing to new disturbances (Ahlgren 1960). Little information is available on the effect of fires on established populations. The proximity of rhizomes to the soil surface suggests they would not survive severe fire very well (McLean 1969). Although seeds have been found in mature forest soil (Karpov 1960 cited in Major and Pyott 1966) it is not known whether they survive fire. The architecture of the diaspore indicates they are primarily adapted to colonizing after fire or other disturbances and Salisbury (1942) states that they only establish on open sites.

Another fire-following species is Pteridium aquilinum. It resembles Epilobium in that it is a widespread species producing a proliferation of disseminules which invade recently burned sites, then spread vegetatively (Salisbury 1942, Oinonen 1967 cited in Harper 1977). Repeated fires, however, are less damaging to Pteridium because

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<sup>1/</sup>Keeley, S. C., J. E. Keeley, S. Hutchinson, and A. W. Johnson. Post fire succession of the herbaceous flora in the southern California chaparral. Unpublished ms.

the rhizomes are deep enough to survive high temperatures (Flinn and Wien 1977). Several other species have a similar life cycle, e.g., Equisetum sylvaticum in Canada (Beasleigh and Yarranton 1974), Pteridium caudatum in Venezuela, and Gleichenia spp. in New Guinea (Gillison 1969).

### Marshes

As used here, marshes refers to herbaceous communities in standing water much of the year. The chance of fire in any given year is low due to the moisture conditions of the vegetation. Periodically, however, severe droughts will cause a drastic drop in water table and produce conditions suitable for burning. Thus, in large part, fire frequency depends on local water table patterns.

The marsh dominants are perennial grasslike species from a variety of monocot families (e.g., Cyperaceae, Poaceae, Typhaceae, Juncaceae, etc.). Dependent upon the latitude, tillers emerge between spring and early summer. Not all tillers flower in a given year; e.g., Carex lacustris and C. rostrata produce tillers which commonly overwinter and flower in their second year then die (Bernard 1976). Most seeds are buoyant and dispersed to some extent by water. In fact, the marsh grass Paspalum has boat-shaped spikelets well adapted for water transport (Crampton 1974). If the study by van der Valk and Davis (1978) is typical, the soil seed pool of freshwater marshes is of considerable size. Seed of emergent species remain dormant until water levels drop and the seeds are exposed. This is also when fires are most likely to occur; thus frequent fires would not be conducive to reproduction.

Characteristic of most marsh species is a well-developed capacity for vigorous vegetative reproduction. Such stolons or "creeping" or "branching" rhizomes commonly reach several meters and more. Regeneration after fire is highly sensitive to fire temperatures. Garren (1943) states that marsh species are killed by dry-season fires because roots near the soil surface are destroyed.

In general it would seem that most marsh species are sensitive to fire due to its coincidence with seedling establishment and the high probability of destruction of below-ground regenerative parts. Nonetheless, marshes throughout the southeastern United States (and other regions of the world) are subject to severe droughts coinciding with lightning ignitions approximately every 30 to 100 years. The outcome of these periodic fires is on one hand to reduce encroaching woody vegetation but on the other hand to destroy marsh vegetation and replace it with submerged aquatics (Cypert 1972).

### Wet Meadows and Tundra

This group includes a heterogeneous collection of plant associations, with the major distinction being that they occupy sites which are moist most of the year. Certain "meadows" occupying drier sites, particularly at lower elevations or latitudes, are structurally similar to what has been discussed as "grasslands." There is also a certain amount of overlap between meadow vegetation and the herbaceous component of adjacent woodlands. Meadows and tundra are extensively developed at high elevations and latitudes. The more or less perennially wet character of the vegetation makes fires of infrequent occurrence and questionable selective importance.

The vast majority of species are perennial; commonly grasses and sedges. The conspicuous absence of annuals may be related to the "closed" nature of the vegetation, i.e., lacking openings for seedling establishment. Many species reproduce sexually infrequently (Salisbury 1942), and this is reflected in small seed pools in the soil (Major and Pyott 1966) and rarity of seedlings (Callaghan and Collins 1976, Callaghan 1976), even after occasional fires (Wein and Bliss 1973). Most species are vigorous vegetative reproducers, either through creeping or branching rhizomes, stolons, or layering. These species can regenerate after the tops are removed, though fires (except when the soil is quite moist) would be damaging since roots and other regenerative parts occur near the surface.

The heavy dependence on vegetative rather than seed reproduction may result from several factors. Salisbury (1942) suggests that lower temperatures at high elevations or latitudes, or lower light levels in woodlands, are not conducive to seed production which is physiologically more demanding. Alternatively, extreme conditions could make vegetative reproduction a safer gamble due to the much greater food reserves available; theoretically, seeds could evolve large reserves, though this may be too risky an investment in an environment where seed crop failures are common and unpredictable. Vegetative reproduction also has greater flexibility in initiating and arresting itself, unlike a germinating seed which is committed to a certain increment of growth before arresting development; a potentially important factor in an unpredictably "extreme" environment. Finally, moist conditions and lack of frequent disturbance, leading to a "closed" community with few openings, is a poor environment for seedling establishment, particularly ones with minimal food reserves (Thomas and Dale 1975).

#### Summary: Herbaceous Vegetation Types

The dominant strategy for surviving in a frequently burned perennial-type grassland is that of a long-lived perennial which, through its capacity to resprout from below-ground parts, appropriates space and holds it for extended periods. Certainly fire is only one aspect of the grassland environment which has selected for this strategy. The intensive selective pressure of droughts is suggested by the extensively developed root systems of most grassland species (occasionally reaching depths of 4 m or more, Weaver 1958). Perhaps to insure some colonizing ability (e.g., into areas subjected to severe drought, intensive grazing, badger building, tornadoes, or fire) seeds of the perennial grassland species are light; consequently they require "openings" in which to become established. In grasslands unburned for extended periods of time, openings may be rare and consequently seedling establishment is also rare. Under long fire-free periods, populations of some species may go extinct although most species are resilient to periods of low fire frequency as well as periods of high fire frequency. The extent to which perennial grasslands are dependent upon frequent fire is related to proximity and invasiveness of woody vegetation.

Mediterranean-climate annual grasslands represent one of the most fire-resilient herb communities; existing under frequent as well as infrequent fires. These annual species demonstrate few specific adaptations to fire per se. They have r-selected attributes and are species adapted to rapid colonization. Although most r-selected species require frequent disturbance to remove invading and more competitive K-selected species, such is not the case for these annual grassland species. Once the original vegetation has been removed, reinvasion is imperceptibly slow and thus r-selected species remain dominant with or without additional disturbance.

The fire-type annual floras of certain Mediterranean regions exhibit the greatest degree of adaptation (specifically) to fire. These species are specialized r-strategists with rapid establishment from stored seed "only" in response to fire; however, they are not good colonizers, perhaps because disturbances are generally widespread. They are not resilient to very frequent fires (return of the shrub cover is required to shade out other more aggressive herb species) but can withstand fire-free periods as long as a century. Thus, fire-type annuals illustrate that specialized adaptations to fire do not necessarily imply adaptation to frequent fires.

Epilobium and Pteridium illustrate strategies adapted to periodic intense fires which do not destroy the parent population but open up nearby areas. Abundant light, wind-dispersed disseminules are well adapted to broadcast colonization of denuded sites, even at some distance from the parent population. It should be recognized, however, that these species are not dependent on fire since they commonly colonize sites opened up by other types of disturbance.

Species common to most marshes, meadows, and tundras appear to be poorly adapted to fire and not resilient to frequent fires. They differ from more fire-adapted communities in that reproduction is predominantly from stolons and shallow rhizomes, structures easily destroyed by fire. Although these three communities can recover from fire, its effect is probably more that of a catastrophe (sensu Harper 1977) in that the selective consequence is to decrease "short-term fitness."

### SHRUB VEGETATION TYPES

The major shrub vegetation types to be considered represent adaptive responses across a spectrum of fire frequencies (table 3).

#### Mediterranean-Climate Evergreen Scrub

The five regions of the world characterized by a cool-winter-rain, hot-summer-drought climate are dominated by a vegetation of closely spaced evergreen shrubs with heavily sclerified leaves. In most of these regions summer droughts are occasionally interrupted by thunderstorm activity resulting in lightning fires carried far by the dense continuous brush cover. Although the five Mediterranean regions are broadly similar there are significant differences. I will focus in detail on the California chaparral since the life histories of these shrubs (coupled with associated trees, see later section) illustrate that species in a fire-type community represent a variety of optima and resiliences to varying fire frequencies.

TABLE 3.--Principal shrub vegetation types, estimated natural fire frequency, and a rough estimate of the minimum and maximum fire-free interval to which they are resilient

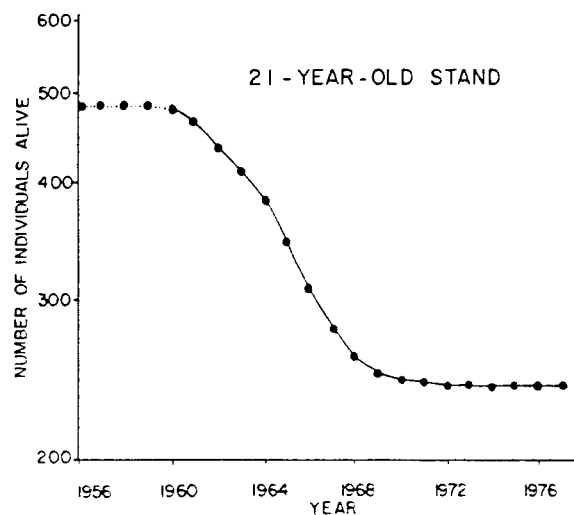
Vegetation type	Modal fire frequency	Resilience	
		Minimum fire-free interval	Maximum fire-free interval
----- <u>Years</u> -----			
Mediterranean-climate evergreen scrub	20 - 50	10	100-200 (?)
Mediterranean-climate deciduous scrub	30 -100	10	100(150?)
Humid evergreen scrub	20 - 30	2 - 5	200 (?)
Arid (desert scrub)	50 -100	10 - 20	(?)
Temperate forest			
successional shrubs:			
Western forest shrubs	20 -100	5	300-400 (?)
Eastern forest shrubs	100 -500	5	∞
Scrub steppe	100 -300	30	∞
Tropical rain forest			
understory shrubs	∞	∞	∞

California chaparral consists of shrubs 1.5 to 3 m tall almost always occurring in stands with an (aboveground) even-age structure (excepting one anomalous shrub, Yucca whipplei). These stands are distributed in a mosaic determined by burning patterns. Presently nearly all of the acreage burned in southern California results from manmade fires (Keeley 1977b). As a consequence fire frequencies vary with proximity to habitations; e.g., fires occur every 2 to 5 years in some heavily used foothills of the San Gabriel Mountains overlooking Los Angeles whereas large portions of the little-used Santa Ana Mountains have never had a recorded fire (USDA For. Serv., unpublished data). The commonly accepted modal frequency of natural fires is 20 to 30 years. Undoubtedly in prehistoric times this varied widely dependent upon elevation and proximity to the coast (Keeley 1977b, Byrne and others 1977).

Chaparral shrubs represent a variety of plant families and life histories. Some species, e.g., Heteromeles arbutifolia, Cercocarpus betuloides, Rhus laurina, and Rhus ovata, are capable of great longevity (100-200 years?) becoming small trees in isolated localities. Others, in particular Ceanothus species, are traditionally considered short-lived (40-60 years), although their longevity is closely tied to stand structure. As shown by Schlesinger and Gill (1978), as the canopy closes in "pure" stands of Ceanothus megacarpus, there is a sudden die-off (fig. 3) presumably due to rapidly increasing competition for light. In older mixed stands, mortality of Ceanothus greggii is apparently constant (Keeley and Zedler 1978) and probably reflects gradually increasing competition for light and soil moisture in this shade-sensitive shallow-rooted species. Thus, if these "short-lived" species escape close competition they can be quite long lived (Keeley 1975, Schlesinger and Gill 1978).

Seed production fluctuates widely from year to year dependent in large part on precipitation patterns. Some species initiate flower buds the year prior to flowering, whereas others do not; thus, seed production is not usually synchronous across species (Keeley 1977a). There is little indication that seed production declines with age, and in one study (Arctostaphylos glauca) seed production was much greater in 90-year-old shrubs than 20-year-old ones (Keeley and Keeley 1977; a similar pattern was found for Adenostoma fasciculatum, Keeley and Keeley unpublished data). Seed dispersal modes vary widely, e.g., the chaparral shrub, Adenostoma fasciculatum produces an abundance of light seeds; however, they are not highly specialized for (and chaparral is not conducive to) wind dispersal and probably are not dispersed widely. Ceanothus and Arctostaphylos species are important chaparral constituents with, for the most part, localized seed dispersal. Quercus dumosa is a common chaparral shrub characterized by erratic production of large acorns potentially widely dispersed but heavily preyed upon. A number of quantitatively minor species, e.g., Heteromeles arbutifolia and Rhamnus crocea, have fleshy fruits which are probably widely dispersed by birds.

Figure 3.--Density of live Ceanothus megacarpus shrubs after fire in 1955 (from Schlesinger and Gill 1978, with permission of Duke Univ. Press., copyright by the Ecological Society of America).



Seed storage in the soil is variable. The most common species, Adenostoma, Ceanothus, and Arctostaphylos, have a seed-coat scarification requirement usually met by intense heat during fire (Stone and Juhren 1953, Quick 1935, Hadley 1961, Berg 1974). Other species such as Quercus dumosa, Rhamnus crocea, Heteromeles arbutifolia, and Prunus illicifolia have no such scarification requirement and will germinate readily (Mirov and Kraebel 1937, Keeley unpublished data). Consequently, seedlings of these species occasionally establish in mature chaparral; Patric and Hanes (1964) recorded several hundred per hectare in very old chaparral. It is doubtful whether these contribute to the mature canopy since they are usually stunted (Patric and Hanes 1964) and many eventually die, in part, from overgrazing by small mammals (Keeley 1973, Horton and Wright 1945). Thus these shrub seedlings seldom establish under mature chaparral or in openings created by dead shrubs (Hanes 1977). Following fire, there is an abundance of seedlings of Adenostoma fasciculatum and certain species of Ceanothus and Arctostaphylos, all from soil-stored seed, germinating in the first postfire year. Postfire seedling establishment of other species is sporadic and often insignificant numerically (Zedler 1977a).

The capacity to resprout from basal parts after fire is widespread in chaparral shrubs, being found in all species except the majority of Ceanothus and Arctostaphylos species. The species which can resprout after fire vary in the proportion of the population which actually survives to do so. Thus, postfire regeneration is either by seedlings from soil-stored seed or resprouts from basal vegetative parts or both. The dependence upon seedlings or resprouts varies from species to species. We can picture this schematically in figure 4 where a point along the abscissa, corresponding to a particular proportion of seedlings vs. proportion of resprouts, describes the reproductive tactic. However, this position will vary spatially (from population to population) and temporally (from one fire to the next); thus a species is best characterized by a reproductive strategy which occupies a region along the abscissa. For example, Quercus dumosa is a vigorous resprouter but seldom establishes seedlings, thus its reproductive strategy is represented by region "a" along the abscissa. The ubiquitous Adenostoma fasciculatum is temporally and spatially quite variable in post-fire resprouting and thus might be described by region "c." There is one significant exception to this pattern; the majority of Ceanothus and Arctostaphylos species do not occupy a region along the abscissa but rather a single point (see the arrow, fig. 4). These species are totally incapable of resprouting under any condition and thus are entirely dependent upon seedling production for postfire regeneration.

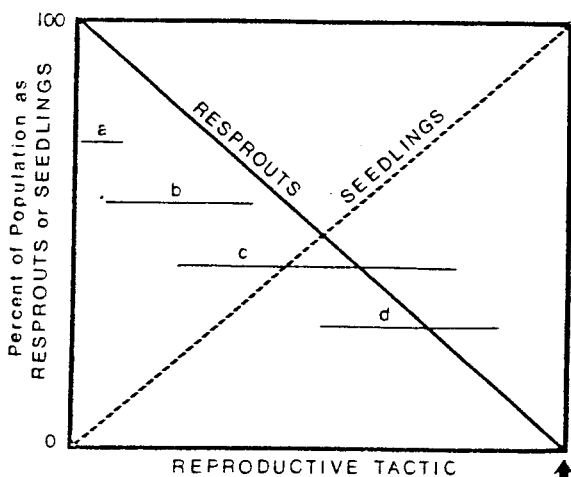


Figure 4.--Reproductive options available to shrubs after fire. See text for further explanation.

A summary of these characteristics is given in table 4. From this we can distinguish two modes. One group, consisting of the most abundant chaparral shrubs (Adenostoma, Ceanothus, and Arctostaphylos), is best developed on the more xeric sites and is shade intolerant. They produce more or less locally dispersed seeds which are stored in the soil until stimulated by fire to germinate. Some resprout, but others do not. The other group consisting of shrubs such as Quercus dumosa, Heteromeles arbutifolia, Rhamnus crocea, and Prunus illicifolia are best developed on the more mesic slopes. They are mostly long-lived, shade-tolerant species capable of outliving, overtopping, and shading out most of the group 1 species. They produce widely dispersed seeds which do not require fire for germination. They occasionally establish seedlings in mature chaparral, but seldom contribute seedlings to the postfire flora. All are vigorous resprouters.

## TWO REPRODUCTIVE STRATEGIES

How can we account for these two different reproductive strategies? In light of modal fire frequency of every 20 to 30 years, the group 1 strategy is easily rationalized: Produce seeds cued to germinate only after the next fire, since (1) seedlings would be unlikely to establish in the shade of existing shrubs, (2) seedlings are likely to be eaten by herbivores, (3) another fire is likely to occur before the mature shrubs die out, (4) because of their smaller size, these later-establishing seedlings or "saplings" would stand little chance of surviving a fire in order to resprout, and (5) the more intense fires on the more xeric sites translate into fewer resprouts and more openings for postfire seedling establishment. Also, since these fires will be quite widespread, little benefit would be derived from dispersing seeds far and wide.

The group 2 strategy is difficult to rationalize in light of frequent fires. Seed production seems to contribute little to the future population; rather, these species depend upon resprouting to maintain population levels. One could argue that perhaps these species are relicts representing an evolutionary dead end in the face of frequent fires. Although there may be some merit to this idea, another explanation might be the following: Since these species are best developed on north-facing slopes, in ravines, and other disjunct mesic sites, widely dispersed seeds would be highly adaptive (Bullock 1978). Once a seed got to one of these more mesic sites, it would be better off germinating directly because the more mesic site would mean that: (1) It is less likely to burn as frequently as a more xeric site. (This seems particularly likely when one considers the mosaic pattern of many fires [Minnich 1974], and the possibility of more infrequent fires in prehistoric times [Wells 1962, Keeley 1977b, Zedler 1977a, Burne and others 1977].) (2) More mesic slopes would mean less intense fires and thus greater postfire resprout survival which would out-compete seedlings establishing after fire. (3) Less intense fires would mean a greater chance for late-establishing understory "saplings" to survive fires and to resprout.

Data necessary to evaluate such ideas, e.g., seed dispersal distances, seedling recruitment rates in group 2 species, successional changes in very old chaparral, and natural fire frequencies, is lacking. For the most part, group 1 species seem most closely adapted to the chaparral fire cycle: (1) They are the most abundant species; (2) they produce refractory seeds dependent upon intense heat for seed-coat scarification; (3) the resprouting species in this group produce large, bulky basal burls or lignotubers, which are specialized starch-storing structures with dormant buds that give rise to resprouts after fire; and (4) many species are highly "specialized" obligate-seeding shrubs.

## LIGNOTUBERS

Jepson (1916) first described basal burls on a sprouting species of Arctostaphylos and later Wieslander and Schreiber (1939) noted that the burl was not a result of sprouting but a normal development the first year. It is this distinction which most



TABLE 4.--Qualitative summary of chaparral shrub characteristics (NS = nonsprouting, S = sprouting, - = poorly developed or absent, + = well developed), see text for complete explanation

Species	Longevity	Shade tolerance	Fruit type	Dispersal	Fire-stimulated germination	Resprouting	Basal burl
<u>Adenostoma fasciculatum</u>	+	-	achene	-	++	+	++
<u>Ceanothus</u> NS spp.	-	-	capsule	-	++	-	-
S spp.	-	+	capsule	-	++	+	+
<u>Arctostaphylos</u> NS spp.	+	-	dry berry	-	++	-	-
S spp.	+	+	dry berry	-	++	++	++
<u>Rhus ovata</u>	++	++	drupe	?	++	++	-
<u>Quercus dumosa</u>	++	++	acorn	++	-	++	-
<u>Heteromeles arbutifolia</u>	++	++	pome	++	-	++	-
<u>Rhamnus crocea</u>	+	?	berry	++	-	+	-
<u>R. californica</u>	++	++	berry	++	-	++	-
<u>Cercocarpus betuloides</u>	++	?	plumose achene	++	-	++	-
<u>Prunus illicifolia</u>	++	++	drupe	++?	-	++	-

clearly separates group 1 and group 2 because some of the latter group's species, e.g., Heteromeles, will sometimes form an irregularly shaped platformlike structure after repeated resprouting. Basal burls or lignotubers are known from sprouting shrubs in other Mediterranean regions, being common in the South African fynbos (Kruger 1977), but most highly developed in the Australian mallee (Kerr 1925). Outside Mediterranean regions lignotubers are rare except in a few arid savannas where they appear to be primarily involved in surviving summer drought, since aboveground parts die back annually regardless of fire (Rawitscher 1948).

Since lignotubers are not a prerequisite for resprouting after fire (resprouting is characteristic of nearly all woody dicots, Wells 1969), perhaps they are not an adaptation to fire per se, but to fire in conjunction with the Mediterranean climate. The unique combination of features found in these regions is one of shrubs growing in nutrient-deficient soils exposed to frequent fires during summer droughts. The result may be problems unique to Mediterranean-climate shrubs; they depend upon an extensive root system to obtain sufficient soil moisture and inorganic nutrients, so when the tops are removed by fire an extensive root system may not be supportable without a ready store of carbohydrates. This would be particularly so after summer fires, since resprouting is commonly postponed until the first fall rains (Sauntier and Wagle 1967, Biswell 1974, Tratz and Vogl 1977). Such an hypothesis would account for why the non-burl-forming sprouting species (group 2) favor the more mesic slopes.

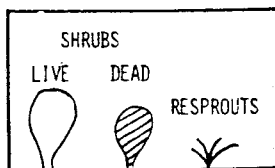
#### OBLIGATE-SEEDING SHRUBS

So lignotubers may not represent a specialized adaptation to fire per se, but to fire within the context of the Mediterranean climate. Another characteristic of reproductive modes in some Mediterranean floras is the high proportion of species (in genera where lignotuberous species are common) totally lacking the ability to resprout after fire. In California, for example, approximately one-third of the Ceanothus and Arctostaphylos species resprout from lignotubers after fire in addition to postfire seedling establishment. The rest of the species are incapable of resprouting and thus are obligate seeders. A similar array of genera with lignotuberous species and obligate-seeding species is found in the Australian mallee (Specht and others 1958) and the South African fynbos (Kruger 1977). Such species, which lack ability to resprout from underground parts, are rare among woody dicots (Wells 1969). That these obligate seeders are "fire-type" species as suggested by Jepson (1916) is supported by their high frequency in the chaparral, mallee, and fynbos and their absence in the Chilean matorral, a Mediterranean-climate region of low natural fire frequency (Mooney 1977b).

The adaptive significance of obligate-seeding species is not obvious. Evidence that the California obligate-seeding species were derived from lignotuberous sprouting ancestors is given by Wells (1969) and Stebbins (1974). Obligate-seeding species likely evolved on sites where high mortality of resprouters favored reallocation of energy from lignotuber to seed production. This would follow because: (1) resprouting is less useful on such sites and (2) fewer resprouts mean less competition for seedlings and thus a greater premium on seedling production. Therefore, obligate seeders are dependent upon fires which create large openings for seedlings at the expense of resprouters. This could come about if fires were sporadic and occasionally there were long periods of time between fires; there would be fewer shrubs alive, thus fewer potential resprouts, and fewer still would survive the more intense fires (fig. 5). Obligate seeders can survive long periods without fire as seeds in the soil. This scenario would be exacerbated on more xeric sites since (1) these sites would have fewer shrubs (and thus fewer resprouts) and (2) fires would tend to be more intense regardless of the age, and thus result in higher mortality of resprouters. It is of interest that obligate-seeding species favor the driest slopes and ridgetops whereas north-facing slopes, which support an abundance of vigorous resprouters, are the least favored sites. Specht (1980) describes a similar situation in the Australian mallee where in humid areas the high density of resprouters tends to suppress obligate seeding, whereas in drier habitats they survive in gaps between the more widely spaced resprouters.

PREFIRE ASPECT

25 years

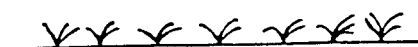
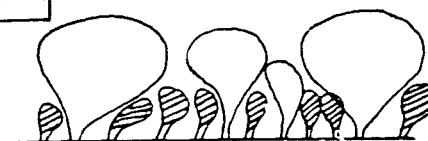


100 years

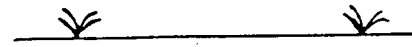
POSTFIRE ASPECT

FIRE  
↓

FIRE  
↓



SHORT FIRE CYCLE



LONG FIRE CYCLE

1. FEWER DEAD SHRUBS PRIOR TO THE FIRE  
THUS, MORE POTENTIAL RESPROUTS
  2. LESS INTENSE FIRES  
THUS, LOWER MORTALITY OF  
SPROUTING SHRUBS
- THE RESULT IS SMALLER OPENINGS  
FOR SEEDLINGS
- CONCLUSION: LOW SELECTION PRESSURE  
FOR OBLIGATE-SEEDING

1. MORE DEAD SHRUBS PRIOR TO THE FIRE  
THUS, FEWER POTENTIAL RESPROUTS
  2. MORE INTENSE FIRES  
THUS, HIGHER MORTALITY OF  
SPROUTING SHRUBS
- THE RESULT IS LARGER OPENINGS  
FOR SEEDLINGS
- CONCLUSION: HIGH SELECTION PRESSURE  
FOR OBLIGATE-SEEDING

Figure 5.--Model of the relationship between successional changes in the density of live shrubs and relative abundance of postfire resprouting shrubs resulting from fires early vs. late in succession (redrawn from Keeley and Zedler 1978). See Brown (1958) for enhanced resprouting under frequent fires and Keeley and Zedler (1978) and Schlesinger and Gill (1978) for thinning (and change from contagious to random distribution) in older chaparral.

Mediterranean-Climate Deciduous Scrub

Most Mediterranean climate regions have a summer deciduous highly aromatic sub-ligneous vegetation on the drier margins of evergreen scrub. From what little is known of this vegetation (for all regions) it seems the southern California Coastal Sage Scrub is representative. This community is characterized by closely spaced shrubs 1-1½ m tall. It is best developed at lower elevations, on xeric sites, in midst of chaparral. Due to its coastal location, it is distant from lightning storms which are concentrated at higher elevations inland (Keeley 1977b). This, coupled with prevailing on-shore winds during thunderstorms, militates against a high natural fire frequency for this vegetation (Sauer 1977, Byrne and others 1977).

The longevity of these shrubs is not well known; in one instance shrubs over 40 years old were quite vigorous (Keeley, unpublished data). All species produce abundant light, wind-dispersed seeds. The extent of seed storage in soil until fire is unknown. However, no coastal sage species is known to require fire scarification to

(Mirov and Kraebel 1937, Keeley unpublished data). Also, seedlings of most coastal sage species readily establish without fire, in openings in coastal sage vegetation (personal observation), or openings in chaparral (personal observation; Patric and Hanes 1964). Postfire regeneration is poorly understood. All species, even the most suffrutescent ones, are vigorous resprouters from caudices and (in some species) root systems (Keeley unpublished data). Postfire resprouting, however, is apparently sensitive to fire intensity since these shrubs (when found in association with chaparral) are often reported as nonsprouters. Apparently most coastal sage species do not store seeds in the soil until fire. This is suggested by the recent discovery that shrub seedling establishment in the first postfire year is nil (J. Keeley unpublished data). Most shrub resprouts, however, flower the first year after fire and establish abundant seedlings the second year.

#### Humid Evergreen Scrub

On poor soils throughout the mild and humid coastal plain of the southeastern United States is a shrub vegetation. On sandy soils in maritime situations it forms a dense scrub whereas in bogs it is interspersed among, and often successional to, other vegetation types (Schlesinger 1978). This region is characterized by precipitation throughout the year and frequent spring and summer lightning storms. Natural fires can occur only in very dry seasons and are not always common (Webber 1935).

The vegetation is a dense tangle of broad-leaved evergreen sclerophyllous-leaved shrubs, distinctly lacking herbaceous understory. Little is known about the reproductive characteristics of these shrubs. Seeds are mostly animal dispersed with some species producing acorns, others fleshy drupes. Seedling establishment is apparently rare under mature shrubs and there is little viable seed storage or none that survives fire, since seedlings do not establish after fire (Webber 1935). Vegetative reproduction is uncommon though all species regenerate vigorously from rootstocks after fire, even in the face of repeated frequent fires. Under natural conditions, the fire frequency is low, since moisture content of the vegetation is usually high and there is no herbaceous vegetation to carry a fire. In fact, the dearth of herbs extends into a "bare zone" around the edge, preventing fires from being carried into the scrub from adjacent savannas (Webber 1935). This scrub vegetation can withstand long fire-free periods since most of the shrubs are long lived, often becoming small trees. They probably owe their existence to occasional periods with frequent fires which eliminate pines and to poor soils which slow reinvasion by the pines or sprouting hardwood trees.

Once scrub vegetation has established, it is maintained by resprouting after fire. Seed production appears to contribute little to continuation of the stand; rather, seeds are dispersed elsewhere. Once in a new area, seeds germinate, and may infrequently establish new shrubs beneath the sparse canopy of certain pine formations. Given a peculiar sequence of frequent fires (which eliminate some pines but allow resprouting shrubs to remain) coupled with infrequent fires (which allow for establishment of new shrubs), there may be slow attrition and eventual replacement of pines with scrub vegetation.

#### Arid (Desert) Scrub

Scrub vegetation in arid regions frequented by summer thunderstorms is common in both the temperates and tropics. Lightning fires are frequent though the spread of fire is often limited by lack of fuel. This vegetation is well developed throughout southwestern North America where it consists mostly of spiny shrubs and subshrubs. Seed production is erratic from year to year. The seed of many species requires scarification and this can come about in a variety of ways. Thus, seedling establishment can occur without a fire, though it is erratic and probably linked to precipitation patterns.

Vegetative spread is poorly developed except for layering in some species. Most shrubs can resprout from basal portions after fire, though some species are more vigorous than others (Box and others 1967). Fires are sporadic, dependent on the buildup of herbaceous fuel coupled with a summer lightning storm. Fires are commonly destructive to seedlings and small "saplings" (Cable 1972). Older shrubs, for the most part, can survive and resprout. Few seedlings establish from soil-stored seed though it is not known whether this is due to low seed storage or fire-killed seeds. Many subshrubs produce light seeds which readily blow in and establish after fire. In general, seedling establishment is not highly dependent upon fire and will occur in all species whenever there is a favorable opening.

#### Temperate Forest Successional Shrubs

For a short time after fire in temperate forests, there is a successional stage of shrubs. Frequency of natural fires and type of understory shrubs is quite different in western and eastern forests of North America.

#### WESTERN FOREST SHRUBS

Coniferous forests, subjected to dry summers interspersed with lightning storms, are occasionally eliminated by crown fires and temporarily replaced by shrub vegetation. Shrubs are 2 to 4 m tall and capable of living 50 to 100 years, but they are normally shaded out much earlier by forest regeneration. Where regeneration is slow, due to peculiarities of the site or its history, this shrub vegetation may remain for extended periods of time.

The shrub species can be conveniently divided into two groups. One, consisting of species of Ceanothus and Arctostaphylos, produces seeds that are not well adapted to widespread dispersal. Substantial seed production begins at ca. 10 years and the seeds accumulate in soil until seed coat scarification which commonly comes about from intense heat during a fire (Cronemiller 1959, Quick and Quick 1961, Gratkowski 1962, Orme and Leege 1976). These species are found at higher elevations throughout the western United States, but as a group are best developed in the Sierra Nevada. The other group of species, e.g., Prunus, Sambucus, Rosa, Rubus, Salix, and Symphoricarpos species, are characterized by production of widely dispersed seeds with no seedcoat scarification requirement. These seeds apparently do not survive fire (Lyon and Stickney 1976) though it is not known whether in the absence of fire they remain in the soil until some other disturbance. Several species of Ribes fit neither group, having widely dispersed seeds which require scarification, usually by fire (Quick 1962).

Vegetative spread by rhizomes is common in group 2 species but not group 1 species. All species, however, can resprout from underground parts after the tops are removed by fire.

Group 1 species (Ceanothus and Arctostaphylos) seem most specifically adapted to fire. Lack of widespread seed dispersal suggests that these shrubs are adapted to widespread fires, i.e., if fires cover large areas, there is low probability of reaching a site which will burn sooner than the parent site. Thus, seeds are deposited into the soil and remain dormant until the next fire. If repeat fire occurs within a few years, these species can resprout from the root crown. As the canopy species recover and shade out the shrubs, the potential for regeneration from resprouts is eliminated. However, soil-stored seeds appear to have a great longevity as evidenced by synchronous establishment of large numbers of seedlings after fire in 400-year-old forests (Gratkowski 1962, Youngberg and Wollum 1976).

Group 2 species are adapted for dispersing into localized disturbed areas but not necessarily ones due to fires, e.g., treefalls. Also, having widely dispersed seeds, they can disperse into areas disturbed after a long disturbance-free period which would

have resulted in the deterioration of the group 1 species soil-stored seed. Since establishment on a given site is highly probabilistic, being dependent upon disturbance followed by a propagule, it is likely that some seeds will arrive sooner than others. Thus, early arriving species can benefit greatly by vigorous vegetative spread, a trait common to group 2 species but not group 1.

#### EASTERN FOREST SHRUBS

The predominantly winter deciduous forests of the east are characterized by cold snowy winters and some precipitation throughout the year. Moisture condition of the vegetation is usually high; consequently lightning fires seldom coincide with burning conditions (Barden and Woods 1973). Therefore, natural fires are infrequent and unpredictable and, if they did not produce conditions similar to other types of disturbance, fires might be considered catastrophes rather than disasters (*sensu* Harper 1977).

The shrub species may be evergreen or deciduous. Most are shade intolerant and thus entirely early successional. Forest regeneration is rapid; consequently, shrubs may survive only 5 to 15 years. Seed production begins early in the life cycle and is frequent and abundant (Johnson and Landers 1978). Seed dispersal mechanisms are well developed in all species. Most produce brightly colored fleshy fruits attractive to a wide variety of birds and mammals, ensuring their widespread dispersal (Smith 1975, Thompson and Willson 1978). Many species have viable seed stored in soil for long periods (Olmsted and Curtis 1947, Moore and Wien 1977), whereas others do not. Seedling establishment is uncommon without disturbance. Many species require an opening in the forest canopy for germination, the cue probably being light (Marks 1974).

Most of the species, e.g., Rubus, Vaccinium, Lonicera, Rosa, Rhus, Sassafras, Crataegus, and Symphoricarpos species, are capable of aggressive vegetative reproduction by stolons or rhizomes. The majority are capable of rapid regeneration from root crowns or caudices (Ahlgren 1960) if disturbance occurs before forest canopy closure has eliminated them. In fact, dependent upon forest structure these species may persist, e.g., Reiners (1967) showed that abundance of Vaccinium in oak-pine forest is proportional to light penetration.

Natural fire frequency for this environment is probably once every 100 to 300 years. However, other sorts of disturbances (e.g., tree falls from tornadoes, cyclones, heavy snowpack, senescence) are common. Such disturbances are localized and distributed mosaic fashion. The reproductive mode of the shrubs is closely tuned to this pattern. When localized disturbance occurs, some viable seed may already be in the soil and other seeds will come in rapidly because bird dispersers (looking for other seeds) are attracted to the openings (Thompson and Willson 1978). Early arriving seedlings will spread vegetatively, attempting to preempt as much space as possible. As the opening becomes more crowded, less energy will go into vegetative growth and more into seeds (Abrahamson 1975) which are dispersed elsewhere.

#### Scrub Steppe

Scrub steppe vegetation occurs in regions with deep soils and severe continental climate. Annual precipitation is low, coming mostly in the form of winter snow. Since storms are concentrated in winter, lightning fires are infrequent (Komarek 1967). In North America this vegetation is known as Great Basin Sage Scrub and natural fires are considered rare (Billings 1951 cited in Beatley 1966). The vegetation is dominated by two shrubs, Artemisia tridentata and Purshia tridentata, in association with a variety of subshrubs and grasses. Artemisia and Purshia are long-lived (100 to 200 years) evergreen "soft-wooded" shrubs, variable in size (0.5 to 4 m), dependent upon the region.

Both shrubs flower and fruit consistently, Artemisia producing an abundance of tiny widely dispersed seeds (Deitschman 1974) and Purshia fewer, larger, less mobile seeds (Deitschman and others 1974). Seeds which accumulate in mature stands contribute new individuals slowly and are greatly reduced in number by fire (Mueggler 1956). Seedling establishment is vigorous in openings or adjacent grassy areas (Humphrey 1962, Sampson and Jespersion 1963) and after fire from seed dispersing in from adjacent areas (Loope and Gruell 1973).

Other than layering on certain extreme sites, these dominant shrubs have no capacity for vegetative reproduction. For the most part neither can resprout after fire; there are exceptions, however. While resprouting is rare in most populations of P. tridentata there are certain regions with vigorous resprouting populations (Blaisdell and Mueggler 1956). That this is genetically controlled is suggested by the observation that resprouting frequency increases in populations in the southern part of its range where it overlaps and hybridizes with the closely related desert resprouting shrub, Purshia glandulosa (Nord 1965). The increase in resprouting from north to south among the two species may be related to a similar gradient in increasing summer thunderstorms and natural fire frequency.

Data from Wyoming indicate that fire frequencies between 10- and 20-year intervals are sufficient to replace A. tridentata with bunchgrasses, but it readily reestablishes given an 80-year fire-free period (Houston 1973), and this time frame is supported by studies in Utah (Pickford 1932). Given a longer fire-free period than this, juniper can invade and replace sagebrush (Barney and Frischknecht 1974). This, however, requires a seed source area immediately available since rapid juniper invasion is generally restricted to ecotonal areas between the two vegetation types (Burkhardt and Tisdale 1976). Thus, long fire-free periods throughout much of the Great Basin probably would not result in juniper invasion.

#### Tropical Rain Forest Understory Shrubs

Scattered short-statured shrubs occur in the understory of lowland tropical forest in both the Old and New World. Precipitation is evenly distributed throughout the year so that the moisture condition of the vegetation essentially precludes natural fires (Phillips 1965). Palms are an important part of this understory vegetation. A typical example is Podococcus barteri, a common African understory palm.<sup>2/</sup> Flowering and fruiting occur over many months and actual seed production may be quite small. Fruits are fleshy and likely animal dispersed. Seedling establishment is not common. Most reproduction is due to clonal spread from stolons. An individual is estimated to live for more than 100 years. It was estimated that stolon production began after about 15 years with flowering beginning after 40 years. In contrast to Podococcus is the New World tropical understory palm Cryosophilia guagara. This species establishes seedlings under the closed canopy. However, a break in the canopy is required for the seedlings to develop further and reproduce (Richards and Williamson 1975).

#### Summary: Shrub Communities

Mediterranean evergreen scrub vegetation represents a number of specialized adaptations to fire. The most prominent have poorly dispersed seeds, fire-stimulated germination, basal burls, or obligate-seeding shrubs. Lack of well-developed seed dispersal mechanisms in the dominant species (90 percent by cover, Bullock 1978) may stem from widespread fires. Seed germination cued to fire reflects the inhospitality of chaparral understory (low light and high predation) coupled with predictability that fire will occur before much of the canopy dies. Basal burls may represent a response to problems unique to Mediterranean shrubs; maintenance of an extensive root system when the tops have been removed but conditions are unsuitable for their

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<sup>2/</sup> Bullock, S. H. Demography of an undergrowth palm in Biafran rain forest. Unpublished ms.

immediate restoration. Obligate-seeding species are another unique feature of most Mediterranean regions. They may have evolved in response to an increasing number of sites on which resprouters could not succeed. The outcome would be twofold: (1) large "openings" for seedlings, thus selection for higher seed production, and (2) less chance of resprouting, thus less intense selection for maintenance of a burl; in sum, a reallocation of energy from burl to seed. This scenario is supported by evidence that California obligate-seeders arose from burl-forming ancestors. This may account for loss of the burl. Loss of sprouting per se may be due to ineffectiveness of resprouting without a burl on the more xeric sites. Thus, Mediterranean scrub represents one of the most specialized vegetations with respect to fire. These adaptations reflect high predictability of fire in the environment. However, they do not reflect the predictability of frequent fires, i.e., the vegetation as a type is degraded by too frequent fires and not obviously affected by fires as few as one per century (Keeley and Zedler 1978).

Southern California Coastal Sage Scrub is a vegetation type further removed than chaparral from natural fire sources, thus fire is more unpredictable. Postfire regeneration occurs from sprouts in some cases and from seed either in the soil or blowing in. If fires are too frequent, coastal sage is replaced with grass. Shrub seedlings can establish in openings and thus this vegetation (unlike chaparral, for example) can regenerate (albiet slowly) in the absence of fire. Its well-developed colonization capacity suggests it may have played a role in a sort of gap phase succession with oak woodland prior to increased fire frequencies (and elimination of much of the oak woodland) upon arrival of hominids in southern California (Wells 1962). Today, coastal sage species colonize chaparral areas thinned out by too frequent fires.

The coastal plain evergreen scrub of the southeastern U.S. resembles Mediterranean-climate scrub in many ways (sclerophylly, evergreenness, small leaves, sprouting, deep roots, lack of herbaceous understory, and sometimes a peripheral "bare zone"). The structural features are general adaptations to a variety of semixerix environments (Axelrod 1975). However, this is where the similarities end. Coastal plain scrub differs from chaparral in that seeds are not stored locally and stimulated by fire to germinate, and there are no burl-forming or obligate-seedling shrubs. Although coastal plain scrub is not as specialized to fire as chaparral, it exhibits much greater resilience to high fire frequency.

Desert scrub vegetation can recover following occasional fires, predominantly from resprouting. Seedling establishment occurs without fire, thus many age classes are present when fire occurs resulting in the younger age classes being killed. Consequently, frequent fires may result in an unstable age structure. In the absence of fire, desert shrubs are capable of maintaining themselves. The fact that summer lightning storms occur and that desert shrubs such as Purshia glandulosa, have evolved or maintained the resprouting ability when a closely related congener, P. tridentata has not, suggests fire may have been a selective agent in this vegetation.

Temperate forest successional shrubs exhibit two strategies. One which is best developed in the more western forests is similar to the predominant chaparral shrub strategy. It involves shrubs which lack vigorous vegetative reproduction and produce poorly dispersed, long-lived, fire-stimulated seeds. The shrubs are all relatively resilient to fire, all able to resprout if fires are too frequent, and all remain dormant as seeds if fires are infrequent. Widespread fires have probably selected against dispersal mechanisms. Local seed storage in the soil results in abundant seedling establishment following fire; consequently, less is to be gained by spreading vegetatively than growing vertically. The second strategy (most highly developed in eastern forests) involves shrubs with vigorous vegetative reproduction and widely dispersed seeds lacking any seedcoat scarification requirement. Widespread seed dispersal suggests adaptation to a more localized disturbance, of which fire may be only one type.



Since disturbances other than fire result in openings for these shrubs, there has been no selection for heat-stimulated germination. Also, a seed reaching an opening first will benefit by spreading vegetatively and preempting space. All of these shrubs resprout after the tops are removed, thus frequent fires are not harmful; nor is the complete absence of fire harmful, since other disturbances are probably common enough to maintain these shrubs.

Steppe-type scrub shows little dependence upon fire except in defining the border between it and juniper woodland at the base of various mountain ranges. The dominant shrubs do not resprout and revegetation following fire requires recolonization from the outside. Thus, this vegetation is not resilient to frequent fires and can maintain itself throughout most of its range without fire.

Tropical understory shrubs probably have had no evolutionary influence from fire. Some resemble temperate forest successional shrubs in dependence upon openings and strategies for getting to them. Others are shade tolerant and not dependent upon disturbances and instead exist as understory shrubs. Vegetative spread is the dominant reproductive mode. Reduced seed production may reflect the dwindling importance of two common functions of seeds: (1) to provide a dormant stage and (2) to provide a dispersal agent.

### TREE VEGETATION TYPES

A list of the major tree vegetation types considered here is given in table 5. Note that in addition to the life history responses listed in table 1, trees, unlike herbs and shrubs, have the capacity to resist fires through their tall growth form in conjunction with self-pruning and thick fire-resistant bark. In some instances, resistance to fire may be as important as (and functionally similar to?) resprouting.

#### Temperate Coniferous Forests

Throughout temperate regions of the world are a variety of coniferous forest types. I will focus here on a few communities and individual species from North America which represent responses from low to high fire frequency.

#### SEQUOIA MIXED CONIFER FOREST

Throughout the Sierra Nevada Range of California, between 1 000 and 2 000 m elevation, is a forest dominated by Pinus ponderosa, P. lambertiana, Abies concolor, and Calocedrus decurrens with scattered groves of Sequoiadendron giganteum. The climate is Mediterranean with most of moisture coming in the winter as snow and the summers subject to droughts. Summer thunderstorms are frequent and although they contribute little to the annual precipitation they provide a source of lightning fires.

Studies of tree-ring chronologies in fire-scarred trees indicate that, during the 18th and 19th centuries, widely separate areas had fire frequencies ranging from 2 to 20 years with an average interval of 5 to 10 years (Wagner 1961, Kilgore 1973). Evidence indicates that aboriginal man who occupied parts of this region for the last 1,000 years contributed substantially to this frequency of fires. Reynolds (1959) provided evidence of this for the central Sierra Nevada by demonstrating the unlikelihood that lightning fire frequency could account for fire scar frequencies in trees of this region. By comparing fire scar frequencies from different historical periods Kilgore and Taylor (1979) have also provided substantial evidence of Indian influence on past fire frequencies for the southern Sierra Nevada. Their data show an approximate five-fold decrease in fire scar formation after the elimination of the Sierran Indian culture (1870's) but before the U.S. fire suppression effort around 1900 (fig. 6). Thus, a "natural" fire frequency (natural in the sense that life history attributes evolved long before Indian occupation) for the mixed conifer forest is lower than the fire scar data indicate.

TABLE 5.--Principal tree vegetation types, estimated natural fire frequency, and a rough estimate of the minimum and maximum fire-free interval to which they are resilient

Vegetation type	Modal fire frequency	Minimum fire-free interval	Maximum fire-free interval
	----- <u>Years</u> -----		
Temperate coniferous forests:			
sequoia mixed coniferous forests	10-100	1-3	600
Lodgepole forest - Sierra Nevada	100-300	?	∞
Lodgepole forest - Rocky Mountains	40- 80	15	200-300
Southeastern pine savanna	20- 50	0	200
Pine barrens	10- 20	1-3	200
Chaparral conifers -			
<u>Cupressus</u>	50-100	20	200?
<u>Pinus</u>	20- 40	10	100
Pinyon-juniper woodland	100-300	100	∞
Boreal forest	20-300	?	∞
Temperate deciduous forest	100-500	25	∞
Tropical rain forest	∞	∞	∞

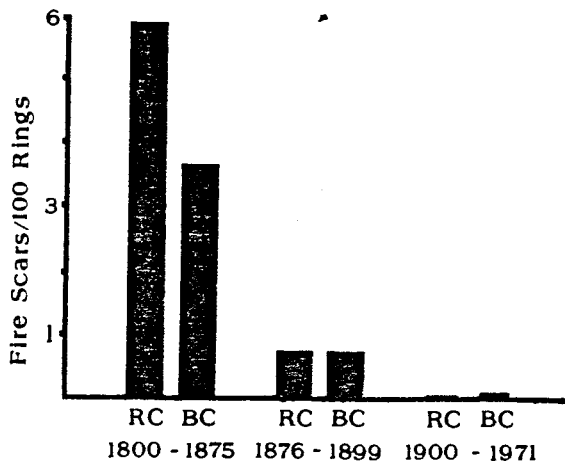


Figure 6.--Number of fire scars per 100 annual growth rings in trees from two sites in the southern Sierra Nevada, presented by historical period; (1) 1800-1875 includes Indian and lightning set fires, (2) 1876-1899 there was no Indian burning, only lightning and settler-set fires, but no fire protection, and (3) 1900-1971 fire protection. RC = Redwood, number of trees = 37; BC = Bearskin Creek, n = 183 (based on data from Kilgore and Taylor 1979).

Extrapolating from Kilgore and Taylor's data, the natural fire frequency is approximately one-fifth of that indicated by tree chronologies. A reasonable range might be 10 to 100 years with a 25- to 50-year mode. Given these bounds, the mixed conifer belt very likely evolved under a temporal mosaic of fire frequencies; e.g., periods of frequent ground fires interrupted by an occasional hiatus in fires and terminated by a severe crown fire. The rugged topography of this region would promote irregular burning patterns and further contribute to this mosaic of frequent ground fires interspersed with severe crown fires. It should be kept in mind that when John Muir stated, "In the main forest belt of California fires seldom or never sweep from tree to tree in broad all-enveloping sheets" (Muir 1938), he was reflecting the fire regime resulting from widespread Indian influence. Notwithstanding, there is evidence of occasional widespread crown fires even during this period (Burcham 1973, Reynolds 1959, Wagener 1961).

The influence of a temporal mosaic of ground fire and occasional severe crown fires is reflected in the life history attributes of the shrubs (see previous section) and trees of this region (Fowells 1965). The dominant trees are long lived, most species surviving 300 to 600 years (P. lambertiana to 1,000 years, S. giganteum to 3,000 years). Substantial seed production begins between 40 and 120 years, with P. ponderosa at the lower end and P. lambertiana and S. giganteum at the upper end. Annual seed production fluctuates with "good" years occurring at intervals of 3 to 9 years. Seeds are wind-dispersed and although most species have winged seeds, the bulk of the seed crop falls within 50 m of the parent tree. However, the small amount dispersed further may be significant in some instances, since seedling establishment in most of these species is dependent upon an exacting set of microsite conditions. For example, P. ponderosa and S. giganteum seedlings require highly lit, mineral-soil sites, whereas A. concolor establishes best in litter beneath the canopy of shrubs or trees. In all species, seed storage in soil is insignificant.

Vegetative reproduction or regeneration from sprouts is essentially unknown in these species. Resistance to fire varies widely both between species and between age classes within a species. In general, seedlings and saplings of all species are sensitive to fire, even light ground fires (Connaughton 1934, Hartesveldt and Harvey 1967). Kilgore and Taylor (1979) found that the youngest age at which fire scars were laid down was between 15 and 20 years in most species, suggesting that trees younger than this did not survive fires. Thus, for the first couple of decades of a sapling's life, survival is greatly enhanced by lack of fire.

Today, the mixed conifer forest is a patchwork mosaic of various species combinations (Kilgore 1973) which very likely reflect differing species' tolerances or optima in fire regime. For example, mature P. ponderosa are tall, thick-barked trees which self-prune and thus can withstand centuries of light to severe ground fires. Seedling establishment requires a local seed source, a relatively open site such as after a crown fire followed by a period of years without fire. Thus, occasional ground fires distributed mosaic fashion, which by chance happen to skip patches of forest for many years, would result in a patchwork of small crown fires near seed source trees. The cohort of seedlings established after such a disaster would in later years be thinned by ground fires and eventually result in a localized even-aged stand which is commonly the case for P. ponderosa (Fowells 1965). Sequoia seems to have a life history adapted to a similar scenario, i.e., ground fires which thin the understory and thus ensure the survival of some seed source trees, coupled with the occasional localized severe fire which opens the forest canopy. In general, S. giganteum seedlings establish and survive best on open sites after severe fires followed by a lack of burning (Hartesveldt and Harvey 1967).

In contrast to these two species, Abies concolor is dependent upon the existence of sites which remain fire free for extended periods. Although their thin bark and lack of self-pruning make them sensitive to ground fires, older individuals can survive light fires. Seedlings, however, do not establish well in openings, rather they do best beneath the canopy of other vegetation. Thus, mature A. concolor is able to survive on sites periodically burned with light ground fires; however, seedling establishment and development to maturity is dependent upon localized sites which remain free of fire for extended periods. Given enough time, conditions suitable for a crown fire can occur in a white fir stand replacing it with ponderosa pine. Increased establishment of A. concolor since presettlement times is well documented and it is generally agreed this is due to decreased frequency of fire. What is not generally appreciated is that, although present densities are unnaturally high due to fire protection, presettlement levels were unnaturally low due to Indian burning. This is illustrated by Kilgore and Taylor's (1979) demonstration that (1) a large surge of Abies following collapse of the Indian cultures (ca. 1870) and (2) most of the Abies establishment occurred prior to fire protection (ca. 1900).

Frequent fires represent an important component of the fire regime of the mixed conifer forest, in large part because they preserve seed source trees by "breaking up" the region and thus prevent widespread crown fires. This is critical since seeds are not stored in the soil and long-range dispersal is poorly developed. However, fires are not ubiquitous, and localized areas throughout the region remain unburned for extended periods. Species such as Abies concolor are dependent upon such sites for establishment, but eventually these localized stands are removed by severe fire and it is upon this sort of event that P. ponderosa is dependent. The other mixed-conifer trees represent adaptive solutions somewhat intermediate to these extremes. In terms of resilience all species can withstand occasional periods of frequent fires as well as extremely long fire-free periods.

#### LODGEPOLE FOREST--SIERRA NEVADA

At between 2 700 and 3 200 m in the Sierra Nevada is forest dominated by Pinus contorta spp. murrayana. The region is characterized by a short growing season, infrequency of droughts, sparse forests, and relative infrequency of lightning fires (Reynolds 1959). Natural fire frequency for this vegetation is apparently very low. This is suggested by results from the Natural Fire Management Zone in Sequoia and Kings Canyon National Parks. This zone includes over 200 000 ha generally above 2 600 m, in which all naturally ignited fires are allowed to burn (Parsons 1977). Over a period of 9 years less than 2 percent of the region has burned, suggesting a recurrence interval for the region of several hundred years. Even when fires do occur after a long fire-free period, fuel and moisture conditions are such as to preclude extensive crown fires.

Pinus contorta, the dominant tree of this forest, is relatively long lived, attaining ages in excess of 600 years. In most respects seed production characteristics are similar to other pines in this region, i.e., production of winged seeds more or less locally distributed establishing best on exposed mineral soil. Unlike populations of P. contorta in the Rocky Mountains, there is no tendency towards serotiny in Sierran populations. Pinus contorta differs from pine species found in more fire-prone regions in that it has relatively thin bark, self prunes poorly, and in more open stands has branches near the ground.

Thus, fires are uncommon in the lodgepole type as are adaptive characteristics for surviving fires. Seedling establishment is generally on sites exposed by tree-falls or in meadows following a change in water table.

#### Lodgepole Forest--Rocky Mountains

In some parts of the Rocky Mountains, Pinus contorta populations produce mostly serotinous cones (Critchfield 1957) and this is apparently genetically controlled (Lotan 1967, Teich 1970). The climate of this region is continental with some precipitation occurring during summer months (particularly accompanying lightning) so that conditions conducive to fires occur at infrequent intervals (Loope and Gruell 1973). Lodgepole pine occurs at lower elevations than in the Sierra Nevada (1 800 to 2 400 m), therefore the growing season is longer and forests more heavily stocked and summer dry periods more likely to occur. Fires are infrequent in this region, but when they occur they tend to be destructive crown fires (Komarek 1967, Muir 1938, Loope and Gruell 1973). Populations with serotinous cones reestablish even-aged populations after fire. Over extended periods without fire, more shade-tolerant spruce and fir will invade (Lotan 1976).

Thus, P. contorta under an infrequent but predictable and severe fire regime has taken on the role of a successional species. An obvious response to this role is the serotinous habitat. However, in many parts of its range, selection has adjusted (genetically) the frequency of serotiny to reflect local predictability of fire (Lotan 1967, Perry and Lotan 1979).

#### Southeastern Pine Savannas and Pine Barrens

The mild-humid forested regions of eastern North America have precipitation distributed throughout the year; therefore, even though spring and summer thunderstorms are common, burning conditions often are not conducive to fires. Drier summer conditions, and therefore fire frequency, increase from north to south, from mountains to coastal plain, and from poorly to well-drained soils (Doolittle 1977). Given an extended period free from disturbance, most of this region would support a forest of mixed hardwoods (Christensen, this volume). There are, however, several pine species prominent as successional species or more permanent members on edaphically severe sites, viz, poorly or excessively drained soils (Fowells 1965).

These pines have a number of common characteristics: (1) they are not long lived (100 to 200 years), (2) they are capable of substantial seed production at 15 to 20 years, (3) seeds are wind-dispersed, most within 50 to 100 m, (4) seed is not stored in soil, and (5) seedling establishment usually requires exposed mineral soil.

The loblolly-shortleaf pine community is the most widely distributed of the successional pine types. Dominants are Pinus taeda and P. echinata and in the absence of disturbance the former persists on very wet sites, the latter on drier low-nutrient sites. Mature individuals of both species can withstand light ground fires and young seedlings (and saplings in P. echinata) can resprout from the root collar after fire. Both pines invade hardwood sites recently cleared by severe crown fires. The tenure of this pine forest is closely tied to the sequence of fires to follow. Without

further disturbance, the hardwood sprouts may overtake and shade out the pines in 50 to 100 years. Light ground fires have little effect on this successional sequence, since the hardwoods resprout vigorously and the pines do not establish in their shade (Little 1973, Baden and Woods 1976). A severe ground fire or repeated light fires will thin the overstory and replace the hardwood understory with grasses resulting in pine savanna; this, however, will be a temporary type since these pines establish seedlings poorly under their own canopy and/or in the face of repeated fires.

These pines therefore require more or less localized disturbances which remove a portion of the canopy, but not all local seed source trees. Both species are resilient to periods of frequent fires since seedlings resprout and mature trees have thick fire-resistant bark. Neither species is resilient to long fire-free periods. Two other pines with a somewhat similar relationship to fire are P. elliotii and P. palustris. These species are less widespread and less invasive, best developed on azonal soils. Pinus elliotii is common in poorly drained flatwoods and on pond margins. Occasional fires allow establishment on better drained sites; however, seedlings and saplings are sensitive to light fires. Pinus palustris occupies sandy, excessively drained sites and has a life cycle closely cued to these xeric conditions. During the first 3 to 7 years (or longer, dependent upon soil-moisture conditions) energy is diverted from stem to root growth, producing a grasslike seedling above ground. After the first year of growth this grass stage is resistant to fire, having buds protected by needles and scales. For a period after stem growth begins, the seedling is somewhat sensitive to fires, because it does not resprout, but soon develops fire-resistant bark.

The greatest degree of adaptation to fire is found in two pines with more localized distributions, P. rigida and P. serotina, both more or less restricted to extreme sites; the former on poor sandy or gravelly soils, the latter on frequently waterlogged sites. These two trees differ from the previous species in that (1) they are more vigorous resprouters (at any age) both from root collar and stem, (2) they produce seeds at an early age (3 to 4 years in resprouts), and (3) they produce serotinous cones to varying degrees (being highly dependent upon fire history of the site [Little 1974]). In light of these specialized fire adaptations and the fact that both these species are resilient to frequent fires, it seems likely they evolved under a more frequent fire regime than associated congeners. This seems reasonable for P. rigida, since it occupies semixerix sites, but not for P. serotina which is generally restricted to bogs. It may be that P. serotina has not been exposed to more frequent fires than other southeastern pines but that fires were more devastating. This could come about in several ways. Growth on these waterlogged sites is commonly stunted, thus relative frequency of fire between stages, e.g., seedling to sapling, may be greater. Stunted growth, exacerbated by fire, would mean the crown would be exposed to severe burning more frequently. This might select for ability to resprout from the stem. Serotiny which is well developed may have been derived for similar reasons, i.e., not necessarily more frequent fires, but more severe fires.

#### CHAPARRAL CONIFERS

Mediterranean-climate scrub in North America is commonly associated with local patches of conifer forests within a chaparral matrix. Dominants include several species of Pinus and Cupressus, each of which have serotinous cones but do not resprout after fire and Pseudotsuga macrocarpa which resprouts but is without serotinous cones.

One species is Cupressus forbesii, a small tree occurring in small even-aged monotypic groves in the midst of dense chaparral in southern California and adjacent parts of Baja California. Substantial seed production does not begin until about 40 years of age, and for the most part seeds are not dispersed until fire opens the cones. The wingless seeds are very poorly dispersed and so seedlings establish more or less within the boundaries of the parent grove. Cupressus forbesii may owe its

existence to long fire-free periods. One advantage of infrequent fires is that it allows time for the parent plant to shade out invading resprouting shrubs which would have a competitive edge over cypress seedlings in the postfire environment (fig. 5). Its dependence upon infrequent fires is suggested by the late age at which seeds are produced, coupled with inability to resprout after fire and indications of impending extinction in stands burned at the present frequency of every 20 to 30 years. Zedler (1977a) has provided good evidence of this last point by showing that stands burned after 21 and 28 years have marked declines in density (table 6). Similar declines in populations subjected to the present man-induced fire frequency of 20 to 30 years have been described by Reveal (1978) for another closed-cone cypress (C. arizonica var. stephensonii).

Closed-cone pines associated with chaparral are similar in many respects to cypress, the major difference being their resilience to more frequent fires (Vogl 1973, Zedler 1977b). The fact that closed-cone pines and cypress seldom occur together and usually not even in the same locality suggests that they may have been segregated according to patterns of natural fire frequency.

Pseudostuga macrocarpa, unlike the other chaparral conifers, does not occur in pure even-aged stands. It is long lived (300 to 600 years) and generally found on mesic, less fire-prone north-facing slopes and ravines in association with Quercus chrysolepis. Seed production does not begin early in life and seeds are not widely dispersed; however, seedlings establish under the canopy in the absence of fire (Sawyer and others 1977). When fires occur the youngest age classes are killed but the oldest can resprout from the stem (Bolton and Vogl 1969). Frequent fires in recent years have apparently eliminated populations at lower elevations, thereby reducing the range of P. macrocarpa (Gause 1966). Thus, P. macrocarpa like Cupressus spp. is not resilient after frequent fires. It is capable, like many nearby chaparral shrubs, of withstanding long fire-free periods.

TABLE 6.--Reconstruction of stand densities based on sample data and conservative extrapolations from data on stand structure and seedling mortality for Cupressus forbesii in San Diego, Calif. (from Zedler 1977a)

Year	Length of time since last fire	Cypress trees/m <sup>2</sup>
<u>Years</u>		
<u>Bigrock Stand</u>		
(1944)	64	( ~1.0)
(1945)	0.5	(>14.0)
1972	28	8.9
1976	1	0.60
<u>Smuggler's Canyon</u>		
(1944)	64	( ~1.0?)
(1945)	0.5	( ~1.5)
1965	21	>1.04
1966	0.5	(0.04)
1972	7	0.03
1976	1	0.02

## PINYON-JUNIPER WOODLAND

Woodland dominated by a few species of Juniperus and Pinus occurs throughout western portions of North America. The climate is continental with sparse precipitation (250 to 500 mm/yr), usually as winter snow. Summers are hot and occasionally interrupted by thunderstorms; although precipitation is generally unavailable to the trees, these storms provide ignition for natural fires. Even so, natural fires are uncommon due to the infrequency of lightning coupled with the sparseness of the vegetation.

The dominant trees, J. occidentalis, J. scopularum, P. edulis, and P. quadrifolia are medium height (10 to 30 m) and relatively long lived (200 to 500 yrs). Seed production begins early (10 to 20 yrs); however, substantial seed production begins at 50 to 100 years. Juniper "berries" and (wingless) pinyon "nuts" are widely dispersed (often over 20 km) by birds, and these dispersed seeds have a better chance of establishing seedlings than locally deposited seeds (Salomonson 1978, Vander Wall and Balda 1977). Juniper seeds can remain dormant in soil for years until conditions are suitable for germination (usually high soil moisture) though pinyon seeds apparently must germinate the first year (Johnsen 1959, Vander Wall and Balda 1977). Seedling establishment is dependent upon chance dispersal to a favorable site (usually the protective cover of a low shrub) and ample rainfall. None of the trees have the capacity for vegetative reproduction or regeneration from resprouts, and resistance to fires is poorly developed (viz, thin bark and low branches). When fires occur in pinyon-juniper woodland, the initial effect is to eliminate the younger age classes. Continued burning will eventually replace woodland with sagebrush because the shrubs can colonize faster than the trees can reestablish.

## BOREAL FOREST

At high latitudes in the Northern Hemisphere, a predominantly coniferous forest exists under a severe continental climate. The growing season is short with precipitation distributed throughout the year. Although thunderstorms are common, burning conditions are usually poor. Fires are most frequent on drier sites, but occasional droughts make widespread areas susceptible. Fires are dependent on dry periods; therefore, in the southern part of the region, fires on some sites may occur every 50 to 150 years (Heinselman 1973), whereas further north the highest frequencies may be one every 100 to 300 years (Viereck 1973), and one every 1,000 years at higher elevations (Wein and Moore 1977). The localized distribution of burning conditions coupled with the stochastic pattern of ignitions produces a mosaic of different habitats (Heinselman, this volume). Perhaps as a result, a diversity of life histories is represented by the dominants.

Pinus banksiana occurs on the driest sites (and thus most frequently burned sites) and has the greatest resilience to frequent fires. In many respects it resembles more southern pine barren congeners; in particular, it has serotinous cones. It probably is not subject to fires as frequent as, for example, P. rigida, and this may account for its lack of resprouting ability.

Populus tremuloides is an aggressive pioneer into burned areas and once established will spread by underground rhizomes and a proliferation of suckers (Viereck 1973). Repeated fires stimulate sucker growth and clones can withstand fires at intervals as short as 3 years (Fowells 1965). Substantial seed production begins after 30 to 40 years. Seeds are very light and, buoyed by long silk hairs, widely dispersed. Dispersal begins in late spring and seedling establishment is dependent upon immediate occupation of a suitable site, specifically a disturbance. Thus they capitalize on a localized burning pattern. Resilience to infrequent fires is low; areas unburned for 80 years may deteriorate from disease or invasion by shade-tolerant species (Loope and Gruell 1973).



Whereas these two species are closely dependent upon fire, two other boreal forest species, Picea glauca and P. mariana, although commonly increasing after fire, are able to persist in its absence. Picea glauca invades disturbed sites by seeds which are wind dispersed. This may be erratic, since good seed crops are sporadic (Viereck 1973), and seed is not stored in the soil (Johnson 1975). The random coupling of disturbance and good seed years probably accounts for the temporally disjunct episodes of regeneration in many areas (Payette 1976). It thrives on lowland sites; thus disturbances resulting from flooding probably create more reliable sites for establishment (Rowe 1970). Picea mariana establishes well after fire because of semi-serotinous cones, and frequently stands are even aged, dating back to the last fire (Zoltai 1975). However, it is not dependent upon fire. Some seed is dispersed every year, more in warm years or when openings in the canopy expose older cones to direct sunlight (Fowells 1965). Also, vegetative reproduction by layering is common in older trees, thus some stands can perpetuate themselves without disturbance (Zoltai 1975).

Abies balsamea requires areas free of disturbance for long periods of time, thus balsam fir is restricted to moister sites. Once established it can regenerate under its own canopy indefinitely in the absence of disturbance (Fowells 1965). Increased frequency of man-caused fires in the last 100 years has drastically reduced A. balsamea in some regions (Janke and others 1978).

#### Temperate Deciduous Forest

Temperate latitudes in both hemispheres support belts of deciduous hardwood forests, e.g., North America's Eastern Deciduous Forest. The climate is one of cold winters and warm-humid summers, with precipitation year round. Thunderstorms are common in spring and summer, but because of the moist-humid conditions natural fires are uncommon (Barden and Woods, 1973). When fires occur it is due to widespread droughts and consequently fires are frequently large (MacLean and Wein 1977). It has been estimated from laminated sediments in Green Leaf Lake, Ontario, that since 770 A.D. fires have occurred at least once every 80 years in the vicinity (Cwynar 1978), though much of this may have been due to extensive burning by Indians (Frissell 1973). It is estimated from the total acreage burned by natural fires since settlement of a tract in Maine, that the recurrence interval of burning for that forest is 800 to 2,000 years (Lorimer 1977). Windfalls (from one to hundreds of trees) are perhaps selectively a more important disturbance in these forests: they are more localized than fires but occur much more frequently (Stearns 1949). Therefore, the Eastern Deciduous Forest emerges as a relatively stable forest in a matrix of frequent local disturbances and occasional widespread fires.

Such a selective environment is reflected in the life histories of the trees. This is illustrated by the size distribution of a forest studied by Goff and Zedler (1968), shown in figure 7. The diagram suggests that the area was disturbed some time in the past and first invaded by Pinus strobus and later by Acer rubrum. Both species have well-developed colonizing features, i.e., they produce many seeds which are light and widely dispersed by wind and have rapid germination and growth once they reach openings. Perhaps a cost of this strategy is less competitive capacity once the more shade-tolerant species (e.g., Acer saccharum, Tsuga canadensis) close in the canopy. This is evidenced by lack of new individuals added to the larger size classes of A. rubrum and P. strobilus. Consequently, seeds of these species must land in another opening to complete their life cycle. For these early successional species (since disturbances are small and haphazardly distributed in time and space), evolution has selected for a variety of ways of enhancing the chances of seedlings establishing in openings and also of being some of the first to establish. For example, figure 7 shows that although A. rubrum does not mature under the forest canopy, it does establish seedlings. These can survive, albeit stunted, for various periods of time. In the event of an opening above them, they exhibit "release" (rapid growth) and thus have a headstart on species like P. strobilus which must disperse in.

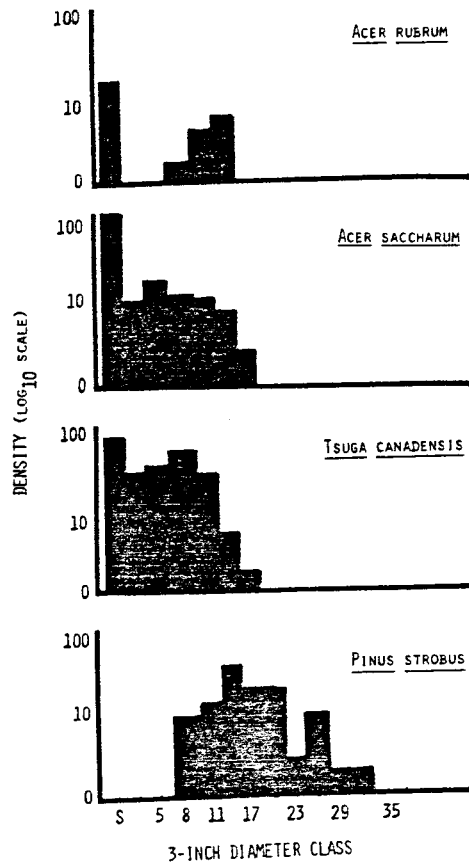


Figure 7.--Density distribution in relation to diameter for a Wisconsin forest (redrawn from Goff and Zedler 1968). S = seedlings.

There are other colonizing strategies found in early successional trees. Prunus pennsylvanica produces an abundance of fleshy drupes which attract many bird species and are widely dispersed (Smith 1975). By being bird-dispersed, the chances of having the seed deposited in an opening are increased (over wind-dispersed seed) since birds are biased towards sunny areas (Thompson and Willson 1978). In the event the seed is not excreted in an opening, it is protected by a hard endocarp and can remain dormant in the soil for many years until disturbance occurs (Marks 1974). Several other ways of ensuring a seed source is available are seen in species of Cornus which mature and reproduce in the understory of better lit portions of the forest or in A. rubrum which can persist a long time in the forest canopy. Regardless of the length of time they persist, the clumped distribution of individuals (relatable to previous disturbances) is sometimes still observable many years after disturbances (Williamson 1975). Most early successional species also exhibit little periodicity in annual seed production (Marks 1974, Wells 1976), reflecting the importance for a rapid invasive capacity; a several-year delay between disturbance and a good seed year could spell failure for a fugitive species.

A few early successional species will fill openings laterally by vegetative reproduction; however, most species do not, and instead attempt to reach the canopy. Essentially all species are capable of resprouting from root collar after the tops have been damaged, and openings are commonly filled by resprouts in both successional and climax species.

Climax species are those which are shade tolerant and therefore capable of establishing beneath their own canopy and replacing themselves. They produce larger seeds which probably are not dispersed as widely as those of early successional species. Larger seeds provide a larger food source for the seedling, a necessity for establishing under the canopy. Lower light levels on the forest floor mean slower growth rates, therefore longer disturbance-free periods are required to establish. Fleshy fruits are uncommon perhaps because the large seed size would require a fruit too large to be effectively dispersed by birds and rapid arrival at openings is of little value due to the slow growth rates. For this reason, too, extreme periodicity in annual seed production (common in climax trees) is of little disadvantage. On the contrary, since these species do not produce an expendable exocarp (as in a drupe) animals attracted to a seed crop destroy much of it, thus many years may serve an antiherbivore function (e.g., Janzen 1976). Another characteristic of the reproductive strategy of "climax" trees is a lack of long-lived soil-stored seed (Olmstead and Curtis 1947). In most respects "climax" species are only quantitatively different from "successional" species since they commonly require subtle disturbances in order to establish or be "released" and enter the canopy (Forcier 1975, VanKat and others 1975, Brewer and Merritt 1978, Harcombe and Marks 1978). The ubiquity of some disturbance-dependence is reflected in Wells' (1976) finding that although some plant families have specialized (ecomorphologically) at the pioneering extreme of the seral gradient, none have a consistent suite of traits specialized on the climax end.

### Tropical Rain Forest

At low latitudes in the Old and New Worlds are forests of broad-leaved evergreen trees existing under a wet-humid tropical climate. Natural fires are essentially nonexistent; however, as in temperate forests, disturbances such as windfalls can be common and when resulting from cyclones or hurricanes they can cause widespread damage (Longman and Janik 1974). Therefore, tropical rain forests, like certain temperate forests, exist as a relatively stable vegetation in a matrix of localized disturbances (Hartshorn 1978). Therefore, one would predict similar reproductive strategies in the dominants. Although much more is known about the reproductive cycles of temperate species, it seems that tropical trees represent a similar seral spectrum of strategies keyed to colonization of disturbed sites. At the pioneering end the Bombacaceae represents a tropical analogue to the temperate Salicaceae in its suite of ecomorphological traits, e.g., light, widely dispersed seeds, rapid growth rate, shade intolerance, and short lifespan (Wells 1976). Like their temperate counterparts, tropical pioneering trees represent a variety of families and adaptive specializations. Also, as in temperate forests, one can detect patches of regeneration which are perhaps related to previous disturbances (Richards and Williamson 1975). In response to disturbance one of the important aspects of the reproductive cycle of tropical trees is their capacity to resprout. In fact, Webb and others (1972) found that 12 years after disturbance, "suckers" were of much greater importance than seedlings. As in temperate forests, the one reproductive strategy not found in climax species is production of long-lived soil-stored seed (Webb and others 1972).

### Summary: Tree Communities

The Sierra Nevada Mixed Conifer Forest has had a long history of relatively frequent ground fires. The rugged topography of this region promotes irregular burning patterns. Once an area is "missed" the burned periphery might act as a firebreak for many years. As a consequence, localized areas may be free of fire for long periods and then the site of a severe crown fire. Thus, the landscape would be a mosaic of different fire frequency patches. Species such as Pinus ponderosa have adapted to more frequently burned patches by being able to resist fires through development of thick bark, self-pruning, etc. Those species such as Abies concolor which have adapted to less frequently burned patches are less fire-resistant but have

shade-tolerant seedlings which can establish in areas free of disturbance. All species are dependent upon maintaining seed-trees throughout the region since seeds are not widely dispersed or stored in the soil. Frequent fires accomplish this by burning around fire-resistant trees and making them "immune" to localized severe fires and by haphazardly missing patches which preserve shade-tolerant fire-sensitive trees. The localized fire-free patches not only provide a haven for fire-sensitive species, but also, because they will eventually be hit by severe fire, will produce optimum conditions for establishing seedlings of shade-intolerant fire-resistant species. Since the more mesic north-facing slopes are likely to remain fire free longer and the dry south-facing slopes burn more frequently. It is not surprising A. concolor is better adapted to the former and P. ponderosa to the latter slope face.

Pinus contorta would not survive the mixed conifer forest burning regime. It is not highly resistant to fire (thin bark, poor self-pruning) and, like most pines, has shade-intolerant seedlings. However, it can adapt to infrequent light fires or periodic severe fires by a (genetically) simple change in behavior.

Several eastern pine species are unique among North American species of the genus in their capacity to resprout; a trait generally lacking in conifers. This may be due to more frequent fires though data to substantiate this is inadequate. Since these pines are on more extreme sites, slower growth rates may mean fires "seem" more frequent to the plant, i.e., a plant on a good site might go from seed to adult without a fire, whereas on an extreme site it might be exposed to several fires between seed and adult stage, even though the absolute fire frequency was the same. The more stunted growth would also place the trees in greater danger of destruction by fires. It is interesting that fire-type serotinous conifers in California are commonly found on edaphically extreme sites also (Raven and Axelrod 1978).

Among chaparral conifers are serotinous species of pine able to withstand frequent fires. Lack of sprouting capacity suggests fires have not been as frequent as in eastern pine barrens. Closed-cone cypress in chaparral suggests natural fires are less frequent than the present fire frequency. They would likely do well with fires every hundred years though they are ultimately dependent upon fire. Pseudo-suga macrocarpa has, like certain cypress species, not fared well under the current 20- to 30-year fire cycle. This is of interest since it resprouts from epicormic buds, a trait which, in light of its wide absence in conifers, was likely selected for by fire. Thus, P. macrocarpa is an example of a species able to survive occasional frequent fires because of a specific "fire-type" adaptation but the species is perhaps most favored by infrequent fires.

Pinyon-juniper conifers are unable to survive fire. They resist fire poorly, do not resprout, and do not store seeds on the plant or in the soil. In event of fire, few if any seed-source trees remain. They are capable, though, of long-distance seed dispersal by birds, a trait unknown in most North American conifers. This may be a response to very infrequent but large-scale fires. Another possibility, however, is that bird dispersal could be the only dispersal option available for the following reasons: Soil moisture is considered the most limiting factor in seedling establishment in these species, and there is circumstantial evidence that seedling establishment, in water limiting environments, is enhanced by larger seeds (Baker 1972). Also, large seeds are poorly dispersed by wind (the prevalent coniferous mode); therefore, animal dispersal could be selected for.

In the boreal forest, frequency of fires is closely linked to substrate. The driest sites support species like Pinus banksiana which resembles many other serotinous pine species. On wetter sites are species such as Picea glauca which can survive well without fire though the chance occurrence of a good seed year and local fire may favor it on burns. Picea mariana is capable of going either way; semiserotinous cones for occasional fires or layering in the absence of fire.

## CONCLUSIONS

An understanding of the evolutionary role of fire in ecosystem development requires knowledge of life history characteristics. Since strategies are under genetic control, having been shaped evolutionarily, their only imperative is continuance. To understand the evolutionary role of fire frequency we need to know how it affects species' ability to remain in that environment. The following conclusions are offered in this light.

1. Since natural fires are randomly distributed in space and time, often a more important focal point than response to the modal fire frequency will be species resilience to the range in fire frequencies encountered. Failure to appreciate species-specific differences in resilience in managing natural ecosystems can spell extinction for some species. For example, it is generally accepted by managers that the chaparral ecosystem is resilient to fire every 15 to 20 years. However, it is apparent that Cupressus forbesii and C. stephensonii are in danger of extinction under this more frequent manmade fire regime.

2. Life history attributes specifically selected for by fire do not imply resilience to frequent fires and vice versa. Annual grassland species are resilient to annual fires. They are not specifically adapted to fire and do well under other annual disturbances. Fire-annual flora species have a life cycle entirely keyed to fire; however, fires at less than 10-year intervals will eliminate most of these species.

3. A component of the fire regime, important to the evolution of reproductive strategies, is the burning pattern, i.e., patchy vs. extensive. Of the four components of the fire regime, season, intensity, frequency, and pattern, the last two exert the greatest selective force, since season is relatively constant across natural systems (generally the driest season) and intensity is a function of frequency (it is largely dependent upon fuel buildup in the fire-free interval). Fire frequency relates to the predictability of fire in time and pattern relates to the predictability of fire in space.

4. There is commonly a whole suite of characteristics associated with a particular pattern of fire predictability. For example, consider the following cases of shrub reproductive strategies in response to different fire regimes.

(a) Frequent fires distributed mosaic fashion (fire is predictable in time but not space): such an environment would select for widely dispersed seeds (to "find" the disturbances), commonly without any imposed dormancy, and with vegetative reproduction (to capitalize on the probability of being one of the first there).

(b) Frequent fires burning extensive areas (fire is predictable in time and space): selection would be for locally dispersed seeds (fire will come to them), which are long lived and require fire stimulation for germination and lacking vegetative reproduction (since germination is locally synchronous).

5. "Other" environmental factors may have a similar selective effect to that of fire. For example, tree falls in many forests are more important than fire, but since they produce a similar type of disturbance, i.e., predictable in time but not in space, the reproductive strategies are similar to those described in 4a.

6. Some strategies are successful across all growth forms. For example, consider the suite of characteristics for an environment in which fire is predictable in time but not space (4a above). One can find examples of this strategy in herbs (Epilobium angustifolium, Pteridium aquilinum), shrubs (Rubus sp., Symphoricarpos sp.), and trees (Populus tremuloides, Salix sp.).

7. In some instances, strategies may be greatly influenced by growth form. For example, both perennial grasslands and chaparral are subjected to fires which are highly predictable in both time and space, yet chaparral shrubs store seed in the soil and perennial grasses do not. However, these grasses can recover from fire and flower and set seed within a few months, an option not available to shrubs. Functionally, such a response may be as fruitful as many years of seed production in a shrub, since it has been shown in at least one study that over 70 years of seed production by a chaparral shrub may result in fewer seeds stored in the soil than can be produced during a single "good" year (Keeley 1977a).

8. Resistance to fire is an attribute unique to trees, and commonly developed through the production of thick bark and self-pruning. Such resistance is required of species to survive frequent fires. As fire frequency decreases, fuel buildup increases, and the resultant fire, because of its intensity, makes resistance a nonviable option. Under very infrequent fires, there is also little selection for resistance to fire.

9. Resprouting after fire is one way an individual in the population can insure a continuance of its genes. It is such a widespread response that it is simpler to list the instances in which it is not found. One example is annual plants, another is obligate-seeding chaparral shrubs. While annual plants in some instances have evolutionarily deserted the perennial condition because of the unlikelihood of surviving a particular season, obligate seeders may have deserted the resprouting mode because of decreasing likelihood of surviving fire. Resprouting in woody dicots is a widespread, apparently conservative trait, which likely evolved many times in response to a variety of conditions; e.g., it allows for rapid recovery after frosts (Mooney 1977a), intense grazing (Sampson and Jespersen 1958), or damage from windfalls (Fowells 1965). Other than the specific instance of obligate-seeding Mediterranean shrubs, the only other common instances of nonsprouting woody dicots are ones which have a predominantly herbaceous ancestry and are currently in a more-or-less fire-free environment, e.g., Artemisia tridentata. In general, to argue that the presence of resprouting capacity in a woody dicot reflects the selective influence of fire is unwarranted. For example, it has been argued that the Hawaiian flora has had a long evolutionary relationship with fire because species resprout when tops are damaged. However, resprouting capacity is ubiquitous among tropical rain forest woody dicots, most of which have had no evolutionary association with fire. Gymnosperms are a different case. Resprouting is uncommon in conifers except where directly attributable to fire.

10. r- and K-selection could be interpreted to predict that growth forms should be favored in an array--herbs:shrubs:trees, relative to decreasing fire frequency. This is true when species must complete a zygote-to-zygote life cycle within the fire-free interval. It is potentially untrue whenever there is the possibility of resistance to fire or regeneration afterwards. Thus, other components of the fire regime, such as fire intensity, need to be considered.

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#### PUBLICATIONS CITED

- Abrahamson, W. G.  
1975. Reproductive strategies in dewberries. *Ecology* 56:721-726.
- Ahlgren, C. E.  
1960. Some effects of fire on reproduction and growth of vegetation in northeastern Minnesota. *Ecology* 41:431-445.

- Albertson, F. W., G. W. Tomanek, and A. Riegel.  
1957. Ecology of drought cycles and grazing intensity on grasslands of central Great Plains. *Ecol. Monogr.* 27:27-44.
- Axelrod, D. I.  
1975. Evolution and biogeography of Madrean-Tethyan sclerophyll vegetation. *Ann. Mo. Bot. Gard.* 62:280-334.
- Baker, H. G.  
1972. Seed weight in relation to environmental conditions in California. *Ecology* 53:997-1010.
- Barden, L. S., and F. W. Woods.  
1973. Characteristics of lightning fires in southern Appalachian forests. *In Proc. Tall Timbers Fire Ecol. Conf.* 13:345-361.
- Barden, L. S., and F. W. Woods.  
1976. Effects of fire on pine and pine-hardwood forests in the Southern Appalachians. *For. Sci.* 22:399-403.
- Barney, M. A., and N. C. Frischknecht.  
1974. Vegetation changes following fire in the Pinyon-Juniper type of West-Central Utah. *J. Range Manage.* 27:91-96.
- Beasleigh, W. J., and G. A. Yarranton.  
1974. Ecological strategy and tactics of Equisetum sylvaticum during a post-fire succession. *Can. J. Bot.* 52:2299-2318.
- Beatley, J. C.  
1966. Ecological status of introduced Bromus grasses (Bromus spp.) in desert vegetation of southern Nevada. *Ecology* 47:548-554.
- Berg, A. R.  
1974. Arctostaphylos Adans. *In Seeds of woody plants in the United States.* p. 228-231. U.S. Dep. Agric., Agric. Handb. 450. Washington, D.C.
- Bernard, J. M.  
1976. The life history and population dynamics of shoots of Carex rostrata. *J. Ecol.* 64:1045-1048.
- Biswell, H. H.  
1974. Effects of fire on chaparral. *In Fire and ecosystems.* p. 321-365. T. T. Kozlowski and C. E. Ahlgren, eds. Academic Press, New York.
- Biswell, H. H., and J. F. Street.  
1948. Wedgeleaf ceanothus, range brush. *Calif. Agric.* 2:3.
- Blaisdell, J. P., and W. F. Mueggler.  
1956. Sprouting of bitterbrush (Purshia tridentata) following burning or top removal. *Ecology* 37:365-370.
- Bolton, R. B., Jr., and R. J. Vogl.  
1969. Ecological requirements of Pseudotsuga macrocarpa (Vasey) Mayr in the Santa Ana Mountains, California. *J. For.* 67:112-116.
- Box, T. W., J. Powell, and D. L. Drawe.  
1967. Influence of fire on south Texas chaparral communities. *Ecology* 48:995-960.
- Bragg, T. B.  
1978. Annual variations in the burning potential of bluestem prairie. *Bull. Ecol. Soc. Am.* 59:109.
- Bragg, T. B., and L. C. Hulbert.  
1976. Woody plant invasion of unburned Kansas bluestem prairie. *J. Range Manage.* 29:19-24.
- Brewer, R., and P. G. Merritt.  
1978. Wind throw and tree replacement in a climax beech-maple forest. *Oikos* 30:149-152.
- Brown, H. E.  
1958. Gambel oak in west-central Colorado. *Ecology* 39:317-327.
- Bullock, S. H.  
1978. Plant abundance and distribution in relation to types of seed dispersal in chaparral. *Madroño* 25:104-105.

- Burcham, L. T.  
 1973. Fire and chaparral before European settlement. In Proc., Living with the chaparral. p. 101-120. M. Rosenthal, ed. Sierra Club, San Francisco, Calif.
- Burkhardt, H. W., and E. W. Tisdale.  
 1976. Causes of juniper invasion in southwestern Idaho. Ecology 57:472-484.
- Byrne, R., J. Michaelsen, and A. Soutar.  
 1977. Fossil charcoal as a measure of wildfire frequency in southern California: a preliminary analysis. In Environmental consequences of fire and fuel management in Mediterranean ecosystems. p. 361-367. H. A. Mooney and C. E. Conrad, eds. USDA For. Serv. Gen. Tech. Rep. WO-3. Washington, D.C.
- Cable, D. R.  
 1972. Fire effects in southwestern semidesert grass-shrub communities. In Proc. Tall Timbers Fire Ecology Conf. 12:109-127.
- Callaghan, T. V.  
 1976. Growth and population dynamics of Carex bigelowii in an alpine environment. Oikos 27:402-413.
- Callaghan, T. V., and N. J. Collins.  
 1976. Strategies of growth and population dynamics of tundra plants. Oikos 27:383-388.
- Canfield, R. J.  
 1957. Reproduction and life span of some perennial grasses of southern Arizona. J. Range Manage. 10:199-203.
- Christensen, N. L., and C. H. Muller.  
 1975. Effects of fire on factors controlling plant growth in Adenstoma chaparral. Ecol. Monogr. 45:29-55.
- Clements, F. E.  
 1920. Plant indicators: the relation of plant communities to process and practice. Carnegie Inst. Wash. Publ. 290, 388 p.
- Connaughton, C. A.  
 1934. Fire damage in the ponderosa pine type in Idaho. J. For. 34:46-51.
- Cooper, W. C.  
 1922. The broad-sclerophyll vegetation of California: an ecological study of chaparral and its related communities. Carnegie Inst. Wash. Publ. 319, 124 p.
- Corbett, E. S., and L. R. Green.  
 1965. Emergency revegetation to rehabilitate burned watersheds in southern California. USDA For. Serv. Res. Pap. PSW-22, 14 p. Pac. Southwest For. and Range Exp. Stn., Berkeley, Calif.
- Crampton, B.  
 1974. Grasses in California. 178 p. Univ. Calif. Press, Berkeley.
- Critchfield, W. B.  
 1957. Geographic variation in Pinus contorta. Maria Moors Cabot Found. Publ. 3, 118 p.
- Cronemiller, F. P.  
 1959. The life history of deerbrush--a fire type. J. Range Manage. 12:21-25.
- Cwynar, L. C.  
 1978. Recent history of fire and vegetation from laminated sediment of Green Leaf Lake, Algonquin Park, Ontario. Can. J. Bot. 56:10-21.
- Cypert, E.  
 1972. Plant succession on burned areas in Okefenokee swamp following fires of 1954 and 1955. In Proc. Tall Timbers Fire Ecol. Conf. 12:199-217.
- Daubenmire, R.  
 1968. Ecology of fire in grasslands. Adv. Ecol. Res. 5:209-266.
- Deitschman, G. H.  
 1974. Artemisia L. Sagebrush. In Seeds of woody plants in the United States. p. 235-237. U.S. Dep. Agric., Agric. Handb. 450. Washington, D.C.
- Deitschman, G. H., K. R. Jorgensen, and A. P. Plummer.  
 1974. Purshia Bitterbrush. In Seeds of woody plants in the United States. p. 686-688. U.S. Dep. Agric., Agric. Handb. 450. Washington, D.C.



- Doolittle, M. L.  
1977. Forest fire occurrence in southern counties, 1966-1975. USDA For. Serv. Res. Note SO-227. South. For. Exp. Stn., New Orleans, La.
- Flinn, M. A., and R. W. Wein.  
1977. Depth of underground plant organs and theoretical survival during fire. Can. J. Bot. 55:2550-2554.
- Forcier, L. K.  
1975. Reproductive strategies and the co-occurrence of climax tree species. Science 189:808-810.
- Fowells, H. A., ed.  
1965. Silvics of forest trees of the United States. U.S. Dep. Agric., Agric. Handb. 271. Washington, D.C.
- Frissell, S. S., Jr.  
1973. The importance of fire as a natural ecological factor in Itasca State Park, Minnesota. J. Quat. Res. 3:397-407.
- Gadgil, M. D., and O. T. Solbrig.  
1972. The concept of r- and K-selection: evidence from wildflowers and some theoretical considerations. Am. Nat. 106:14-31.
- Garren, K. H.  
1943. Effects of fire on vegetation of the southeastern United States. Biol. Rev. 9:617-654.
- Gause, G. W.  
1966. Silvical characteristics of bigcone Douglas fir (Pseudotsuga macrocarpa (Vasey) Mayr). USDA For. Serv. Res. Pap. PSW-31, 10 p. Pac. Southwest For. and Range Exp. Stn., Berkeley, Calif.
- Gill, A. M.  
1973. Effects of fire on Australia's native vegetation. In CSIRO Div. Plant Ind. Annu. Rep. p. 41-46. Canberra, Aust.
- Gillison, A. N.  
1969. Plant succession in an irregularly fired grassland area - Doma Peaks region, Papua. J. Ecol. 57:415-427.
- Goff, F. G., and P. H. Zedler.  
1968. Structural gradient analysis of upland forests in the Western Great Lakes Area. Ecol. Mongr. 38:65-86.
- Gratkowski, H. S.  
1962. Heat as a factor in germination of seeds of Ceanothus velutinus var. laevigatus T. and G. Ph.D. thesis. Oreg. State Univ., Corvallis.
- Hadley, E. B.  
1961. Influence of temperature and other factors on Ceanothus megacarpus seed germination. Madrono 16:132-138.
- Hadley, E. B., and B. J. Kiekhefer.  
1963. Productivity of two prairie grasses in relation to fire frequency. Ecology 44:389-395.
- Hanes, T. L.  
1977. California chaparral. In Terrestrial vegetation of California. p. 417-469. M. G. Barbour and J. Majors, eds. John Wiley and Sons, Inc., San Francisco.
- Hanson, H. C.  
1950. Ecology of the grassland. II. Bot. Rev. 16:283-360.
- Harberd, D. J.  
1967. Observations on natural clones of Holcus mollis. New Phytol. 66:401-408.
- Harcombe, P. A., and P. L. Marks.  
1978. Tree diameter distributions and replacement processes in southwest Texas forests. For. Sci. 24:153-166.
- Harper, J. L.  
1977. Population biology of plants. 842 p. Academic Press, San Francisco.
- Harper, J. L., and J. Ogden.  
1970. The reproductive strategy of higher plants. 1. The concept of strategy with special reference to Senecio vulgaris L. J. Ecol. 58:681-698.

- Hartesveldt, R. J., and H. T. Harvey.  
1967. The fire ecology of Sequoia regeneration. In Proc. Tall Timbers Fire Ecol. Conf. 7:65-77.
- Hartshorn, G. S.  
1978. Tree falls and tropical forest dynamics. In Tropical trees as living systems. p. 617-638. P. B. Tomlinson and M. H. Zimmerman, eds. Cambridge Univ. Press, New York.
- Heady, H. F.  
1958. Vegetational changes in the California annual type. Ecology 39:402-416.
- Heady, H. F.  
1977. Valley grassland. In Terrestrial vegetation of California. p. 491-514. M. G. Barbour and J. Major, eds. John Wiley and Sons, Inc., San Francisco.
- Heinselmann, M. L.  
1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. J. Quat. Res. 3:329-382.
- Hervey, J. F.  
1949. Reaction of a California annual plant community to fire. J. Range Manage. 2:116-121.
- Hodgkins, E. J.  
1958. Effects of fire on undergrowth vegetation in upland southern pine forests. Ecology 39:36-46.
- Holler, L. C., and W. G. Abrahamson.  
1977. Seed and vegetative reproduction in relation to density in Fragaria virginiana (Rosaceae). Am. J. Bot. 64:1003-1007.
- Horton, J. S., and C. J. Kraebel.  
1955. Development of vegetation after fire in the chamise chaparral of southern California. Ecology 36:244-262.
- Horton, J. S., and J. T. Wright.  
1945. The wood rat as an ecological factor in southern California watersheds. Ecology 25:341-351.
- Houston, D. B.  
1973. Wildfires in northern Yellowstone National Park. Ecology 54:1111-1117.
- Humphrey, R. R.  
1962. Range ecology. 235 p. Ronald Press, New York.
- Janke, R. A., D. McKaig, and R. Raymond.  
1978. Comparison of presettlement and modern upland boreal forests on Isle Royale National Park. For. Sci. 24:115-121.
- Janzen, D. H.  
1976. Why bamboos wait so long to flower. Annu. Rev. Ecol. Syst. 70:347-391.
- Janzen, D. H.  
1977. What are dandelions and aphids? Am. Nat. 111:586-589.
- Jepson, W. L.  
1916. Regeneration in manzanita. Madroño 1:3-11.
- Johnsen, T. N., Jr.  
1959. Longevity of stored juniper seeds. Ecology 40:487-488.
- Johnson, A. S., and L. L. Landers.  
1978. Fruit production in slash pine plantations in Georgia. J. Wildl. Manage. 42:606-613.
- Johnson, E. A.  
1975. Buried seed populations in the subarctic forest east of Great Slave Lake, Northwest Territories. Can. J. Bot. 53:2933-2941.
- Keeley, J. E.  
1975. The longevity of nonsprouting Ceanothus. Am. Midl. Nat. 93:540-507.
- Keeley, J. E.  
1977a. Seed production, seed populations in soil and seedling production after fire for two congeneric pairs of sprouting and nonsprouting chaparral shrubs. Ecology 59:820-829.

- Keeley, J. E.  
 1977b. Fire-dependent reproductive strategies in Arctostaphylos and Ceanothus. In Environmental consequences of fire and fuel management in Mediterranean ecosystems. p. 391-396. H. A. Mooney and C. E. Conrad, eds. USDA For. Serv. Gen. Tech. Rep. WO-3. Washington, D.C.
- Keeley, J. E., and S. C. Keeley.  
 1977. Energy allocation patterns of sprouting and nonsprouting species of Arctostaphylos in the California chaparral. *Am. Midl. Nat.* 98:1-10.
- Keeley, J. E., and P. H. Zedler.  
 1978. Reproduction of chaparral shrubs after fire: a comparison of the sprouting and seeding strategies. *Am. Midl. Nat.* 99:142-161.
- Keeley, S. C., and A. W. Johnson.  
 1977. A comparison of the pattern of herb and shrub growth on comparable sites in Chile and California. *Am. Midl. Nat.* 97:120-132.
- Kenman, T. C. D.  
 1971. The effects of fire on two vegetation types at Matopos, Rhodesia. In *Proc. Tall Timbers Fire Ecol. Conf.* 11:53-58.
- Kerr, L. R.  
 1925. The lignotubers of eucalyptus seedlings. *Proc. Royal Soc. Victoria* 37:79-96.
- Kerster, H. W.  
 1968. Population age structure in the prairie forb Liatris aspera. *Bioscience* 18:430-432.
- Kilgore, B. M.  
 1973. The ecological role of fire in Sierran conifer forests. *J. Quat. Res.* 3:496-513.
- Kilgore, B. M., and D. Taylor.  
 1979. Fire history of a Sequoia mixed conifer forest. *Ecology* 60(1):129-142.
- Komarek, E. V., Jr.  
 1967. The nature of lightning fires. In *Proc. Tall Timbers Fire Ecol. Conf.* 7:5-41.
- Kruger, F. S.  
 1977. Ecology of Cape fynbos in relation to fire. In *Environmental consequences of fire in fuel management in Mediterranean ecosystems*. p. 391-396. H. A. Mooney and C. E. Conrad, eds. USDA For. Serv. Gen. Tech. Rep. WO-3. Washington, D.C.
- Levin, D. A.  
 1973. The age structure of a hybrid swarm in Liatris (Compositae). *Evolution* 27:532-535.
- Levin, D. A., and H. W. Kerster.  
 1978. Rings and age in Liatris. *Am. Nat.* 112:1120-1122.
- Lippert, R. D., and H. H. Hopkins.  
 1950. Study of viable seeds in various habitats in mixed prairie. *Trans. Kans. Acad. Sci.* 53:355-364.
- Little, S.  
 1973. Eighteen-year changes in composition of a stand of Pinus echinata and P. rigida in southern New Jersey. *Bull. Torr. Bot. Club* 100:94-102.
- Little, S.  
 1974. Effects of fire on temperate forests: northeastern United States. In *Fire and ecosystems*. p. 225-250. T. T. Kozlowski and C. E. Ahlgren, eds. Academic Press, New York.
- Longman, K. A., and J. Jenik.  
 1974. Tropical forest and its environment. 196 p. Longman, London.
- Loope, L. L., and G. E. Gruell.  
 1973. The ecological role of fire in the Jackson Hole area, northwestern Wyoming. *J. Quat. Res.* 3:425-433.
- Lorimer, C. G.  
 1977. The presettlement forest and natural disturbance of cycle of northeastern Maine. *Ecology* 58:139-148.
- Lotan, J. E.  
 1967. Cone serotiny of lodgepole pine near West Yellowstone, Montana. *For. Sci.* 13:55-59.

- Lotan, J. E.  
1976. Cone serotiny--fire relationships in lodgepole pine. In Proc. Tall Timbers Fire Ecol. Conf. 14:267-277.
- Lyon, L. J., and P. F. Stickney.  
1974. Early vegetal succession following large northern Rocky Mountain wildfires. In Proc. Tall Timbers Fire Ecol. Conf. 14:355-373.
- MacArthur, R. H., and E. O. Wilson.  
1967. The theory of island biogeography. 203 p. Princeton Univ. Press.
- McLean, A.  
1969. Fire resistance of forest species as influenced by root systems. J. Range Manage. 22:120-122.
- McLean, D. A., and R. W. Wein.  
1977. Nutrient accumulation for postfire jack pine and hardwood succession patterns in New Brunswick. Can. J. For. Res. 7:562-578.
- Major, J., and W. T. Pyott.  
1966. Buried, viable seeds in two California bunchgrass sites and their bearing on the definition of a flora. Vegetatio 13:253-282.
- Marks, P. L.  
1974. The role of pin cherry (Prunus pennsylvanica L.) in the maintenance of stability in northern hardwood ecosystems. Ecol. Monogr. 44:73-88.
- Martin, R. E., R. L. Miller, and C. T. Cushwa.  
1975. Germination response of legume seeds subjected to moist and dry heat. Ecology 56:1441-1445.
- Minnich, R. A.  
1974. The impact of fire suppression on southern California conifer forests: a case study of the Big Bear fire, November 13 to 16, 1970. In Proc. Living with the Chaparral. p. 45-47. M. Rosenthal, ed. Sierra Club, San Francisco, Calif.
- Mirov, N. T., and C. J. Kraebel.  
1937. Collecting and propagating the seeds of California wild plants. USDA For. Serv. Res. Note 18, 27 p. Calif. For. and Range Exp. Stn., Berkeley, Calif.
- Mooney, H. A.  
1977a. Frost sensitivity and resprouting behavior of analogous shrubs of California and Chile. Madroño 24:74-77.
- Mooney, H. A., ed.  
1977b. Convergent evolution in Chile and California: Mediterranean climate ecosystems. 224 p. Bowden, Hutchinson and Ross, Inc., Stroudsburg, Pa.
- Moore, J. M., and R. W. Wein.  
1977. Viable seed populations by soil depth and potential site recolonization after disturbance. Can. J. Bot. 56:2408-2412.
- Mueggler, W. F.  
1956. Is sagebrush seed residual in the soil of burns or is it windborne? USDA For. Serv. Res. Note 35, 10 p. Intermed. For. and Range Expt. Stn. Ogden, Utah.
- Muir, J.  
1938. John of the mountains. 459 p. Houghton Mifflin Co., Boston, Mass.
- Naveh, Z.  
1967. Mediterranean ecosystems and vegetation types in California and Israel. Ecology 48:445-459.
- Naveh, Z.  
1974. Effects of fire in the Mediterranean region. In Fire and ecosystems. p. 401-434. T. T. Kozlowski and C. E. Ahlgren, eds. Academic Press, New York.
- Nord, E. C.  
1965. Autoecology of bitterbrush in California. Ecol. Monogr. 35:307-334.
- Olmstead, N. W., and J. D. Curtis.  
1947. Seeds of the forest floor. Ecology 28:49-52.
- Orme, M. L., and T. A. Leege.  
1976. Emergence and survival of redstem (Ceanothus sanguineus) following prescribed burning. In Proc. Tall Timbers Fire Ecol. Conf. 14:391-420.

- Parsons, D. J.  
1977. The role of fire in park management. *Parks* 2:1-4.
- Patric, J. H., and T. L. Hanes.  
1964. Chaparral succession in a San Gabriel Mountain area of California. *Ecology* 45:353-360.
- Payette, S.  
1976. Succession ecologique des forets d'epinette blanche et fluctuations climatiques. Poste de la Baleine, Nouveau Quebec. *Can. J. Bot.* 54:1394-1402.
- Perry, D. A., and J. E. Lotan.  
1979. A model of fire selection for serotiny in lodgepole pine. *Evolution* 33(3):958-968.
- Philips, J.  
1965. Fire as master and servant, its influence in the bioclimatic regions of trans-Saharan Africa. *In Proc. Tall Timbers Fire Ecol. Conf.* 4:7-109.
- Pianka, E. R.  
1970. On r and K selection. *Am. Nat.* 104:592-597.
- Pickford, G. D.  
1932. The influence of continued heavy grazing and of promiscuous burning on spring-fall ranges in Utah. *Ecology* 13:159-171.
- Pitt, M. D., and H. F. Heady.  
1978. Responses of annual vegetation to temperature and rainfall patterns in northern California. *Ecology* 59:336-350.
- Quick, C. R.  
1935. Notes on the germination of Ceanothus seeds. *Madroño* 3:135-140.
- Quick, C. R., and A. S. Quick.  
1961. Germination of Ceanothus seeds. *Madroño* 16:23-30.
- Raven, P. H., and D. I. Axelrod.  
1978. Origin and relationships of the California flora. *Univ. Calif. Publ. Bot.* 72:1-134.
- Rawitscher, F.  
1948. The water economy of the vegetation of the campos cerrados in southern Brazil. *J. Ecol.* 36:237-268.
- Reiners, W. A.  
1967. Relationships between vegetational strata in the pine barrens of central Long Island, New York. *Bull. Torr. Bot. Club* 94:87-99.
- Reveal, J. L.  
1978. The autoecology and status of Cuyamaca cypress (Cupressus arizonica var. stephensonii). Unpubl. ms. USDA For. Serv., Cleveland Natl. For., San Diego, Calif.
- Reynolds, R. D.  
1959. Effects of natural fires and aboriginal burning upon the forest of the central Sierra Nevada. M.S. thesis. Univ. Calif., Berkeley.
- Rice, E. L., and R. L. Parenti.  
1978. Causes of decreases in productivity in undisturbed tall grass prairie. *Am. J. Bot.* 65:1091-1097.
- Richards, P., and G. B. Williamson.  
1975. Tree fall and patterns of understory species in a wet lowland tropical forest. *Ecology* 56:1226-1229.
- Rowe, J. S.  
1970. Spruce and fire in northwest Canada and Alaska. *In Proc. Tall Timbers Fire Ecol. Conf.* 10:245-254.
- Salisbury, E. J.  
1942. The reproductive capacity of plants. 244 p. Bell, London.
- Salmonson, M. G.  
1978. Adaptations for animal dispersal of one-seed juniper seeds. *Oecologia* 32:333-339.
- Sampson, A. W.  
1944. Plant succession and burned chaparral lands in northern California. *Univ. Calif. Agric. Exp. Stn. Bull.* 685, 144 p. Berkeley.

- Sampson, A. W., and B. S. Jespersen.  
1963. California range brushlands and browse plants. Univ. Calif. Agric. Exp. Stn. Manual 33, 162 p. Berkeley.
- Sauer, J. D.  
1977. Fire history, environmental patterns, and species patterns in Santa Monica mountain chaparral. In Environmental consequences of fire and fuel management in Mediterranean ecosystems. p. 383-386. H. A. Mooney and C. E. Conrad, eds. USDA For. Serv. Gen. Tech. Rep. WO-3. Washington, D.C.
- Saunier, R. E., and R. F. Wagle.  
1967. Factors affecting the distribution of shrub live oak (Quercus turbinella Greene). Ecology 48:35-41.
- Sawyer, J. O., D. A. Thornburgh, and H. R. Griffin.  
1977. Mixed evergreen forest. In Terrestrial vegetation of California. p. 417-469. M. G. Barbour and J. Major, eds. John Wiley and Sons, Inc., San Francisco.
- Schall, B. A.  
1978. Age structure in Liatris acidota (Compositae). Oecologia 32:93-100.
- Schlesinger, W. H.  
1978. On the relative dominance of shrubs in Okefenokee Swamp. Am. Nat. 112:949-954.
- 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.
- Shultz, A. M., J. L. Launchbaugh, and H. H. Biswell.  
1955. Relationship between grass density and brush seedling survival. Ecology 36:226-238.
- Smith, A. J.  
1975. Invasion and ecesis of bird-disseminated woody plants in a temperate forest sere. Ecology 56:19-34.
- Smith, E. F., and C. E. Owensby.  
1972. Effects of fire on true prairie grassland. In Proc. Tall Timbers Fire Ecol. Conf. 12:9-22.
- Smith, T. A.  
1970. Effects of disturbance on seed germination in some annual plants. Ecology 51:1106-1108.
- Specht, R. L.  
1980. Responses of heathlands and related shrublands to fires. In Fire and the Australian Biota Symposium. A. M. Gill, R. H. Groves, and I. R. Noble, eds. Aust. Acad. Sci.
- Specht, R. L., P. Rayson, and M. E. Jackman.  
1958. Dark island heath (Ninety-mile Plain, South Australia). VI. Pyric succession: changes in composition, coverage, dry weight, and mineral nutrient status. Aust. J. Bot. 6:59-88.
- Stearns, F. W.  
1949. Ninety years change in a northern hardwood forest in Wisconsin. Ecology 30:349-358.
- Stebbins, G. L.  
1974. Flowering plants evolution above the species level. 399 p. Harvard Univ. Press, Cambridge, Mass.
- Stone, E. C., and G. Juhren.  
1953. Fire-stimulated germination. Calif. Agric. 7:13-14.
- Swan, F. R., Jr.  
1970. Post-fire response of four plant communities in south-central New York State. Ecology 51:1074-1082.
- Sweeney, J. R.  
1956. Responses of vegetation to fire: a study of the herbaceous vegetation following chaparral fires. Univ. Calif. Publ. Bot. 28:143-250.
- Teich, A. H.  
1970. Cone serotiny and inbreeding in natural populations of Pinus banksiana and Pinus contorta. Can. J. Bot. 48:1805-1809.

- Thomas, A. G., and H. M. Dale.  
1975. The role of seed reproduction in the dynamics of established populations of Hieracium floribundum and a comparison with that of vegetative reproduction. Can. J. Bot. 53:3022-3031.
- Thompson, J. N., and M. F. Willson.  
1978. Disturbance and the dispersal of fleshy fruits. Science 200:1161-1163.
- Tratz, W. M., and R. J. Vogl.  
1977. Postfire vegetational recovery, productivity and herbivore utilization of a chaparral-desert ecotone. In Environmental consequences of fire and fuel management in Mediterranean ecosystems. p. 426-430. H. A. Mooney and C. E. Conrad, eds. USDA For. Serv. Gen. Tech. Rep. WO-3. Washington, D.C.
- Valk, A. G. van der, and C. B. Davis.  
1978. The role of seed banks in the vegetation dynamics of prairie glacial marshes. Ecology 59:322-335.
- Van der Wall, S. B., and R. P. Balda.  
1977. Coadaptions of the Clark's Nutcracker and the pinyon pine for efficient seed harvest and dispersal. Ecol. Monogr. 47:89-111.
- Vankat, J. L., W. H. Blackwell, Jr., and W. E. Hopkins.  
1975. The dynamics of Hueston Woods and a review of the question of the successional status of the southern beech-maple forest. Castanea 40:290-308.
- Viereck, L. A.  
1973. Wildfire in the taiga of Alaska. J. Quat. Res. 3:465-495.
- Vogl, R. J.  
1970. The role of fire in the evolution of the Hawaiian flora and vegetation. In Proc. Tall Timber Fire Ecol. Conf. 9:5-60.
- Vogl, R. J.  
1973. Ecology of knobcone pine in the Santa Ana Mountains, California. Ecol. Monogr. 43:125-143.
- Vogl, R. J.  
1974. Effects of fire on grasslands. In Fire and ecosystems. p. 139-194. T. T. Kozlowski and C. E. Ahlgren, eds. Academic Press, New York.
- Wagener, W. W.  
1961. Past fire incidence in Sierra Nevada Forests. J. For. 59:739-747.
- Weaver, J. E.  
1958. Classification of root systems of forbs of grassland and a consideration of their significance. Ecology 39:393-406.
- Weaver, J. E., and F. W. Albertson.  
1956. Grasslands of the Great Plains: their nature and use. 395 p. Johnsen Publ. Co., Lincoln, Neb.
- Webb, L. J., J. G. Tracey, and W. T. Williams.  
1972. Regeneration and pattern in the subtropical rain forest. J. Ecol. 60:675-695.
- Webber, H. J.  
1935. The Florida scrub, a fire-fighting association. Am. J. Bot. 22:344-361.
- Webster's Seventh New Collegiate Dictionary.  
1969. 1223 p. C. C. Merriam Co., Springfield, Mass.
- Wien, R. W., and L. C. Bliss.  
1973. Changes in arctic Eriophorum tussock communities following fire. Ecology 54:845-852.
- Wien, R. W., and J. M. Moore.  
1977. Fire history and rotations in the New Brunswick Acadian Forest. Can. J. For. Res. 7:285-294.
- Wells, P. V.  
1962. Vegetation in relation to geological substratum and fire in the San Luis Obispo quadrangle, California. Ecol. Monogr. 23:264-267.
- Wells, P. V.  
1969. The relation between mode of reproduction and extent of speciation in woody genera of the California chaparral. Evolution 23:264-267.

- Wells, P. V.  
 1976. A climax index for broadleaf forest: an n-dimensional, ecomorphological model of succession. In Proc. First Central Hardwood Forest Conf. p. 131-176. J. S. Fralish, G. T. Weaver, and R. C. Schlesinger, eds. South. Ill. Univ. at Carbondale.
- Went, F. W., G. Juhren, and M. C. Juhren.  
 1952. Fire and biotic factors affecting germination. *Ecology* 33:351-364.
- Werner, P. A.  
 1978. On the determination of age of Liatris aspera using cross-sections of corms: implications for past demographic studies. *Am. Nat.* 112:1113-1120.
- West, D.  
 1971. Fire, man and wildlife as interacting factors limiting the development of climax vegetation in Rhodesia. In Proc. Tall Timbers Fire Ecol. Conf. 11:121-145.
- Westman, W. E.  
 1976. Vegetation conversion for fire control in Los Angeles. *Urban Ecol.* 2:119-137.
- White, K. L.  
 1966a. Structure and composition of foothill woodland in central coastal California. *Ecology* 47:229-237.
- White, K. L.  
 1966b. Old-field succession on Hastings Reservation, California. *Ecology* 47:865-868.
- Wicklow, D. T.  
 1977. Germination response in Emmenanthe penduliflora (Hydrophyllaceae). *Ecology* 58:201-205.
- Wieslander, A. E., and B. O. Schreiber.  
 1939. Notes on the genus Arctostaphylos. *Madroño* 5:38-47.
- Wilbur, H. M., D. W. Tinkle, and J. P. Collins.  
 1974. Environmental certainty, trophic level, and resource availability in life history evolution. *Am. Nat.* 108:805-817.
- Williamson, G. B.  
 1975. Pattern and seral composition in an old-grown beech-maple forest. *Ecology* 56:727-731.
- Zedler, P. H.  
 1977a. Life history attributes of plants and the fire cycle: a case study in chaparral dominated by Cupressus forbesii. In Environmental consequences of fire and fuel management in Mediterranean ecosystems. p. 451-548. H. A. Mooney and C. E. Conrad, eds. USDA For. Serv. Gen. Tech. Rep. WO-3. Washington, D.C.
- Zedler, P. H.  
 1977b. The status of Bishop Pine (Pinus muricata) on Vandenberg Air Force Base and recommendations for its management. Unpubl. ms. Air Force Off. Sci. Res., Vandenberg Air Base, Vandenberg, Calif.
- Zedler, J., and O. L. Loucks.  
 1969. Differential burning response of Poa pratensis fields and Andropogon scoparius prairies in central Wisconsin. *Am. Midl. Nat.* 81:341-352.
- Zoltai, S. C.  
 1975. Structure of subarctic forests on hummocky perma-frost terrain in Northwestern Canada. *Can. J. For. Res.* 5:1-9.