Fire Adaptations of Some Southern California Plants

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Shortly after arriving in California six years ago, I was asked to give a biology seminar lecture on my research. This was the usual procedure with new faculty and I prepared a lecture on my fire research in Wisconsin (Vogl 1961). These seminars were open to the public, since the college serves the city and surrounding communities. As I presented my findings, I became conscious of the glint of state and U. S. Forest Service uniforms in the back rows. These back rows literally erupted into a barrage of probing questions at the end of the lecture. The questions were somewhat skeptical and were intended to discredit. They admitted that I almost created an acceptable argument for the uses and effects of fire in the Midwest, but were quick to emphasize that they were certain that none of these concepts or principles of fire would apply out here in the West.

I consider this first California Tall Timbers Fire Ecology Conference a major step towards convincing the West that fire has helped shape its vegetation and is an important ecological factor here, just as it is in the Midwest, Southeast, or wherever in North
America. I hope that southern Californians attending these meetings or reading these *Proceedings* are not left with the impression that the information presented might be acceptable for northern California but cannot be applied to southern California because the majority of contributors worked in the north.

Southern Californians are thoroughly convinced that all fire is synonymous with destruction. Indeed, at times, living in southern California with its smog, traffic, and ravaging fires is perhaps analogous to going to hell early. Even southern California scientists, who are presumably open-minded and unbiased, think of fire in an emotional, illogical, and prejudiced manner. This can be illustrated by the following account. Many of the steeper hills around our campus are controlled burned each spring to eliminate the fire hazard created by drying stands of brome grasses (*Bromus* spp.), wild oats (*Avena* spp.), and mustards (*Brassica* spp.). As I left the campus one evening in the spring of 1966, I was preceded by two chemistry professors who were startled by the freshly blackened hills behind the parking lot. Neither could understand why the hills had been burned. One suggested that perhaps the burning was conducted to kill the grass and weed seeds. The other thought it might have been an accidental fire, but both agreed that whatever the reason or cause, the burning was foolhardy because the hills would wash away with the first rains. They were certain of this because they had viewed on television the floods and erosion that follow California fires. However, the following winter rains did not wash the hills away, just as rains after at least ten previous annual burns had not affected the hills.

Some past investigators have tried to discredit fire as a positive ecological factor in California. Show and Kotok (1924) were credited with producing incontrovertible evidence that sounded the “death knell” for light burning in California forests (Woolsey 1925). Burcham (1959) claimed that fires were almost non-existent prior to the arrival of European settlement, since the first explorers encountered dense woods and brush which were interpreted as indicating a paucity of fires. Burcham felt that the Indian’s use of fire was ineffective and, therefore, decided that southern California’s vegetation was not subjected or adapted to frequent fire.
The role of lightning as a source of fire has been greatly underestimated, particularly in southern California. It has been assumed that lightning is confined to high elevations and therefore is considered to only influence the vegetation of upper coniferous forests. The assumption that lightning only strikes the tallest objects on the highest peaks can be dispelled by the yearly occurrences of lightning at lower elevations and in valley cities of southern California. Accounts of lightning fires at low elevations and lightning damage to city facilities are common (Anonymous 1966, Berman 1966, Copeland 1967, Houston 1967, Leadabrand 1967). In pristine times, when vegetation types were continuous and contiguous, fires could burn large areas or through several vegetation types without stopping. Even present-day southern California fires burn for long distances, despite many kinds of man-made firebreaks and man's efforts, until stopped by massive natural firebreaks or changes in climatic conditions (Kinucan 1965). A little lightning, then, could have gone a long way, particularly when thunderstorms coincided with the dry season. The driest and hottest season in southern California usually occurs in late summer and early autumn (Kinucan 1965, Pirsko and Green 1967). This is the time when desert thunderstorms are pushed westward into California as they curve up from the Gulf of Mexico. During the last few days of August, 1967, for example, seven lightning fires occurred in the Angeles National Forest and 11 occurred in the San Bernardino National Forest while air temperatures were over 100°F. (Anonymous 1967a).

Another misconception is that lightning fires cannot burn downhill. Calkins (1925) stated that lightning fires were “reluctant” to travel downhill from their origins in timbered mountain tops and, therefore, could not have affected lower elevational brush and grassland. Under normal circumstances, fires do not readily burn downhill, particularly for long distances. Conditions prior to, and during thundershowers, however, are often atypical since storms are accompanied by downdrafts which produce heavy radial winds (Davis 1959). Fires often originate from “sleepers” which may not spread until long after a storm has passed. Under normal southern California coastal weather conditions, strong downslope winds augmented by offshore winds commonly occur at night and can push fires down-
Southern California mountains are also frequented by high-velocity foehn winds. These ground-hugging winds, known locally as "Santa Ana" winds, are hot and dry descending winds which have been observed to push fires downhill as rapidly as normal upslope fires spread.

**SOUTHERN CALIFORNIA VEGETATION**

The major vegetation types found in southern California as well as in the entire state are coniferous forest, woodland-savanna, chaparral, grassland, and desert (Munz 1963). These vegetation types, with the possible exception of desert, have been influenced by the presence of fire throughout their development. About one-half of California is covered by forest, woodland, and brush (Stone 1964). Agriculture and urbanization occupy another one-fourth which was once primarily covered with native grasslands (Benson and Walkington 1965). Fire, then, helped to shape three-fourths of the state's vegetation but is still largely considered a negative destructive force. Even the role of fire in the life histories of many economically important species has been ignored or de-emphasized.

But what about the remaining one-fourth of the state occupied by desert? North American deserts are not generally considered to have been influenced by fire because their scant or sparsely scattered vegetation appears incapable of supporting fire. I find it difficult to accept that some 270,000 square miles (Brown 1963) could have escaped the influence of fire, particularly since desert vegetation is highly flammable and subject to periodic lightning. Only infrequent fire would be necessary to produce pronounced effects, since plant succession is slow in the extremely harsh and dry desert environment.

Large portions of desert ecotones have been classed as desert grasslands. This type still exists in many areas including parts of the Sonoran Desert in Arizona and Mexico, and has been considered a fire type (Humphrey 1962). Desert grassland is not described for the California portion of the Sonoran Desert or for the Mojave Desert (Munz 1963). But, historical and present evidence indicates that cattle and sheep ranches once dotted these California deserts.
Surely, grasses and forbs must have been present to support the livestock on these ranches. The Angeles National Forest bordering the Mojave Desert, for example, was once threatened by bands of Basque sheep in quest of summer range (Muir 1907). Reminders of this past desert empire are the die-hard ranches still in operation and the recent opposition of desert home owners and wildflower fanciers to the remaining roving sheep herds. I feel that grasslands existed in these western deserts. These grasslands were precariously balanced on low winter precipitation supplemented by undependable traces of summer rain and probably expired in the face of combined drought and continual heavy grazing. Today these areas appear to be without fire, but this is only a recent condition created since the arrival of Europeans and their livestock.

Jepson (1921) witnessed a similar situation in Sierra forests. He observed that the forests were changing from the type first seen by white man. He felt that studies of the remaining unchanged and undisturbed portions would reveal that “...fire will be found to have been a factor of great biological importance, and will reveal and explain many things which are now hidden.” I think this statement can be applied equally well to California deserts.

Higher desert elevations (2,000 to 6,000 ft.) and desert-forest transitions are occupied by desert woodland (Munz 1963). Joshua trees (Yucca brevifolia), pinyon pines (Pinus monophylla), and junipers (Juniperus spp.) are dominant over large areas. Lightning fires commonly occur or spread into this woodland. The following statements are based on preliminary results of a current study of a series of wildfires along the west edge of the Mojave Desert. Pinyon and juniper are fire-tender species whose expansion and dominance correlate with the absence of fire. Joshua trees are capable of producing vigorous stump or root sprouts after burning. A burned Joshua tree is usually survived by a close group of resprouts. Fire appears to be important in the production and maintenance of pure Joshua tree stands. A combination of adequate moisture and a high fire frequency may have produced the dense Joshua tree stands in Walker Pass and in the west end of Antelope Valley. These individuals have been separated as Yucca brevifolia var. herbertii and are described as having many stems arising from rootstocks forming
clumps up to 10 meters in diameter (Munz 1963). Large-sized Joshua trees attain fire resistance as they lose their trunk shag of dried leaves. The flaky alligator-like bark on older trunks functions as a firebreak between surface fuels and the shag on upper limbs that otherwise would allow fire to torch up to the terminal buds. These growing points are protected from fire and its heat on large trees as they are held aloft 30 or more feet and are sheathed with thick green leaves.

Other Yucca species occurring with Joshua trees and reacting similarly to fire, or occupying similar desert ecotones are the Mojave yucca (Y. schidigera), banana yucca (Y. baccata), and the Lord’s candle (Y. whipplei). In some desert edges, Yucca species are poorly represented and are replaced by other members of the agave family including Nolina parryi, N. bigelovii, Agave utahensis, and A. deserti (Bradley 1964, Whittaker and Niering 1965).

Although these thick fibrous-leaved monocots are rich in desert-forest ecotones, an explanation of their high densities was not found. The desert ecotones have extreme environments. Temperatures range from below freezing to above 100° F. Precipitation fluctuates from almost none to heavy rain, or more often, snow. Surface fuels are continuous and dry, and lightning storms are frequent. These members of the agave family, like most monocots such as the Gramineae, Cyperaceae, Juncaceae, Typhaceae, and Palmae, have wide amplitudes of tolerance making them tough enough to withstand extreme environmental conditions, including the ability to survive repeated fires.

Fires also occur in desert scrub. Desert blackbush (Coleogyne ramosissima) communities consist of closely spaced individuals that are tinder dry and susceptible to fire (Beatley 1966). On the southern Nevada Desert Game Range, grasses were more abundant in burned blackbush communities (Bradley 1965). J. R. Koplin (personal communication, 1966) noted the effects of fire throughout the Nevada Desert Game Range. He observed a lightning fire start in Joshua tree woodland on July 18, 1959 that burned vigorously for one day and continued to smolder until July 29th when a thunder-shower contained it. The fire burned through desert scrub, desert woodland, and yellow pine forest on Spring Mountain. Further
investigation is needed to uncover and document the role of fire in California desert vegetation.

**CALIFORNIA FAN PALM**

The California fan palm (*Washingtonia filifera*) occurs around seeps and springs as far north as the Turtle and Cottonwood Mountains of California south into the Sierra Juarez, San Pedro Martir, and Sierra Pinnate Mountains of Mexico. Man-caused and natural fires are considered important factors affecting the palms and the oases in which they grow (Vogl and Mc Hargue 1966). Effects of fire were observed in all oases along the San Andreas Fault (Fig. 1). Jaeger (1959) found burned trees in all the palm canyons he visited south of the border in Mexico. Burning of palms by Indians during religious ceremonies removed the highly flammable, persistent dead palm thatch believed to harbor evil spirits (Henderson 1961). The fertilizing effects of the ash deposited around each tree increased the size and production of fruit (James 1907). Burning entire oases made them accessible, facilitated hunting, and increased the flow of the life-giving oasis springs.

Fires are also started by lightning (Gardner 1961, Henderson 1961). E. C. Jaeger (personal communication, 1966) suspected that a palm oasis deep in the Eagle Mountains was burned by a lightning fire since it was too inaccessible to have been burned by man. Desert thunderstorms are typically accompanied by lightning, but evidence of lightning is often difficult to find since palms do not generally show lightning disfigurement (Sharples 1933, Komarek 1965). Decapitated palms presumably killed by crown rot have been observed in San Andreas Fault Oases (Fig. 1) (Vogl and Mc Hargue 1966). Perhaps crown rot is not the primary cause of death, but only secondarily attacks lightning-damaged terminal buds as Sharples (1933) found in coconut palm plantations. Gardner (1961) found burned oases by using a helicopter in remote canyons of Baja California which could not have been visited by land travel. He suggested that static electricity generated in dead fronds produced the fires. Although this is feasible, undetected lightning is a more probable cause. Another source of fire might have been sparks generated from rock
slides or falling stones. Steep-walled canyons and undercut cliffs are common in wash oases and constantly lose surface rock and talus to dry scour and gravity. Sparks from these falling rocks could start fires in the dry, and often, prodigious fuels of the oases.

Besides man and lightning, the most likely cause of fire is spontaneous combustion in the hydric portions of oases which produce dense, subtropical growth with heavy accumulations of litter. Spontaneous combustion occurred naturally in Louisiana marshes (Viosca 1931), and parts of oases are similar in composition and environment.

Desert oasis fires occur at any time of the year, including immediately following a rain or a wet period. Oasis fuels are usually so prodigious, due to a year-around growing season, and so desiccated, due to continual high temperatures and low humidities, that lightning, even when occasionally accompanied by heavy rain, can readily produce persistent fires.

California fan palms are not usually killed by the burning of thatch or by repeated burning, and appear to be adapted to fire as are other members of the palm family (Fig. 1). Each successive fire kills and removes some of the outer vascular bundles, causing a reduction in trunk diameter and a corresponding reduction in crown size. This trunk and crown reduction may effectively reduce the transpiration and water-pumping capacity of these phreatophytic trees. This would serve to insure the survival of a species dependent on a stable water supply by making more of the limited supply available for palm reproduction or for a larger palm population. Although repeated burning decreases trunk diameters, trees are seldom burned off by fire. Burning experiments indicated that the fibrous trunks are difficult to ignite and almost impossible to flame. The greatest consumption of outer vascular fibers occurs with the initial burning of the attached flammable thatch. Hot fires are sometimes repeated when new thatch in tree tops detaches and slides down the burned trunk to ring the base with fresh fuel. Subsequent fires burn lesser amounts of the trunk but succeed in charring the surface. This charring increases the fire resistance of the already burned trunks. The blackened surface serves to check deep burning that might result in the felling of palms. The presence or absence of recent or recurring fires may be partially responsible for some of the confusion sur-
rounding the classification of the genus *Washingtonia*, since trunk, thatch, crown, fruit, and frond characteristics all vary with fire and have been used in its taxonomy.

Fire releases young palms suppressed by the shade of arborescent woody species. Passing fires burn off and finally kill these fire-intolerant woody species, but leave scorched palms surviving in full sun. The release of the shade-intolerant palms is important in wet oases which typically produce heavy shrub growth. Elimination of shrubs and understory species reduces transpirational losses and increases spring flow and available soil moisture. This retards understory succession and benefits fire-tolerant palms and palm reproduction. Fire consumes accumulated palm fronds and other heavy litter, exposing enriched, moist mineral soils necessary for the establishment of new palms. Juvenile palms grow vigorously on this open ground free from water competition and subsequent fire. The increase in surface water may also help to temporarily reduce the high alkalinity of the soils thus favoring palm germination and growth (Vogl and Mc Hargue 1966).

Fire, then, determines the vegetational composition of the understory by reducing or eliminating fire-intolerant species. It affects the physiognomy of the palms and the reproduction and maintenance of palms by producing and perpetuating moist pioneer conditions.

**SOUTHERN CALIFORNIA CYPRUS**

Four cypress species occur south of Point Conception and the Sierra Nevada Mountains. The most widespread of these rare species is Tecate cypress (*Cupressus forbesii*), followed by lesser amounts of Sargent cypress (*C. sargentii*), Piute cypress (*C. nevadensis*), and Cuyamaca cypress (*C. stephensonii*) (Armstrong 1966). Groves of these species are located in a winter wet climate with a prolonged summer drought accompanied by fires. Most groves are adjacent to and crowded by combustible chaparral that is adapted to fire. The groves of all species contain evidence of being burned. Even-aged stands date back to known fires (Fig. 2, 3). Groves in Orange and San Diego Counties have all burned at least once in the last 22 years. The average interval between fires in Tecate cypress stands was 25
years, ranging from 15 to 63 years. Trees tend to grow in dense thickets that are conducive to crown fires (Fig. 2, 3). All species were able to produce mature ovulate cones in about 14 years, which is less than the minimum fire interval (Armstrong 1966).

Cypress cones generally remain unopened until they are burned. Unburned cones detached from trees do not open as completely as burned cones, or fail to open, resulting in negligible seed shed. Heat generated by fire breaks the resinous seal between ovuliferous scales, allowing them to open. Seeds are shed from these opened cones for several months following burning.

Fire plays a delicately balanced role in the life history of southern California cypress. Frequent fires might destroy a cypress grove, since young trees could be eliminated before producing cones. Eastern hemlock (*Tsuga canadensis*) groves occurring on the edge of its range have been eliminated by severe fires and the isolated cypress groves could possibly meet the same fate (Wackerman 1925).
FIG. 3. A seventeen-year old thicket of Tecate cypress which originated after a November fire. Prodigious amounts of seed produced this dense growth which has resulted in excessive competition and stunting. These crowded stands are susceptible to crown fire.

However, fires more frequent than the time required to produce cones have not occurred in the stands studied, and individuals or islands of trees within a grove often escape fire (Fig. 4). The complete elimination of fire would be more likely to lead to their extinction since this would effectively prevent reproduction. As over-mature trees died, little or no seed would be released. If small amounts of seed were shed, the chances of establishment would be almost nil because of the small amounts, dense competition, unbroken canopies, and heavy ground litter.

The fire release of cypress seed is naturally tuned to optimum conditions. The majority of cypress fires occur in the fall of the year (Armstrong 1966). Strong winds and low humidities commonly accompany or follow these fires (Kinucan 1965). This insures maximum cone opening, jactitation of seeds from the suspended opened cones, and widespread dispersal (Fig. 2). Seeds reach mineral sites complete with pioneer conditions and minimum competition. Suc-
Successful seedlings require full sunlight and mineral substrates (Fig. 3). Winter rains usually terminate the fire season, providing adequate moisture at the most crucial time, since the thin-coated cypress seeds readily lose their viability due to desiccation.

It has been demonstrated experimentally that heat can be used to increase mutation rates or growth abnormalities. Komarek (1965) reported that multiples of the normal chromosome number and gene mutations might be induced by the heat of fires occurring at the critical time of meiosis. Microsporogenesis in Tecate cypress, as opposed to most conifers, occurs in late summer and early fall at the time when it is most subject to fire. Heat intensities produced in cypress fires vary, and strobili on the same tree or different trees may be completely destroyed, exposed only to high temperatures, or remain completely unaffected. Within this range of variability, the right conditions for heat-induced mutations could occur (Komarek, 1965).
FIRE ADAPTATIONS OF SOME SOUTHERN CALIFORNIA PLANTS

marek 1965). Grove sizes have been noted to fluctuate from fire to fire. An example of this is the Greenhorn Mountain grove of Piute cypress. In 1961, fire reduced the grove from three mature trees to a single tree. The burned trees responded to the fire by producing approximately 40 seedlings. A recurring surface fire could reduce the grove to a single tree. It is conceivable that the sole survivor of a fire could be a cypress that had been genetically altered by fire. This individual would become a founder tree that could be responsible for repopulating a grove with altered stock. Cuyamaca cypress may have become separated from Tecate cypress as a result of fire-induced change (Wolf and Wagener 1948, Armstrong 1966, Little 1966). Fire may have served as a mutagenic agent in other species in which meiosis coincides with their fire season. Perhaps fire should also be considered as a factor contributing to the high degree of endemism in California's flora. Most of California has been subjected to fire and fire could have helped contribute to species diversity, particularly in those genera in which flowering occurs during the dry season.

BIG-CONE DOUGLAS FIR

Big-cone Douglas fir (*Pseudotsuga macrocarpa*) is a southern California conifer commonly associated with chaparral. It is most widespread on north-facing slopes between 3,000 and 5,000 ft. elevation. Because of its distribution, big-cone Douglas fir is subject to fire, as are the surrounding plant associations.

An outstanding adaptation of this species is its ability to resprout after it has been burned. Big-cone Douglas fir is apparently one of the few western conifers possessing this trait. Burned trees produce epicormic shoots in the axils of branches or branch stubs on trunks and larger stems (Fig. 5). These trunk meristems remain dormant until a tree’s apical meristems are injured. Basal, stool, or root sprouts were not observed. Resprouting trunk meristems produced by burning only occur in trees. Seedlings and saplings (under 4 inches dbh) are generally killed by fire (Fig. 6). Apparently the thin bark of saplings offers little fire protection to the cambium and latent meristems. Trees, however, contain thicker bark composed of heavy layers of cork separated by thinner wood-like plates. Trees over 40
FIG. 5. This big-cone Douglas fir had all of its foliage removed by a crown fire but has responded by producing epicormic shoots along the trunk and larger branches.

inches dbh, for example, possessed bark 6-8 inches thick (Bolton and Vogl 1968). This thicker bark insulates the trunk meristems and cambium from the heat of crown fires, just as the thick bark of many tree species protects the cambium against damage from surface fires (Davis 1959).

Not all trees respond to burning by resprouting. Some trees, including occasional large specimens, are killed or appear to have been fire killed. Dead, non-sprouting trees are sometimes found immediately adjacent to living ones of the same size that have resprouted (Fig. 7). This differential response to fire is difficult to explain. Possibly the non-sprouting trees were decadent prior to burning, or burning conditions were locally severe because of immediate variations in fuels, associated vegetation, or topography. The dead trees could have been weakened sufficiently by fire to be subsequently killed by insects or fungi, or could have lost the ability to resprout by having resprouted after a previous fire or fires. The ability to
The ability to produce trunk resprouts is related to tree size in big-cone Douglas fir. The sapling on the left is dead since it failed to resprout, whereas the young tree on the right has resprouted after being burned.

Resprouting trees in the Santa Ana Mountains of southern California ranged from 5 to 45 inches dbh and from 25 to 300 years old, but no clear-cut correlation was found between tree age or size and resproutability. The only definite relationship established was that saplings, 4 inches dbh or smaller, were consistently killed by fire (Bolton and Vogl 1968).

Big-cone Douglas fir reproduction on burned areas is vigorous and dense. Seedlings in unburned stands are suppressed by shade. Burned sites contained up to 3,500 seedlings per acre in the Santa Ana Mountains. One burned site contained hardy, 12 to 15-year old stock that averaged 4 ft. in height, while trees of the same age in unburned areas were only one-half to 1 ft. tall and had no definite leaders. Fire establishes the same optimum conditions for big-cone Douglas fir as it does for Douglas fir (Isaac 1943) by preparing the seedbed, reducing the existing understory, and opening the canopy.

Although big-cone Douglas fir is fire adapted, it is not as well
adjusted to the total semi-arid environment of southern California as is chaparral. Chaparral is dominant on lower mountain slopes rather than big-cone Douglas fir, possibly because chaparral is better adapted to the continual interruption by drought and severe fires. Big-cone reproduction is not as successful under these xeric conditions and cannot compete with chaparral species (Bolton and Vogl 1968). Reproduction can invade decadent chaparral only during wet years and in the absence of fire. These invasions are most often terminated with fire unless the conifers have been able to reach tree size and attain some degree of fire resistance during the fire-free period. Impenetrable chaparral on gentle slopes appears to be resistant to big-cone encroachment even during wet years (Wilson and Vogl 1965).

Like many conifers, big-cone reproduction does well on open sites. In the rugged topography of southern California mountains,
openings are created by fire and erosion. Since young trees are susceptible to fire, big-cone stands often become limited to openings with a low fuel content. Steep slopes devoid of competitive chaparral provide almost fire-proof sites for big-cone Douglas fir establishment. Continuous chaparral cover is absent from these steep slopes since the angle of repose promotes continual geological disintegration and soil movement. On more level sites, established big-cone stands tend to eliminate understory vegetation as trees mature and canopies close. This inhibits sun penetration, increases moisture conditions, and reduces the fire frequency and intensity. Thus big-cone Douglas fir maintains itself by occupying relatively fire-free sites or by creating conditions which reduce the fire problem.

Fire has played a major role through time to help produce a quasi-equilibrium between chaparral and big-cone Douglas fir. Both vegetation types are adapted to fire, but have become separated into different habitats by responding differently to fire frequency and intensity. The interfaces along the semi-stable sites of these two types serve as unceasing battlefronts that fluctuate as environmental factors of drought, precipitation, and fire assert themselves.

**JEFFREY PINE**

Jeffrey pine (*Pinus jeffreyi*) is endemic to California, Baja California, and small adjacent areas in Oregon and Nevada (Fowells 1965). It is closely related to the more widespread ponderosa pine (*P. ponderosa*) and both species are commonly classified as western yellow pine. In southern California, Jeffrey pine generally occurs between 6,000 and 9,500 ft. elevation, whereas ponderosa pine is usually found between 5,000 and 7,500 ft. (Haller 1962). In Baja California, Jeffrey pine is most common from 6,000 to 8,000 ft., but does occur down to 3,000 ft. where it possibly replaces ponderosa pine which is absent (Wiggins 1940).

Extensive observations of Jeffrey pine in southern California indicate that lightning is an important part of its environment (Jepson 1921, Vogl and Miller 1968). The pine-covered slopes of Mt. Pinos, California, for example, receive as many as 600 lightning strikes during the summer months, with single storms often producing well
over 100 strikes. Some bolts do not strike the vegetation. Others hit pines and cause damage but only rarely kill trees (Fig. 8). Pines struck by lightning seldom die from the shock unless badly shattered (Hopping 1925). Sometimes struck trees are ignited but are immediately extinguished by rain. Other times trees continue to burn, particularly those previously injured by lightning, fire, wind, or fungi. Fires may spread immediately to the surrounding vegetation, or remain as “sleepers” for a time. These “sleepers” are often more effective in starting fires in the surrounding forest than are the initial lightning strikes. Lightning is often accompanied by rain or
Fig. 9. This even-aged group of Jeffrey pines probably originated after one of the many local spot fires that have occurred on Mt. Pinos. These small fires recreated pioneer conditions for the re-establishment of the pines.

Adverse burning conditions, whereas "sleepers" can smolder until the surrounding fuels are dry. Drying conditions are usually accompanied by winds, and winds accelerate the enclosed burning and topple fire-weakened trees. The falling trees shatter the glowing shell of the trunks in all directions. These fire-brands burst into flame as they are exposed to air, and increase the chances of fire reaching additional fuels. However, these "sleeper" fires generally do not spread far because of the lack of continuous understory in southern California (Fig. 8). Scant growth of shrubs, grasses, and forbs is
characteristic of southern California Jeffrey pine forest (Jepson 1921, Whittaker and Niering 1965, Vogl and Miller 1968). This tends to discourage widespread surface fires, and makes the spread of crown fires almost impossible. This is perhaps reflected in the 1966 fire records for the San Bernardino National Forest, where 97% of the fires were under 15 acres in size (Anonymous 1967b). Lightning on Mt. Pinos produced small fires averaging under four acres in size (Fig. 9). These fires burn individual trees, the immediate duff and understory, or crown and burn a close group of trees (Fig. 10). Thirty-two percent of the Jeffrey pines between 7,000 and 8,800 ft. had lightning damage in the form of conspicuous spiraled trunk splits (Fig. 8) (Vogl and Miller 1968). This percentage was considered conservative since trees with damaged tops were excluded because wind and lightning damage could not be readily separated. Older scars healed with age were undoubtedly missed. In the vicinity of Dawson Saddle in the San Gabriel Mountains, 33% of the Jeffrey pines sampled had evident lightning damage. An average of 24% of the fires in this range are caused by lightning each year (U. S. Forest Service 1964). This high incidence of lightning, which is usually accompanied by little rain, is common in southern California’s pineland. The greatest amount of lightning occurs during late summer or autumn which coincides with the dry season. I. L. Wiggins (personal communication, 1966) observed lightning and its effects in remote Jeffrey pine forests in Baja California. He related an account in which Mexican sheep herders above the Meling Ranch warned him not to camp under a grove of large Jeffrey pines because they were “lightning trees.” To humor the Mexicans he followed their advice only to later witness lightning striking the very trees he intended to camp under.

Jeffrey pine may differ from ponderosa pine because of its continuous high exposure to lightning as a result of its higher elevational location. The possible differential treatment and subsequent response of Jeffrey pine to long-term hammering by lightning might warrant investigation of lightning as an evolutionary and ecological force contributing to the separation of the two species. The distribution of Jeffrey pine, which is still inadequately explained, may coincide with high-country areas receiving a high incidence of lightning.
Despite repeated lightning, few pines are killed each year. Old trees on exposed crests and ridges contain evidence of repeated strikes. Jeffrey pines are able to absorb considerable amounts of lightning without suffering fatalities (Fig. 10). Only 2.5% of the trees sampled on Mt. Pinos were dead. An unusual feature of Jeffrey pine is that its resins or turpentines are not composed of terpenes as they are in most pines, but instead are composed of normal heptane, one of the paraffin hydrocarbons with a small admixture of fragrant straight-chain aldehydes (Schorger 1919, Mirov 1929, 1938, Fowells 1965). Lightning-damaged trees are susceptible to attack by bark beetles (Hopping 1925), and are often ultimately killed by the insects. About 80% of mature ponderosa pine struck by lightning were attacked and killed by the western pine beetle (Johnson 1966). The presence of resin aldehydes may produce a resistance of Jeffrey pine to some species of bark beetles (Fowells 1965). These aldehydes
might be altered by the heat, electrical charge, and ionization of a lightning bolt, which might further enhance the suspected protective nature of these gasoline-like resins. Studies of lightning and the chemical composition of Jeffrey pine are needed before definite interrelationships can be established.

One of the characters used to separate Jeffrey and ponderosa pine is the bark. Fissures in Jeffrey pine bark are usually deep and close together, whereas those in ponderosa pine are shallower and wider apart. As a result, Jeffrey pine bark generally consists of a series of narrow ridges and ponderosa pine is composed of large flat plates. The bark of both species is composed of laminated scales shaped like pieces of a jigsaw puzzle (Haller 1962). These bark characters may function as fire and lightning adaptations. One species may be more resistant to shattering by lightning because of its bark structure. In addition, the ease with which these species shed their laminated bark scales when struck by lightning or ignited by fire may make one species better fire adapted. Fire-fighters relate that fires climbing the trunks of these pines are sometimes extinguished when ignited scales are shed from the heated trunks.

Mature Jeffrey pines survive lightning-caused fires because of their thick bark and moderately high, open tree crowns (Fig. 8) (Jepson 1921). Most old pines carry deep “cat-faced” basal wounds (Fig. 10). Fifty trees with a 21 inch average dbh had a 2.1 inch average bark thickness on Mt Pinos. Jepson (1921) found Jeffrey pine to possess bark 2 to 5 inches thick. Pines grow in small even-aged groups over less than one-quarter to one acre and date back to local spot fires (Vogl and Miller 1968).

Although lightning fires were small, they had pronounced effects on Jeffrey pine forests because of their high frequencies. Jepson (1921) stated that yellow pine forests showed “...marked reactions to millennial fire conditions...” Since the understory of these forests in southern California is discontinuous or lacking, the high incidence of lightning would produce similar overall vegetational effects as caused by widespread surface fires in continuous understoreys such as those found in Rocky Mountain forests. Fires in Jeffrey pines consume litter and create pioneer conditions. In addition, fires accelerate decomposition which is normally slow in these high semi-arid
mountains. Surface fires reduce the existing tree reproduction and any other understory, enabling the overstory to obtain more of the limited moisture. Lightning acts as a predator as it most often strikes old trees and eliminates over-mature, insect or disease-infested individuals (Keen 1929, 1960). All trees with lightning evidence on Mt. Pinos were over 8 inches dbh. Each burned tree opens the canopy releasing younger pines. Spot fires prepare the seedbed for pine reproduction. The total effect of lightning is to continually check succession so that Jeffrey pine replaces itself, since it is the best adapted species to re-colonize the fire-altered community. Jeffrey pine forest has existed for centuries under continual bombardment from lightning and a subsequent patchwork of small fires (Jepson 1921). Frequent lightning, then, serves to cull the forest of over-mature or infested trees, reduce tree and understory competition, and create soil conditions for reproduction. The pine forest withstands lightning without showing detrimental effects. In fact, the life history of virgin Jeffrey pines is considered to be inseparably linked to lightning.

**KNOBCONE PINE**

A study of knobcone pine (*Pinus attenuata*) in the Santa Ana Mountains of southern California is currently being completed. This species is restricted to a few isolated places in southern California, and the Pleasants Peak location in the Santa Ana Mountains is the southern-most stand in the United States. The trees occur within a one-mile radius of the peak and are restricted edaphically. The geological type limiting the distribution of the pine is composed of intrusive rocks of volcanic origin. These ferromagnesian-rich hornblende diorites are a serpentine or a hydrothermal alteration of serpentine. Much of the substrate is in the form of silica carbonate rock cut by veinlets of iron oxide. The surrounding chaparral vegetation occurs on soils derived from hornblende andesites classified as Santiago Peak Volcanics.

The specialized knobcone pine soils derived from the serpentine vary from young chalky white soils of a friable cinder texture to older finely decomposed yellow clays. Soluble salts of calcium, mag-
nesium, and sodium are deficient, containing only one-half the amount found in adjacent chaparral. Soluble nitrate-nitrogen and phosphate-phosphorus were limited to about one-third the amount found in the surrounding soils. The average pH of the pine soils was 4.9 and of the chaparral soils was 6.3. Water retaining capacity and saturation percentage of mineral knobcone soils were twice as high as those of chaparral soils, indicating that the altered serpentine can hold twice as much moisture as neighboring soils. Chemical and physical differences between pine and chaparral soils became less marked on serpentine sites in which the pines have grown undisturbed for 60 or more years. Although knobcone pine requires pioneer conditions for its establishment, it does not appear to have special properties enabling it to thrive on these poor soils. Instead, the serpentine soils, with their low mineral content and possible toxic effects, restrict the normal dense chaparral growth and reduce chaparral competition with the pines. Knobcone pine, like many other pines, is restricted to these specialized soils because of its tolerance for poor soil conditions, but more importantly because it cannot compete with the more aggressive chaparral.

Knobcone pine stands are open and usually located on steep slopes which expose the light-colored substrate. An average of 49% of each pine stand was without vegetational cover, while only 13% of each chaparral stand was devoid of cover. The serpentine sites supported a single strata of dwarf chlorotic chaparral 1 to 2 ft. in height. This discontinuous shrub layer was mixed with taller, but stunted pines. Sixty-year old trees were often only 10 to 14 ft. tall and less than 2 inches dbh. In contrast, the non-serpentine produced a dense growth of various chaparral shrubs which produced a continuous mantle 6 to 8 ft. tall. In older pine stands, differences in plant cover and vigor were minimized by the accumulations of litter and soils which neutralize the deficient or toxic nature of the serpentine.

Several areas of Pleasants Peak have been burned in recent years. Pines within a given watershed or on a given slope were even-aged and dated back to past fires. No reproduction was found in unburned stands. Fifty-five to 65-year old stands contained dying or dead trees. The oldest dead tree was 76 years, a tree killed in a recent fire. The oldest living tree was 74 years old. Burned stands were heavily
stocked with knobcone reproduction. The species requires pioneer conditions of full sun and mineral soils for its germination, establishment, and development.

Knobcone pine belongs to a group of California pines classed as close-coned pines (Munz 1963). The serotinous cones of this Santa Ana Mountain variety (Newcomb 1962) remain unopened and attached to the tree for life. Cones continue to remain closed even after a tree has died and fallen. High temperatures generated by fire

Fig. 11. Cones produced each year by knobcone pines remain closed on the trees until large numbers have accumulated. The heat of a fire as it burns through the trees melts the resinous seals on the ovuliferous scales which gradually open to shed large amounts of seeds.
are required to break the varnish-like resinous seal, permitting the cone's scales to open. Young trees produce cones after ten to twelve years, perhaps occasionally even earlier. Sixty-year old trees averaged 176 cones per tree (Fig. 11). Trees produce cones in groups of fours, or sometimes fives, all firmly attached on dowl-like branches around a stem in a tight whorl (Fig. 12). The heavy cones protect the seeds from fire damage and the tightly arched ovuliferous scales open slowly for several days after burning. The large accumulation of cones insures a generous seed supply with burning. The firmly
attached cones are not burned off and remain fixed to the trunks to shed seeds in the wind (Fig. 11). Fire is essential for the completion of the pine’s life cycle by releasing seed that would otherwise be indefinitely imprisoned in the cones. Cones of over-mature or dead trees must be opened by fire to perpetuate the groves before the trees succumb and add the unopened cones to the decomposing litter.

Fires in the Pleasants Peak stands create pioneer conditions by removing the organic matter, surface soil, and vegetational cover. Heavy rains following fire accelerate erosion on steep southern Cali-
fornia mountain slopes (Krammes 1960). These rains scour the denuded slopes, causing soil erosion and exposing fresh unaltered serpentine (Fig. 13). This erosion assures the knobcone pine of a site for its re-establishment, maintenance, and continued survival. This isolated locale of specialized substrate enables the pine to withstand engulfment by the surrounding sea of chaparral.

**SUMMARY**

1. Lightning is considered an important source of fire in southern California at lower as well as higher elevations.
2. Fire has influenced all the major vegetation types in southern California, including desert. Desert woodland, desert grassland, and desert scrub carried fire before the arrival of Europeans and their livestock. Joshua trees and other members of the agave family exhibit fire adaptations.
3. Fire determines the vegetational composition of the understory of California fan palm oases by reducing or eliminating fire-intolerant species. Fire affects the physiognomy of the palms. The burning of palm oases benefits the reproduction and maintenance of palms by creating and perpetuating moist pioneer conditions.
4. Fire plays a delicately balanced role in the life history of southern California cypress as it opens cones and prepares the seedbed. Fires are ensued by optimum conditions for dispersal and germination. Speculation is given concerning fire as a mutagenic agent in cypress. Fire may be a possible factor contributing to the high degree of endemism in California's flora.
5. Big-cone Douglas fir possesses the ability to resprout after it has been burned. Fire establishes the same optimum conditions for it as it does for Douglas fir. Big-cone Douglas fir maintains itself by occupying sites with a lower fire frequency than the surrounding chaparral.
6. The high elevational distribution of Jeffrey pine is postulated as coinciding with areas of high lightning incidence. The chemical composition of Jeffrey pine resins may provide protection of lightning-struck trees from insect attack and subsequent fatalities. Bark characters may function as fire and lightning adaptations. Frequent lightning serves to cull the forest, reduce tree and understory competition, and create soil conditions for reproduction. In this way, Jeffrey pine forests are perpetuated.
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7. Fire is essential for the completion of the life cycle of Santa Ana Mountain knobcone pines, since it is necessary to release seeds from the serotinous cones that otherwise remain sealed indefinitely. Fire creates conditions of full sun and mineral soils which are necessary for the germination, establishment, and growth of the pines. Fire also plays a special role in these edaphically restricted stands by exposing the steep friable slopes to accelerated erosion. This erosion removes the accumulated effects of plant succession and soil genesis, thereby renewing the site and insuring the continued survival of the pines in the Santa Ana Mountains.

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