Proceedings: 8th Tall Timbers Fire Ecology Conference 1968

Fire Ecology in Southeastern Australian Sclerophyll Forests

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INFREQUENT, periodic, forest fires (bushfires) are an integral part of the natural physical environment of Australian sclerophyll forests, and they have evolved a degree of fire tolerance in response to this (Brough *et al.*, 1924; Petrie, 1925; Jarrett & Petrie, 1929; Ellison, 1952; Jacobs, 1951, 1955; Gardner, 1955; and Harris, 1956). Although fires have occurred naturally during the evolution of the Australian sclerophyll forests they have become much more frequent since European settlement (Costin, 1954; Costin *et al.*, 1959; Rodger, 1961). Some of the changes resulting from this increased frequency will be noted in this paper which will discuss the fire ecology of sclerophyll forests in Victoria and South Australia, in the southeast of the world's driest continent.

DISTRIBUTION OF AUSTRALIAN SCLEROPHYLL FORESTS

These forests are associated characteristically with skeletal and leached podzolic soils (Wood, 1939) and are found in a 100-mile-wide band along the eastern littoral in New South Wales, south-eastern Victoria, and in extreme southwestern West Australia

(Herbert, 1929; Wood and Williams, 1960; Cochrane, 1967). They occur discontinuously in southwestern Victoria and in Tasmania, in scattered locations in Queensland, and in a narrow tongue in the Mount Lofty Ranges in South Australia (Cochrane, 1963b). Generally they are confined to areas with over 25 inches annual average precipitation with cool winters and warm to hot summers. Some 'dry' sclerophyll forests, such as the inland box-ironbark communities, occur in regions with annual rainfall from 16 to 25 inches (Cochrane *et al.*, 1968). Summer temperatures are often high (90–100°F), relative humidities very low, and strong, hot, dry, westerly and northerly winds blowing from the arid interior are common (Leeper, 1960; Cochrane *et al.*, 1962). Some sclerophyll forest associations experience periods of acute water stress (Pook, Costin, and Moore, 1966) though both the length and the frequency of drought conditions varies widely from place to place and from time to time.

STRUCTURE OF AUSTRALIAN SCLEROPHYLL FORESTS

All Australian sclerophyll forests are dominated by short, medium, or tall Eucalyptus trees with long boles and flattish, interlacing, or nearly continuous crowns. Leaves are evergreen, leathery and simple in shape but widely varied in size. An understorey of sclerophyllous, microphyllous shrubs is common.

Although there are broad similarities in structural and other features within the Australian sclerophyll forest formation (equals Schimper's [1903] evergreen hardwood forest) there are important differences, firstly, between the 'tall' or 'wet' and the 'dry' sclerophyll forest subformations, and secondly between associations within the formation. Broadly, 'wet' indicates that such communities are often three-tired with mesic elements in the understorey and in the low, broadleaf tree layer. The tall tree dominants are sclerophyllous. Such communities occur where rainfall is over 50 inches or on deep moist soils in sheltered areas with over 35 inches rainfall and no long period of moisture stress. They are characterized by very tall, straight, cleanboled *Eucalyptus* dominants (up to 250 ft. and higher) such as mountain ash (*E. regnans*), manna gum (*E. viminalis*), alpine ash (*E. delegatensis* syn. *E. gigantea*), mountain grey gum (*E. gonio-*

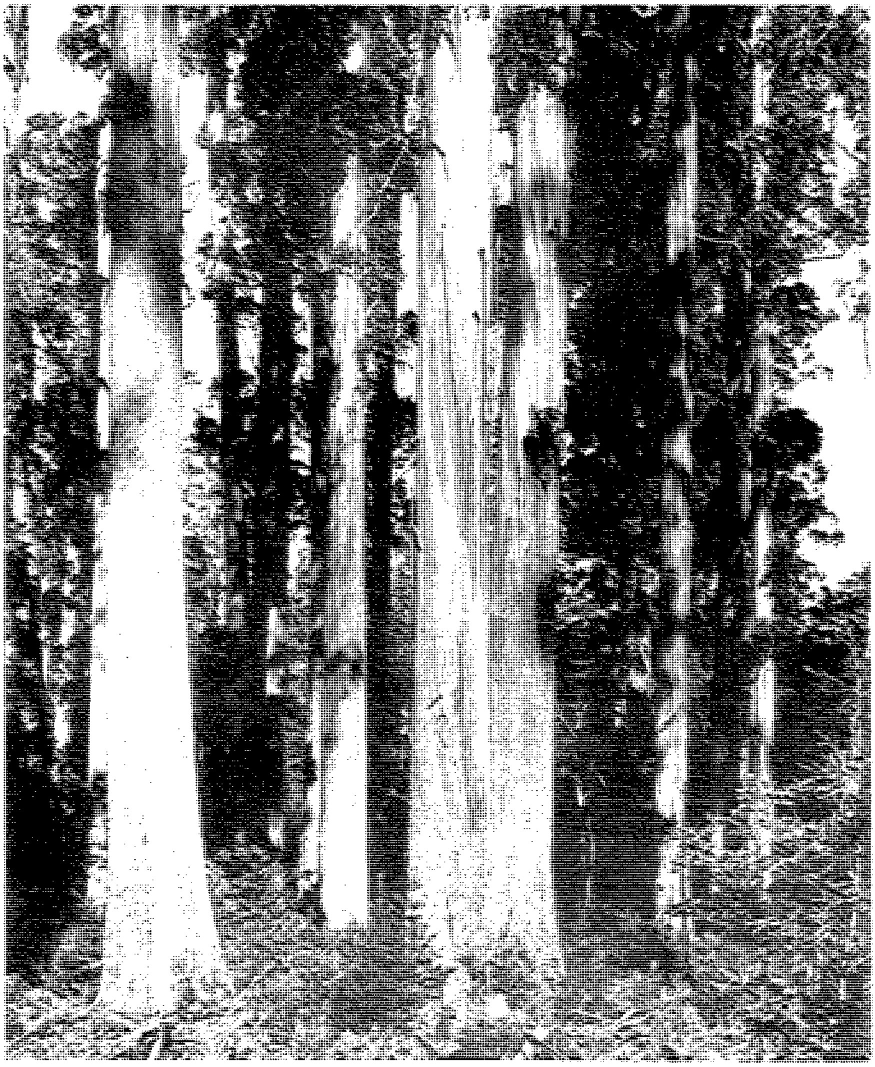

Fig. 1. Wet sclerophyll forest of tall mountain ash, *Eucalyptus regnans*. Note the long ribbons of thin dead bark which carry fire very readily, and the discontinuous secondary tree layer. Bushfires cause great damage in these forests. (Photo: Forests Commission, Victoria.)

calyx), *E. fastigata*, *E. dalrympleana*, Victorian blue gum (*E. globulus*), and Sydney blue gum (*E. saligna*). Many of these provide valuable hardwood and have been extensively milled (Fig. 1).

'Dry' sclerophyll forests are lower and essentially two-tiered. The tree canopy is frequently between 35 to 80 feet high, although it can be very much higher, and the understorey is normally of low or dwarf, harsh, xeromorphic shrubs with sclerophyllous microphylls (Fig. 2). A grass or herb layer may be present. These characteristics are discussed more fully elsewhere (Cochrane, 1963a, 1963b and 1967).

On very xeric sites within 'dry' sclerophyll forests the shrub layer may be largely or entirely replaced by fibrous grasses even though there is no appreciable decrease in tree density. On stony ridges with shallow skeletal soils and facing north or west to the warm afternoon sun, red stringybark (*E. macrorrhyncha*) associations in the Dandenong Range, Victoria, have an understorey of wallaby grass, *Danthonia semiannularis*, *D. pallidus*, and kangaroo grass, *Themeda australis*, with only a few *Acacia stricta* shrubs present (Fig. 3).

Yacca, *Xanthorhorrea australis*, is a prominent member of the understorey of brown stringybark, *E. baxteri*, associations on leached lateritic ironstone soils in South Australia.

In addition sclerophyll forest plant associations clearly reflect differences in aspect (Pook and Moore, 1966), variations in exposure to insolation and dessicating winds, soil depth, texture and moisture (Specht & Perry, 1948), and canopy influences such as shade, as well as the broader changes associated with orographic rainfall gradients (Cochrane, 1968).

Apart from these broad differences, variations between associations within both 'wet' and 'dry' sclerophyll forests in important behaviour differences both during the passage of a bushfire (wildfire) and in the post-fire seral stages (Lawrence, 1939; Gardner, 1955; Cremer, 1960, 1962a, 1962b). Differences in the height of trees, depth of crown, density of canopy, crown-bole ratio, bark texture, thickness and burning characteristics, quantities and kinds of volatile oils in leaves, ground fuel characteristics, i.e. height, density, and nature of understorey and of ground litter are all important in the fire ecology of these forests (Newman, 1955; Gilbert, 1959; Hodgson, 1967).

FIRE FACTORS

For fire to occur fuel, oxygen, and heat are required. These are all usually abundantly available in summer and early autumn when

Fig. 2. Dry sclerophyll forest of messmate, *Eucalyptus obliqua*. The relatively flat canopy allows much light through enabling a low, dense, continuous, sclerophyll understorey of harsh, xerophytic shrubs to develop.

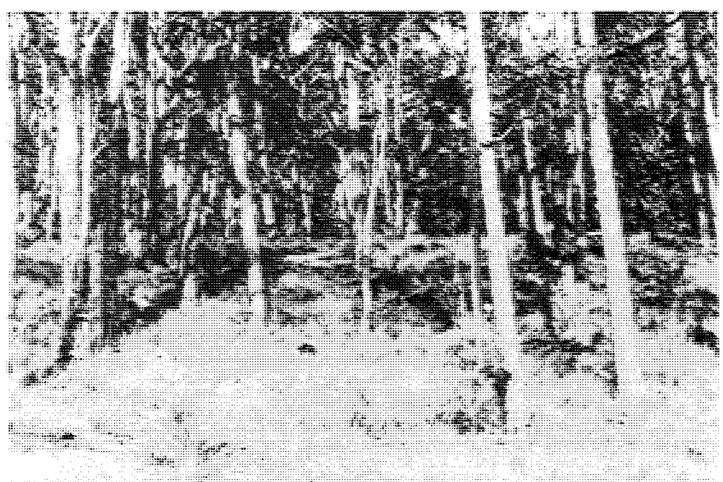

Fig. 3. Dry sclerophyll forest of red stringybark, *Eucalyptus macrorrhyncha*. Thick, fibrous (ropey) bark, a few scattered sclerophyllous shrubs and a continuous low understorey of xeric grasses characterizes this association.

most bushfires occur in southeastern Australia. Vegetation, the fuel, varies—as already noted—particularly in density and structure. Both the quantity and the quality of ground fuel are important. Differences in combustibility, density, and dryness affect the rate of passage and the heat intensity of bushfires (Beadle, 1940; Byram, 1959; Hatch, 1959; Cochrane *et al.*, 1962; McArthur, 1962; Cochrane, 1963b). Much of the understorey vegetation is dry and readily flammable. This results both from its xeromorphic habit and from the climatic and seasonal factors influencing growth in these areas. Climatic variability is high with frequent though irregular alternation of dry and wet years. Also winters are generally cool and moist but summers are dry and hot with periods of century temperatures. These conditions favour lush growth and subsequent drying out so that much dry matter accumulates as potential ground fuel for bushfires.

The prevailing flatness or lack of major relief over much of the continent of Australia (Hills, 1960), and the marked contrasts in atmospheric pressures both within and beyond the continent (Leeper, 1960) means that moderate to strong winds are commonplace. There is no lack of oxygen for bushfires. Once a bushfire is underway strong winds, regardless of temperature, speed its progress (Luke, 1961).

Strong, hot, searing, summer winds and low atmospheric humidity are common. Many of these winds blow from the hot, arid interior supplying both heat and oxygen so once ignition occurs, conditions are ideal for fire to spread rapidly. In Melbourne, Victoria, 75 to 80 percent of strong winds over 30 mph are from the north or northwest, and 90 percent are from northerly or westerly quarters. Whittingham (1964) showed that annual maximum winds gusts at Melbourne, in 1962, follow a similar pattern. These wind directions are important for bushfires in South Australia also (Cochrane *et al.*, 1962; Cochrane, 1963b).

The January 13, 1939, Victorian bushfire, which claimed 71 lives and caused $28,000,000 damage, was associated with above 100°F temperatures (Melbourne 118°F), low humidity, and strong northerly winds. Sclerophyll forest areas in southeastern and southwestern Australia share with Southern California the unenviable reputation of being the most bushfire hazardous areas in the world. It is sobering to recall that fires throughout Australia, in 1965 destroyed 2,620,000 acres of forest and caused damage estimated at an average of $1,-160,000 a week throughout the entire year. Fires cost Australia an average $1,200,000 a week throughout 1966. Unfortunately, the pattern has been repeated for 1967 and bushfires are already figuring prominently in 1968.

Topography exerts important local effects upon the passage of bushfires. In deeply dissected hill country, fires speed upslope regardless of the general wind direction. At the heads of valleys convective updraughts are channelled into the tree canopies, causing explosive burning of the highly volatile canopy leaves of stringybark eucalypts, spotting, and crown fires. These fires burn very rapidly down-wind starting many new understorey fires. Fires burning rapidly upslope are often less hot than slower-burning ones on gentler slopes. Underground parts of plants are often but little affected where fire passage has been rapid (Beadle, 1940). Numerous geophytes are among the first plants to appear after firing along with shoots from root clumps, such as rushes, sedges, and wallaby grass, fronds from bracken fern (*Pteridium esculentum*) rhizomes, and vigorous coppice shoots from hardy root stocks, such as *Astroloma*, *Leptospermum* and some *Acacia* spp.

Both prefire and postfire climatic and seasonal conditions modify burn and regeneration patterns. Very dry conditions before a bushfire usually result in a hotter burn with many species killed and much seed burned. Few underground parts of plants escape destruction from the intense heat. Conversely, little damage results to underground parts of plants if soils are moist. Desiccation and dehiscence of many woody fruits by the heat of the fire results in great numbers of seedlings appearing after moderate intensity bushfires. Dry conditions after firing result in very much slower regeneration than if moist conditions occur. Regrowth 18 months after a fire in 1958 in the Adelaide Hills, South Australia, in the drought conditions of 1959 was much less than that observed on some favourable sites in the Dandenong Range, Victoria, only 4 months after the very severe 1962 bushfires. However, moist conditions followed the latter fire, favouring plant regrowth. If heavy rains wash away the ash from the bushfire and strip away much of the unprotected topsoil by sheetwash and gullying, vegetation re-establishment is a slow process.

EFFECTS OF BUSHFIRES

Bushfires in sclerophyll forests in Australia generally result in (1) the complete destruction of the understorey which is burned to the ground, and (2) the defoliation but not death of the *Eucalyptus* tree layer (Fig. 5) with the notable exception of mountain ash (*E. regnans*), which is easily killed by bushfires (Fig. 4) (Cunningham, 1960; Cochrane, 1969).

This is in marked contrast to exotic tree species, such as *Pinus, Malus, Prunus* and so on which are killed by firing. Many apple

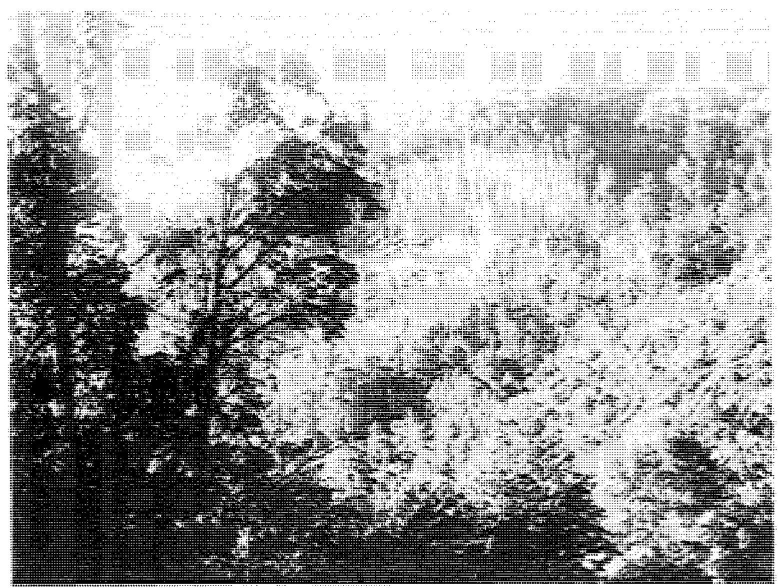

FIG. 4. The January, 1962, Dandenong Range bushfire burned over this entire area killing the fire-sensitive mountain ash, *Eucalyptus regnans*, but merely defoliating all the other eucalypts. Two and a half years later, the dead mountain ash trunks remain starkly bare and bleached in contrast to the other vigourously regenerating tree species.

FIG. 5. The January 14–17, 1962, bushfire was very severe near this area. Many trees near the foreground were completely burned. In the background, fire intensity was less, but all trunks and many leaves were burned.

orchards were killed from the radiant heat from nearby dry sclerophyll forests burned during the 1957 Adelaide Hills bushfire. The *Eucalyptus* trees, which were in the midst of the conflagration, were merely defoliated. Similarly *Pinus radiata* trees and plantations in the Mount Lofty Ranges were completely destroyed by the same fire. Seven hundred acres of *Pinus* plantation were also completely killed by the 1962 Mount Dandenong bushfire. Adjacent burned areas of *E. obliqua* and *E. radiata* were defoliated by the same fire but were not killed.

Many small local variations to these general results of the effects of bushfires on sclerophyll forests can be observed but they are relatively minor differences caused by: (1) particular vagaries of

FIG. 6. Within one week after the passage of the January bushfire long ribbons or 'wicks' of peeling bark hang down from these mountain grey gum, *Eucalyptus goniocalyx*, trees. The smooth bark, unlike the stringybark, does not burn unless already shed but is killed by fire and rapidly splits and peels after fire.

the fire path, (2) changes in wind direction during the fire, (3) slope differences, (4) soil moisture, (5) age of vegetation, (6) density of plant cover, (7) upwind or downwind burning, and (8) species composition, especially relative fire tolerance. Combinations of any of the above factors can result in selective burning both between and within different associations.

Five broad classes of bushfires can be recognized, each of which has different effects. These are: (1) *Very severe bushfires* which burn all vegetation, kill and completely raze all understorey species, kill many of the tree layer species and completely burn many trunks and roots (Fig. 5). (2) *Severe bushfires* which burn and completely raze the understorey layer and kill some trees (Figs. 4 and 6). No scorched grass tussocks, no branches, no shrub stems and no unburned organic litter remain on the bare blackened ground. Some tree canopy leaves are burned from spotting and crown fires, but radiant heat from the understorey fire defoliates most of the canopy trees. The intensity of these ground fuel fires can be appreciated when one considers that tree canopies, especially in wet sclerophyll forest, are often 150–250 ft. and more above the fire. The intensity of radiant heat can be expressed as $r = 1/d^2$, where r = radiant heat and d = distance from radiating source. That is, the intensity of radiant heat varies inversely to the square of the distance from the source. (3) *Moderate bushfires* where much undergrowth is completely burned and the remainder killed by light burning, but left standing above ground level. Trees are rarely burned although bark is commonly charred on stringybark and box eucalypts. Defoliation of the tree canopy results from radiant heat from the ground fuel fire. (4) *Light bushfires* where foliage, twigs, grass and ground litter are burned but many of the stems and main branches of larger shrubs are only scorched and blackened. Trees are defoliated by radiant heat. Upper levels of tall trees, if present, escape fire damage and remain green. (5) *Very light bushfires* where the understorey is burned without markedly affecting the tree canopy. Scorched, blackened stems of shrubs are present. This type of fire is not very common. Also included in this category are shrub and tree or only shrub layers that have been defoliated from radiant heat from adjacent burned areas. This situation is usually of localized rather than widespread occurrence.

Classes 2 and 3, severe and moderate bushfires, are the most frequent. Most bushfires in southeastern Australia, then, burn all the ground fuel (i.e. the understorey layers and accumulated litter of bark, leaves and branches), leaving the ground blackened and bare between the tree trunks, and defoliate but do not kill the dominant trees. The gross structural characteristics of the tree layer remain (Figs. 5, 6, and 10). There are important tree canopy differences between regeneration and climax stages, which exert significant influences upon understorey seral stages, but the gross structure of the tree layer remains. This is in direct contrast with the understorey which begins completely from bare ground.

REGENERATION AFTER BUSHFIRES IN SCLEROPHYLL FORESTS

We have earlier observed that both prefire and postfire climatic and weather conditions may exert important influences upon subsequent vegetation regeneration after bushfires. Marked variations in regeneration of both the tree and understorey vegetation, appear to be closely related to weather conditions. Studies of regeneration following bushfires, in 1957, 1958, 1959, 1960, 1961, 1962, 1964 and 1965 in South Australia and Victoria, demonstrated that the immediate postfire weather conditions were probably the most critical for regeneration. Weber and Olson (1967), analysing change in sycamore and yellow poplar seedings under conditions of water stress—a quite different but related problem—came to a similar conclusion: "*that the level of water stress at the time of leaf formation was more critical than at later stages.*" They measured leaf reflectance of the near and mid-infrared spectral bands (infrared reflectance is largely a function of internal leaf structure) and found that water stress during leaf formation exerted greater influence on foliar reflectance than did the level of water stress at the time of later reflectance measurements.

It is not intended to analyse these climate-regeneration patterns here—the broad trends have been outlined earlier—but rather to discuss specific differences between associations that all experienced uniform postfire conditions. In mid-January, 1962, the Dandenong Range bushfire, fed by a great accumulation of highly combustible ground fuel, favoured by low humidities, and fanned by strong, hot winds ravaged wide areas causing extensive damage and considerable loss of life. Despite the combined efforts of organized fire-fighting groups, enormous numbers of volunteer fire fighters, police and armed services this wildfire raged completely out of control until put out by rain 3 days later. Shortly afterwards steady soaking rains occurred that thoroughly moistened the ground. Throughout the autumn, rains were sufficient to keep the soils moist. The postfire period of the 1962 Dandenong Range bushfire was an optimum one for vegetation regeneration. The subsequent differences in regeneration patterns are the result of genetic makeup, and local and microhabitat variation, not of seasonal climatic differences.

The Dandenong Range, near Melbourne, is a steeply dissected dacite area which rises abruptly, to over 2000 ft., on its western flank from the coastal plain. Rainfall varies from 30 to over 50 inches, is largely from the south, and falls chiefly in winter. Strong, desiccating winds from the north and northwest are common. Dry scleraphyll forest, containing several distinct *Eucalyptus* associations and alliances, is found on the western and northern slopes. Wet sclerophyll forest is found on the wettest, sheltered positions on the eastern and southern slopes. It is also restricted chiefly to areas above 1000 ft. elevation where orographic effects result in rainfall of 45 inches or more. Dry sclerophyll forest reappears at lower elevations on southern and eastern slopes (Cochrane, 1968, 1969).

Within the dry sclerophyll forest messmate or stringybark (*E. obliqua*) is found at the highest elevations where rainfall is over 40 inches; red stringybark (*E. macrorrhyncha*) occurs on the driest, most xeric sites. It is prominent on thin skeletal soils of lower slopes and ridges exposed to the west and north (Fig. 3). Brown stringybark (*E. baxteri*) occupies similar sites but is less widespread, and is usually at intermediate elevations between messmate and red stringybark. Broad-leaf box (*E. elaeophora*) is prominent on the lower slopes where rainfall is under 38 inches. It exists as an association and also frequently forms an alliance with red stringybark. Narrow-leaf peppermint (*E. radiata*) has a broad ecological valence and ranges throughout the dry sclerophyll forest. It forms an important alliance with messmate above 1500 ft. elevation. Mountain grey gum (*E. goniocalyx*) is present at high elevations with.messmate and at lower elevations in moist sheltered valleys or on moist southern slopes.

Mountain grey gum also occurs as wet sclerophyll forest on the eastern and southern slopes. Mountain ash (*E. regnans*), which grows as a single species, usually even-aged stand, is the most prominent wet sclerophyll forest association (Fig. 1). It alone of the sclerophyll forest trees is killed by fire (Fig. 4) yet fire, occasional catastrophic fire, seems necessary for its regeneration. Pertinent observations may be found in Ashton (1956), Gilbert (1959), Cremer (1962b) and Cochrane (1969). *E. delegatensis* is also fire sensitive and damaged by bushfires but seedling survival is best in fire ash beds (Grose, 1957).

Narrow tongues of swamp gum (*E. ovata*) occur in poorly drained, narrow valleys. Manna gum (*E. viminalis*) may flank the former as a narrow band on moist but drained soils. Candlebark gum (*E. rubida*), either alone or as an alliance with manna gum, has a very localized distribution in sheltered locations on deep alluvial silts.

All these species exhibit distinctive regeneration. They differ in time of starting after the bushfire, in form, in vigour, in rate, in density, and in stage of transition towards mature canopy. These variations reflect inherent genetic characteristics, themselves largely an expression of environment in general and of habitat in particular. The regeneration patterns of the trees in turn exert important influences upon the habitat of the understorey species.

TIME AND FORM OF LEAF REGENERATION

Although some individual trees may be killed from very severe firing, most sclerophyll forest eucalypts regenerate after a bushfire from dormant epicormic shoots. In some species these are present along the entire trunk, in some along the trunk and main branches, and in others only along upper branches. Yet others have few on the bole or main trunk and more on upper branches. In the adult trees the bole is relatively long and essentially leafless: the leaf canopy is relatively flat and shorter in depth than the bole. The death of the canopy leaves from fire effects allows vigorous sprouting of the dormant buds. This results in marked differences in tree leaf cover form between regeneration and climax canopy stages. Progress towards climax canopy form varies with different species. It is generally longer than 3 years after a bushfire before the upper canopy is dominant and the many trunk laterals suppressed.

Sprouting from trunks of long-leaf box was observed first just 2 weeks after the bushfire. These forced their way through cracks in the charred rugose bark (Fig. 5). Three weeks after the fire clumps of shoots spaced at approximate 8–10 inch intervals in a spiral up the trunks were present on many long-leaf box trunks. Mountain grey gum regeneration began one month after the bushfire. Leaf shoots

FIG. 7. Two-month regeneration of long-leaf box. Comparison of Figs. 5 and 7 demonstrate the vigour of leaf growth. Note the absence of regenerating foliage on the trunks of the red stringybarks behind.

were largely associated with the long vertical cracks that appeared in the outer bark prior to its later peeling. Narrow-leaf peppermint regeneration began at about the same time with a similar spiral arrangement to that observed for long-leaf box.

Within 2 months all these 3 species had many short laterals clothing the trunks so that they appeared as erect green plumes. Length of laterals ranged from 8–12 inches in narrow-leaf peppermint, 18 inches in long-leaf box (Fig. 7) and 18–24 inches and occasionally 36 inches in mountain grey gum. Much of the fire-blackened trunks of long-leaf box and of narrow-leaf peppermint were masked by dense juvenile foliage—blue-green on the former and light green on the latter—3 months after the fire (Fig. 8). The thick, smooth, brownish to grey bark of the mountain grey gum trunks was largely masked also by a dense growth of short lateral shoots supporting blue-green juvenile foliage (Fig. 9).

Isolated cases of sparse sprouting from messmate occurred after 4 months but generally regeneration of this species—other than on poles and saplings—was not prominent until 6 months after firing. Even then it was largely absent from trunks, much less vigorous than for the other 3 species, and largely confined to main upper

FIG. 8. Three-month regeneration of long-leaf box (left) and narrow-leaf peppermint (right). Leaf shape and colour differ markedly but the dense 'pluming' of juvenile foliage clothing the trunks of both species is broadly similar.

branches (Fig. 9). Brown stringybark regeneration was even slower and more sparse. Red stringybark was slowest and least of all. Very few sprouts had appeared even 7 months after the bushfire. The fire-charred, thick, fibrous bark on the trunks of these stringybarks remained conspicuous when the trunks of the other species were hidden beneath a dense plume of leaves.

Wherever the bushfire had burned the understorey of mountain ash communities the trees were killed. No regeneration occurred (Fig. 4). Direct heat on the trunks kills the cambium which is close to the surface of the thin bark. In localities where both the understorey and the mountain ash trees were defoliated from radiant heat but not burned, some mountain ash survived. Slow regeneration from epicormic shoots occurred on the highest branches. This did not begin until 7 months after the bushfire. Unfortunately, these trees that survived the fire were later felled for timber so their regeneration pattern could not be compared with the other species.

Candlebark, gum, and manna gum followed a similar form to mountain grey gum except their regeneration was much slower. Foliage from laterals was less dense and more widely spaced. Both these species had very restricted distribution.

FIG. 9. Seven-month regeneration of messmate is confined to the upper limbs. The conspicuous, blackened, leafless trunks contrast with the densely leafy mountain grey gum trunks further back.

HETEROPHYLLY

Apart from these gross differences in the form of regenerating leaf canopy all these eucalypts display striking heterophylly. Juvenile, intermediate and adult leaves differ markedly in shape, size, arrangement, attachment, and colour. Juvenile foliage is so distinct and so readily observed following a bushfire that this constitutes a very exact means of identification of sclerophyll forest *Eucalyptus* species. Hybrid swarms of *E. elaeophora* x *E. goniocalyx* were readily differentiated from adjacent *E. elaeophora* and *E. goniocalyx* in one locality on the southern slopes on the basis of juvenile leaves. This area had been observed prior to the bushfire when identification had proved very difficult. Differentiation between *E. obliqua* and *E. baxteria* was much more easily achieved from inspection of juvenile foliage and regeneration pattern following the bushfire than was possible beforehand from inspection of the closely similar adult leaves of the unburned trees. Leaves, buds, flowers and fruit high

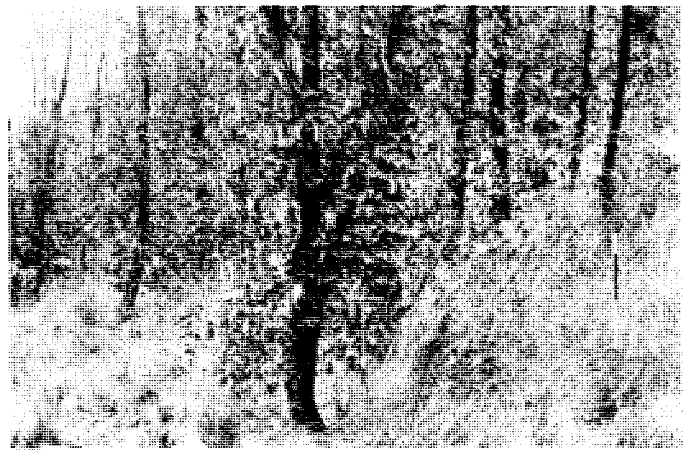

FIG. 10. Two and a half year's regeneration of the same long-leaf box shown at earlier stages in Figs 5 and 7. Note the grass socies in the open areas, but the presence of a variety of shrubs in the 'insolation lee' of the trees. Long, sickle-like, adult leaves are replacing the smaller, rounded, juvenile leaves and intermediate leaves.

up in the canopy are much more difficult to observe than juvenile foliage at ground and at eye level.

Although intermediate leaves frequently appear quite early, they become common about 1 year after the bushfire. Adult leaves become conspicuous about 2½ years after fires (Fig. 10). Even 3½ to 4 years after a bushfire it is not uncommon to still see all 3 leaf forms—juvenile, intermediate and adult—present on individual plants.

RATE AND DENSITY OF TREE CANOPY

The early vigour of leaf regeneration demonstrated by *E. elaeophora*, *E. goniocalyx*, and *E. radiata* also characterized the later growth of these species. After 1 year the trunks of most of these species were thickly clothed with leafy lateral branches 2 ft. to 3 ft. long. The mass of leaves, in most cases, masked the trunks. This pattern continued through the next 2 years. Lateral branches became longer and leaf density increased. Where trees were closely spaced, the dense plumes of foliage reaching from ground level to the apex of the tree, formed a tall 'hedge' or 'shelter-belt effect.'

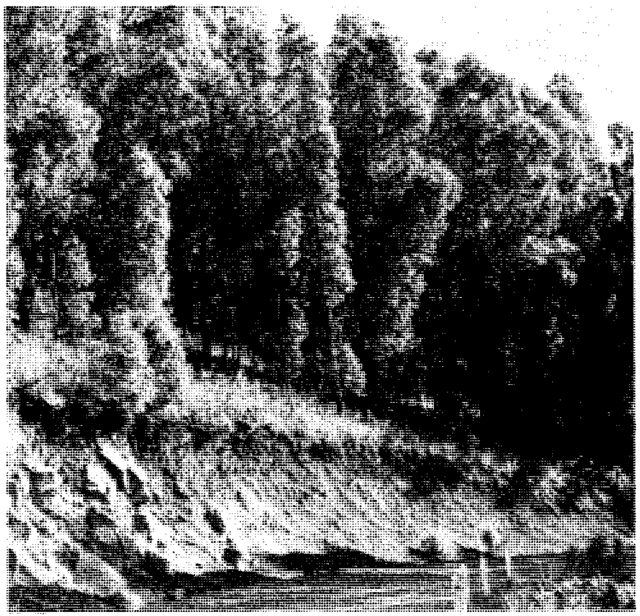

FIG. 11. Two and a half year's regeneration of dry sclerophyll forest trees. The 'insolation wall' produced by the plumed growth of short, leafy, lateral branches on narrow-leaf peppermint contrasts with the lack of trunk laterals and the openess of the messmate canopy at the left. These differences exert an important influence upon the regenerating understorey.

Stringybark leaf regeneration remained slower than for the three former species. After 3 years it was much less dense and was found chiefly on the upper branches. Adult stringybarks remained starkly gaunt with conspicuous fire-blackened trunks and a sparse upper canopy. Except on youthful *E. obliqua,* lateral branches along the trunk were short, infrequent and widely spaced. In contrast, saplings and poles generally had numerous leafy laterals. These were longest near ground level and became shorter towards the top of the tree. Although leaf canopy was less dense than on the broad-leaf box, narrow-leaf peppermint and mountain grey gum trees these messmate saplings and poles formed relatively compact, pyramidal, leafy forms. Canopy conditions of the stringybarks, although by no means the same as in the unburned forest were, nevertheless, broadly similar in their influence upon conditions of the environment. This was not so with the other eucalypts.

UNDERSTOREY REGENERATION

The canopy effects of the trees with dense plumed laterals differs very markedly from that resulting from the open canopy and branchless lower trunks of the climax unburned forest. As most of the trees in the Dandenong Range occur on steep slopes, the dense barriers that their vertical, "plumed" foliage presented to wind and to incident solar radiation (Fig. 11) resulted in the presence of distinct microclimates in their lee. Habitat conditions differed markedly between lee and exposed sites within non-stringybark communities. Differences were also prominent between lee sites and sites under or near stringybark trees. In many places the tree regeneration pattern resulted in a veritable wall of vegetation shading areas from the low-angle, incident radiation so characteristic of the winter months. Cochrane (1966) has shown that

> . . . the duration, intensity and quality of insolation received on the ground is governed by the species, the form, the density, and the spacing of the forest dominants . . . Insolation variations engendered by tree regeneration patterns are reflected in measurements of temperature, relative humidity, windiness and net radiation. Abrupt transitions as well as gradual change in understorey regeneration patterns appear to be strongly influenced by tree canopy differences.

The relatively uniform understorey beneath unburned areas of the sclerophyll forest (Figs. 2 and 3) was not repeated on the burned areas. A complex mosaic of seral socies matched the patterns of shade and light resulting from variations in tree foliage regeneration (Figs. 10 and 12). The rate and pattern of understorey regeneration showed a close parallel to insolation. Similarly, the variations in numbers and types of species, in structural and floristic composition, in range of plants and in total biomass of the ground communities demonstrated that the canopy influence is a primary regulating factor in their regeneration (Figs. 10–14).

Within 1 year after the fire a dense ground cover of mesic species

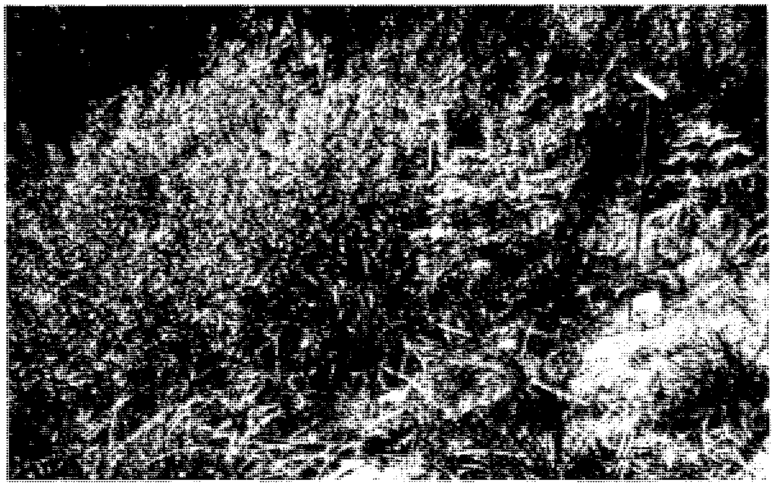

FIG. 12. Two and a half year's regrowth of understorey. Tree canopy influences cause these sharp differences in sclerophyll scrub regeneration patterns. Stringybarks, with their sparse, very open, upper branch, leaf regeneration and lack of stem laterals, allow maximum insolation to reach the areas behind and beneath them.

was found in areas in the lee of *E. goniocalyx* (Fig. 13). Sparse growth of small hardy grass was beginning under *E. macrorrhyncha* and *E. baxteri.* Ground cover was 100 percent under the mountain grey gum and less than 10 percent on the red and brown stringybark sites. Regrowth was also slow under many areas of *E. obliqua* where the lack of foliage resulted in high total values and high intensity insolation reaching the ground. Outgoing longwave radiation was also higher from the bare open stringybark sites.

Different seral socies occurred under *E. radiata* on northern slopes than on southern slopes. This reflected both local and microclimatic factors, but the influence of dense or sparse spacing of trees was clearly reflected in the density and composition of the seral understorey socies.

Striking variations in the understorey occurred on slopes uniformly exposed to desiccating northerly winds and maximum exposure to insolation. Within a few feet of one another seral socies of the grass, *Danthonia semiannularis* (Fig. 11), of the hardy xeric shrub, *Acacia*

FIG. 13. Two and a half year's regeneration. A *Pultenaea scabra* socies closely adjacent to the sites shown in Figs. 10, 11 and 12. With slight variations in insolation and with less wind exposure this socies replaces *Acacia myrtifolia*. With increased shade, wire grass, *Terarrhena juncea*, and other more mesic shrubs like *Goodia lotifolia* and *Indigofera australis*, replace the *Pultenaea* communities.

stricta, of the more mesic shrub, *A. leprosa*, of bracken fern, *Pteridium esculentum*, and grasses, *D. semiannularis* and *Themeda australis*, of the shrub, *A. myrtifolia* (Fig. 12), and of the relatively more mesic shrub, *Pultenaea scabra* (Fig. 13). Each of these are very distinct and are closely associated with shade patterns of regenerating trees.

Many other examples could be cited of the close control of understorey regeneration by the form, rate, and density of foliage on regenerating eucalypt trees (Fig. 13). Throughout the burned areas this micromosaic pattern is present. No large areas of uniform vegetation are found for the first 3 years. This contrasts with the relative uniformity, over wide areas, of climax unburned scrub layers (Figs. 2 and 3).

About 4 years after firing, the lower laterals on the trees gradually die. As apical dominance becomes more prominent the trees

FIG. 14. Two and a half year's regeneration. Dense, exotic scrub of Canary Island broom, *Cytisus canariensis*, (at right) actively invading indigenous scrub of *Acacia*, *Daviesia* and *Pultenaea* species. This whole area was burned bare. Broom has grown 2.5 to 3 metres tall: the native scrub is 0.5 metres high. Total biomass of the broom is nine times greater per unit area than the native scrub. This aggressive intruder, which is highly fire adapted and produces great quantities of inflammable ground fuel, becomes established if frequent firing—albeit intentional or otherwise—is practised.

slowly regain their prefire form. Much more insolation reaches the understorey than formerly and a gradual change occurs (Fig. 13). Many of the more mesic species disappear and a distinct dwarf layer develops in many dry sclerophyll forest communities. The change is relatively slow as the understorey itself affords shelter. If left undisturbed changes occur until the relatively more uniform climax communities develop. This rarely occurs before 7 to 10 years. It is commonly much longer.

FIRE ECOLOGY PROBLEMS

The fire ecology of these sclerophyll forests present problems that are not present in fire management in other forests. Accumulation of ground fuel is very uneven in the early years following bushfires. Ground fuel cannot be burned too soon after fire as further damage to the lateral shoots could kill the trees. In areas milled for timber, such a fire, even if it did not kill the tree, would further retard tree growth. Although the trees regenerate after bushfires the firing slows their rate of growth severely. Annual incremental timber growth is negligible for up to 8 years after a bushfire.

Another problem is that of variation in density and dryness of vegetation. In 3 years, some areas with early plumose foliage shelter, grow great quantities of mesic ground vegetation which is difficult to burn until it is replaced by later seral vegetation. When sufficiently dry to burn the accumulation of fuel is dangerous.

Too frequent firing, by prescribed burning, to control accumulation of ground fuel can result in modification of the environment that favours the invasion of these forests by exotic plants that are better adapted to frequent firing than are the indigenous shrub species (Fig. 14). In the Mount Lofty Range, in South Australia, exotic scrubs produced a greater volume of more flammable fuel quicker than the native scrub following modification of the forest environment (Cochrane, 1963b).

Hodgson (1967) has drawn attention to problems of fuel character and fuel accumulation in sclerophyll forests in Australia. Fire control is not easy. Fire management is very difficult in the sclerophyll forests of southeastern Australia because most of the *Eucalyptus* forests occur on difficult, broken country. Distribution of communities is very varied. Stands of economically valuable forests occur within areas of less valuable species and access is frequently difficult. Varied and distinctive bushfire regeneration of trees and the resultant influences upon seral scrub regeneration create additional complexities. More fundamental research in the fire ecology of sclerophyll forest species is needed so that bushfire damage can be countered by sound practices. Bushfires are an urgent and costly problem in Australia.

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