The Causes of Eucalypt Crown Dieback: A Review

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Contents

4	B TO THE B	OD	T	CALL A	T
	INTR				 V

2. DEFINITION OF TERMS

- 2.1 Diebacks
- 2.2 Cause

3. AGENTS REPORTED TO CAUSE DIEBACK

- 3.1 Abiotic agents
- 3.1.1 Drought
- 3.1.2 Cold
- 3.1.3 Fire and lightning
- 3.1.4 Flooding
- 3.1.5 Nutrient deficiencies, toxicities and pollutants

3.2 Biotic agents other than the fungi

- 3.2.1 Toxic exudates and decomposition products
- 3.2.2.. Insects
- 3.2.3 Nematodes
- 3.2.4 Other animals
- 3.2.5 Parasitic flowering plants
- 3.2.6 Mycoplasmas, viruses, bacteria and algae

3.3 Fungi

- 3.3.1 Foliar pathogens
- 3.3.2 Branch canker pathogens
- 3.3.3 Vascular wilt pathogens
- 3.3.4 Root-rotting pathogens

4. THE EUCALYPT CROWN DIEBACKS

- 4.1 General
- 4.2 Jarrah dieback
- 4.3 Dieback on the Brisbane and Otway Ranges, Victoria
- 4.4 Tasmanian east coast dieback
- 4.5 Tasmanian gully dieback
- 4.6 Tasmanian regrowth dieback
- 4.7 Tasmanian high altitude dieback
- 4.8 Eucalypt diebacks in New South Wales
- 4.9 Eucalypt diebacks in eastern Victoria

5. CONCLUSION

6. REFERENCES

1. INTRODUCTION

This review collates what is known of the causes of the ill-defined group of diseases called eucalypt dieback. Concern has arisen because the more damaging of them have drastic effects upon the structure and composition of important forest communities and greatly reduce yields of forest products.

Much effort has been made to determine their causes, motivated chiefly by a desire to predict their potential and because knowledge of cause is a prerequisite to development of sound control measures. With few exceptions our knowledge is inadequate for these purposes. We have no simple definition of what is meant by eucalypt dieback and no generally-agreed concept of what the term 'cause' should encompass. For the purposes of this review the author defines his concept of the terms of reference as follows.

2. DEFINITION OF TERMS

2.1 Diebacks

Australian usage of the term dieback is loose and not restricted to convention, viz. 'Progressive dying back from the tips of twigs, branches or tops' (Society of American Foresters 1950). This symptom in individual eucalypts is not necessarily an indication of disease. The primary leaf bud systems in *Eucalyptus* are naked and extend rapidly when conditions are favourable for growth. Such bud systems are vulnerable to defoliation, but epicormic shoots develop from secondary bud systems and may allow the crown to refoliate rapidly. In environments where defoliation by fire, drought, and insects is recurrent, some degree of dieback is a feature of forests which can be otherwise regarded as healthy. Dieback cannot be defined therefore as the replacement of primary leaf systems by a secondary crown.

The term dieback is generally used by Australian foresters to refer to diseases which result in spectacular damage and mortality. The disease syndrome may include sudden wilt and death of trees as well as the classic symptoms of progressive dieback. In some trees progressive dieback may proceed rapidly with only a single weak flush of secondary shoots before death. In others it may be protracted over many years, with alternating periods of partial recovery and further dieback. In such cases refoliation from secondary bud systems may lead to crown replacement by epicormic branching of the second and third order.

This review treats both the serious and the minor diseases because (i) the early symptoms of these serious diseases are often difficult to distinguish from those of a range of minor diebacks and (ii) in altered circumstances some diebacks of minor importance may assume more serious proportions.

2.2 Cause

The interdependence of function among the various organs of a tree in the exchange of nutrients, water and photosynthates needs no emphasis, however there are more subtle and complex interactions. It is now evident, though not fully understood, that the health and co-

ordinated development of the various organs of plants is determined by balances between auxins produced in the foliar meristems and cytokinins produced in the roots (Fox, 1969; Thimann, 1969). Further, there is increasing evidence that some factors which determine the resistance of foliage to infection by pathogens have their origins in root systems and that resistance to root rot may be influenced by principles located in the foliage.

Dieback in individual trees is a non-specific symptom of malfunction which may have its locus in any part of the tree. Defoliation, disruption of the translocation system, and root decay all affect a number of functions. Such disruption may be initiated by a great variety of biotic and abiotic agents; the activity of these causal agents and the effects they exert upon eucalypts are all influenced by the environment. Thus, all diebacks are the result of the interaction of multiple factors whether the damage is due to attack by a virulent pathogen on a single type of organ, or to the action of a complex succession of pathogens on several parts of a tree. A study of the cause of any dieback should take into account the nature and locus of primary malfunction, the principal causal agent or agents, and the circumstances in which the change from a healthy to a diseased condition has occurred. Often diagnosis of the locus of primary malfunction and of the causal agent is possible only on trees in the earliest stage of disease and before marked symptoms of dieback are evident.

The extent to which any of these agents cause serious damage varies greatly and appears to depend upon three major factors; firstly the extent to which there has been adaptive selection between the eucalypt in question and the particular pathogenic agency; secondly the extent to which natural balances have been disturbed; and thirdly the influence which environment exerts upon the hosts, the pathogens and their interactions, particularly that of environment upon the infected host.

There is no forest which is entirely free of disease. Most forests have a variable but generally low level of disease which is caused largely by fluctuations in the forest environment or by the action of native pathogens. These pathogens are part of a heterotrophic flora which is essential for the recycling of energy and nutrients via the processes of decay. Such forests have usually evolved, by adaptive selection with their pathogens, a balanced state of tolerance in which pathogen and host are able to reproduce. Climatic change or physical disturbance by cataclysmic agencies or man may change the environment and the balances so that serious disease develops. Some forests are inherently unstable, particularly those which are seral stages in successions to climax. In these cases severe dieback and mass death are natural processes in successional sequences, though in terms of man's preferences they may seem disastrous.

The most destructive diseases are those which are due to recent introductions of virulent pathogens among inherently susceptible hosts which have not been subjected previously to such selection pressure. Even so the effects of the introduction are conditioned by the environments, and there are many examples of coexistence of susceptible hosts and virulent pathogens in environments which limit the activity and effects of the pathogen. Serious disease develops only where the susceptible host is also vulnerable, i.e. in environments unusually favourable to the action and effects of the pathogen.

Examples of these situations, all of which occur among the eucalypt diebacks, are discussed below.

3. AGENTS REPORTED TO CAUSE DIEBACK

In the literature, diebacks have been attributed to a great variety of agents. The evidence to support a claim that a particular pathogen is responsible is often no more substantial than a claim of guilt by association. Rarely have Koch's postulates been satisfied. Some reports are based upon detailed study; others on little more than casual observation. In many cases it is not possible to check the validity of taxonomic diagnoses of the alleged pathogens. Because of the limitations of time it has not been possible to examine all the evidence and evaluate the various claims. The following section of this review is therefore more often a summary of the literature than a critical analysis of the various claims made therein.

3.1 Abiotic agents

3.1.1 Drought—Climatic stress including climatic change may influence the incidence of dieback and decline both directly and indirectly (Clark and Barter, 1958; Tryon and True, 1958; Hepting, 1963; Weaver, 1965; Leaphart and Stage, 1971). Among the atmospheric influences which cause eucalypt dieback, drought and frost have perhaps the most important direct effect. There has been a number of reports of dieback attributed to drought (Day, 1959; Pook, 1967; Pook, Costin and Moore, 1966; Cremer, 1966, 1969). Most eucalypts seem adapted to short periods of extreme heat and internal water deficits, but protracted water deficiency is damaging to all species. Internal water deficits may also be induced by low soil temperatures (Hopkins, 1964), but whether this contributes to dieback is unknown.

Low plant moisture levels affect resistance to infection. The efficiency of wound periderm formation in roots is impaired (Butin ,1955) and the resistance of bark to invasion by canker-forming fungal pathogens is lowered (Bier, 1964). Drought not only depletes carbohydrate reserves (Cremer, 1966) but also predisposes trees to attack by insects, particularly cerambycid borers (Hepburn, 1964; Cremer, 1966; Carne, 1973(b)), and by fungi (Peace, 1962). The chances of survival of trees infected by fungi which cause rot of feeder roots are much influenced by the timing and duration of seasonal drought (Newhook and Podger, 1972).

3.1.2 Cold—Severe cold has caused leader dieback and death on an extensive scale in some exotic plantings of eucalypts, particularly in temperate regions of the northern hemisphere (Martin, 1948; Magnani, 1957; Gentilli, 1961; Linnard, 1969; Anonymous, 1973).

Eucalypts are particularly susceptible to cold damage during periods of rapid shoot extension, and in the early stages of growth. Partially recovered mature trees exhibit gross symptoms similar to those of dieback due to other causes (see the illustrations in Martin, 1948; Magnani, 1957).

Cold hardiness is an important character governing the natural distribution of eucalypt species (Jacobs, 1955; Gentilli, 1961; Ellis, 1968). A number of studies of intraspecific variation have demonstrated that the degree of frost resistance of a particular population is almost always correlated with the climate in their native habitat (Pryor, 1956; Ashton, 1958; Boden, 1959; Sherry and Pryor, 1967; Karschon, 1966; Green, 1969; Pryor and Byrne, 1969; Eldridge, 1971; Layton and Parsons, 1972; Paton, 1972; Awe, 1973). Despite this, frost damage has occurred in native eucalypt forests particularly in regenerated areas (Bond, 1945; Redmond, 1953; Carr, 1954; Ashton, 1958; Tasmanian Forestry Commission, unpublished). Much of this damage has occurred where eucalypts have been regenerated on large areas of land cleared of natural forest (of the same species) and where changes in the patterns of cold air drainage have created frost flats. Because it may not always be practicable to use seed of local provenances or suitably resistant alternatives for the regeneration of large clear-cuts and plantations, it might be expected that the incidence of dieback due to frost will increase.

3.1.3 Fire and lightning—Fire is recognised as one of the most damaging agents in eucalypt forests. Severe fires in wet sclerophyll forests have drastically altered the structure and composition of forest stands in a number of places. Among the most notable examples is the elimination of tall forests of E. regnans and replacement by scrub and bracken on extensive tracts in Victoria as a result of a sequence of wildfires between 1851 and 1939 (Ashton, 1958). Similar effects have been described in Tasmania by Gilbert (1958) and by Jackson (1968). Even in fire-resistant communities severe fires may kill twigs and branches of many species so that the partially recovered crown of epicormic shoots have a stagheaded appearance which may be confused with dieback. Given freedom from further fire damage and disease, the epicormic shoots develop vigorously and form healthy branched crown units typical of healthy trees and quite distinct from those affected by dieback.

It is possible however that fire may contribute indirectly to dieback. Repeated fires in dry sclerophyll forests may severely damage crowns of the dominants without markedly reducing their numbers. Beneath these stands there often develops an excessive stocking of regrowth which competes with the dominants and further weakens them so that they dieback further. Fires may also lead to dieback by creating points of entry for wound pathogens and wood decaying fungi. Where heavy accumulations of fuel are burned and roots are damaged, crown deterioration may follow.

Lightning causes deaths in patches of eucalypt forest, but there are no accounts of these patches extending. In other species, trees which are not killed outright may suffer damage to their deep roots so that delayed mortality may give the appearance of disease spread (Peace, 1962).

3.1.4 Flooding-Though marked differences in the tolerance of eucalypts to waterlogging have been reported (Boden, 1962; Podger, 1967) there is little information on the mechanisms of damage or on its influence on the development of dieback. Three recent papers reflect the complexity of the subject. Burrows and Carr (1969) found that flooding of the root systems of sunflower affected the cytokinin content of xylem sap; these substances are known to be important factors in disease resistance. MacManmon and Crawford (1971) found that the root exudates of flood-tolerant plants shifted to a malic acid dominance over ethanol when flooded, whereas flood-intolerant plants produced a greater proportion of ethanol. Allen and Newhook (1973) have since shown that these shifts in root exudate balance have important effects upon the chemotaxis of zoospores of P. cinnamomi toward roots.

3.1.5 Nutrient deficiencies, toxicities and pollutants—Both deficiencies and excesses of certain nutrient elements have direct and indirect effects upon the health of plants. Some have been associated with eucalypt diebacks. With the exception of boron there is little detailed information on the subject (Snowdon, 1970).

Dieback of eucalypts in plantations has been attributed to boron deficiency in Africa (Savory, 1962; Steyn and Straker, 1969; Cooling and Jones, 1970) and in New Guinea (White, 1964). Applications of borax to soils have controlled the disease. In plants boron is relatively immobile, intimately involved in translocation of sugars, respiration, reproduction, and water relation of cells; deficiency causes disintegration of terminal meristems (Hacskaylo et al., 1969). The element is required continuously in the sapstream and a few hours of acute deficiency can result in meristem damage. Boron deficiency and drought are often associated (Elmer and Gosnell, 1963). Because boron is concentrated in the top few centimetres of soil and because grasses are efficient competitors for boron, dieback due to this deficiency is often associated with erosion and severe grass competition. In excess, the element causes symptoms of toxicity (Pratt et al., 1971) in some tree species including E. saligna (Gibson, 1964). An important indirect effect of added boron is improved resistance of root tissues to fungal infection. This has been demonstrated for Fusarium wilt of tomatoes (Edgington and Walker, 1958) and flax (Keane and Sackston, 1970), and for P. cinnamomi root rot of lupin (Jehne and Snowdon, unpublished).

There are few if any reports of calcium deficiency in field grown eucalypts, but bud dieback has been induced in seedlings grown in calcium-deficient media (Haag et al., 1967; Will, 1961; Kaul et al., 1966). Like boron, calcium is immobile in the plant, essential in the structure and functional integrity of cell membranes, and actively involved in plant growth and development. Deficiency leads to injury of shoot and root meristems

(Hacskaylo et al., 1969). Plants with inadequate calcium supply have increased susceptibility to root rotting pathogens (Edgington and Walker, 1958; Keane and Sackston, 1970; Bellany et al., 1971) and this effect is aggravated by poor soil-aeration. These and other complex effects which soil chemical factors exert upon the pathogenic activity of soil micro-organisms have been reviewed by Chapman (1965). Excessive levels of soil calcium may induce dieback in larch (Peace, 1962) and iron deficiency, chlorosis in E. camaldulensis seedlings (Thirgood, 1956; Karschon, 1968a; Neuman and Waisel, 1966). Iron deficiency and manganese toxicity are intimately related. Winterhalter (1963) reported that manganese toxicity in E. gummifera seedlings could be corrected by iron chelate application. He found also that eucalypt species varied in their tolerance of manganese. Andrew and David (1959) reported iron deficiency in E. dives. Although copper deficiency causes dieback of citrus (Stakman and Harrar, 1957) there is no record for Eucalyptus.

Pollutants produced by heavy industry and by petrochemical combustion can cause severe damage to trees (Forestry Commission, London, 1971; Greywacz and Wazny, 1973). The increasing importance of such damage to plants is reflected in the fact that in the eleven volumes of Annual Review of Phytopathology so far published there have been five reviews of the subject (Rich, 1964; Darley and Middleton, 1966; Heck, 1968; Treshow, 1971; Heagle, 1973). The only information on pollution damage to eucalypts encountered is a comment on eucalypt dieback observed near the Bell Bay alumina plant in Tasmania (Pratt, 1972) and a report from the Los Angeles Aboretum that 9 of 29 eucalypts examined were sensitive to photochemical pollution (Hanson, 1972). Though we need to know more about this subject for planning amenity plantings near sources of pollution, there is no evidence that pollution contributes significantly to the serious diebacks in our forests and plantations.

3.2 Biotic agents other than fungi

3.2.1 Toxic exudates and decomposition products—Plant substances released into the environment in small concentration by decomposition or excretion from plant organs may inhibit the growth of other vegetation including other plants of the same species (Patrick et al., 1964; Schroth and Hildebrand, 1964; Savory, 1966; De Bell, 1970). Some of these phytotoxins may increase the susceptibility of plants to pathogens (Patrick and Tousson, 1965). The best known examples of this type of disease include the specific replant diseases (Savory, 1966) and the decline of Sequoia in stands where litter has accumulated for long periods (Florence, 1965, 1967).

Leachates from eucalypt litter have been shown to differentially inhibit the development of eucalypt seedlings (Florence and Crocker, 1962). Allelopathic compounds which are produced in litter beneath *E. globulus* and in fog drip from its leaves have been shown to accumulate in soil and inhibit sensitive plants (del Moral and Muller, 1969).

In succession toward climax ecosystems, changes may occur in soil nitrogen metabolism from nitrate to ammonium dominance (Rice and Pancholy, 1972). This may affect the health of seral dominants. It has been shown that the form of nitrogen affects vigour, root characteristics and calcium uptake in *Eucalyptus* and that various species differ in their responses to the two sources of nitrogen (Moore and Keraitis, 1971).

Although such effects are known to affect susceptibility to root pathogens (Smiley and Cook, 1973) there is no direct evidence that such changes contribute to

eucalypt dieback.

3.2.2 Insects—The number of insect species which feed upon eucalypts is legion. Several have been studied in considerable detail (Carne, 1962, 1965, 1966, 1967; Carne et al., 1974; Campbell, 1960, 1962; White, 1973). Though most insects cause little conspicuous damage, a number cause severe reduction of growth and a few are the direct cause of severe dieback and mortality.

The more important pests have been listed in several reviews (Clark, 1938; F.A.O., 1958; Greaves, 1961; White, 1962; Waterhouse and Carne, 1964; New South Wales Forestry Commission, 1964; Hepburn, 1964; Zondag, 1964; Campbell, 1966). They include:

- (i) leaf-eaters such as ants of the genera Atta and Acromyrmex in Brazil, (F.A.O., 1958), the beetles Paropsis charybdis and Gonipterus scutellatus in New Zealand, the beetles Anoplognathus and Chrysophtharta spp. in Australia, the phasmatids, larvae of sawflies, and the gumleaf skeletonizer Uraba lugens;
- (ii) sap-suckers, such as the psyllids, and the scale insect *Eriococcus coriaceus*;
- (iii) borers such as cossid moth larvae and the cerambycid *Phoracantha semipunctata*.

The extent of damage done depends upon the part of the tree attacked, the degree of attack, its frequency, and its timing (Greaves, 1966; Kulman, 1971; Carne, 1973(b)). These in turn are dependent upon biological characteristics of the various pest species such as their feeding preferences and gregariousness. Insects which repeatedly defoliate young foliage and buds throughout the growing season deplete reserves and reduce the production of growth substances more seriously than those pests which consume mature foliage outside the main growing season. Carne et al. (1974) have observed that winter defoliation by sawfly larvae has less severe effects upon growth and tree health than does summer defoliation by adults of the Christmas beetles Anoplognathus spp. In turn Christmas beetle attack is less damaging than defoliation by Chrysophtharta spp. because defoliation of buds and young leaves by both larvae and adults of Chrysophtharta may be continuous from spring through summer and autumn.

The attack by many insects is primary but there are others which require predisposition of the tree host. Hepburn (1964) notes that the borers *Phoracantha semipunctata* and *P. recurva* are most troublesome on drought-stricken trees. This observation is confirmed by Carne (1973(a)) who reports (i) that frost predisposes some eucalypts to psyllid and *Eriococcus* infestations;

(ii) that grass competition may predispose trees to cossid larvae attack.

Damage by one insect species may predispose eucalypts to attack by another, for example, cossid attack is most severe on *E. grandis* already affected by psyllids and chrysomelids (Carne 1973(b)). It is well known that some insects, notably borers and sap-suckers transmit bacterial and fungal wilt pathogens, but there are few if any specific records for *Eucalyptus*.

Conspicuous insect damage to eucalypts is most common in open woodland formations, on planted trees or on trees at the forest margin. In such situations insects have caused severe dieback and widespread mortality. Carne (1973 (a) & (b)) is of the opinion that most of the dieback he has seen on a 1000 km transect in woodland on the southern tablelands and slopes during 16 twice-yearly surveys is due to insects, though environmental stress may also be involved.

In contrast, insect damage to closed forest communities is relatively minor (Campbell, 1966; Carne, 1973 (a) & (b)). There are however important problems of declining growth, dieback and mortality in which insects play a prominent role.

The most spectacular of these is due to phasmatid plagues which have flared periodically since at least 1881 (Macleay, 1881; Froggatt, 1905; Richards, 1953; Shepherd, 1957; Hadlington and Hoschke, 1959; Campbell, 1960, 1961; Newman and Endacott, 1962; Mazanec, 1966, 1967, 1968; Readshaw and Mazanec, 1969). A variety of eucalypt species and phasmatid genera are involved. Dieback and death is due to defoliation and depletion of starch reserves (Bamber and Humphries, 1965). Species which have low starch reserves tend to be most susceptible to dieback following defoliation. Another problem which has developed and extended rapidly is defoliation due to jarrah leaf miner (Newman and Clarke, 1926; Wallace, 1970; Mazanec, 1973) a pest which causes chronic growth loss, but so far little dieback or mortality. Leaf miner attack has been severe also on E. pilularis (Moore, 1963). At Ourimbah, New South Wales, psyllids and borers are involved in a third problem (Moore, 1959, 1962) which is discussed in detail in section 4.8.

Because the insect pests of Eucalyptus in Australia are almost all native it might seem reasonable to expect that stable balances should exist between the pests and their hosts and that the problems are due to environmental changes. There have been a number of explanations offered to account for the breakdown of these supposed stable systems. It has been suggested for example that phasmatid outbreaks are due to the exclusion of fire. Campbell (1961) presented evidence that periodic fire effects considerable control over plague buildup. From this it might be suggested that European man's intervention in altering the natural patterns of fire in forests is the cause of the plagues. However this need not be so, as Readshaw (1965) concluded that the outbreaks are a natural and recurrent phenomenon and not merely the result of intervention by man. He suggested that outbreaks are periodically released where parasites and predators are rendered ineffective. In cooler-than-average summers the activity of parasitic wasps is reduced. There is also a tendency for predatory birds to concentrate at outbreak areas so that on other areas, originally less heavily populated by phasmatids, unchecked buildup of population proceeds. It has been proposed that it is the mobility of parasites and predators which give rise to the apparent buildup, spread and decline of outbreaks, and not migration of the phasmatids. Carne (1973 (a) & (b)) has pointed to the possible influence which weather plays in the maintenance or breakdown of host-parasite balances and suggests that plague outbreaks occur where synchronous buildup of pest, predator and parasite populations is disrupted. Plagues of psyllids are also believed to be a natural phenomena in undisturbed woodlands and forests (White, 1969). Large populations of these insects develop on trees with high foliar nitrogen, a condition which may occur during periods of physiological stress following drought of periods of soil saturation which damage roots.

Outbreaks of gum-leaf skeletonizer on E. camaldulensis have been attributed by Campbell (1962) to man's intervention. The reduced frequency of flooding due to water storage schemes in the Murray Valley is said to have reduced the activity of a fungal parasite (Aspergillus sp.) which previously kept larvae of Uraba lugens

in check.

Carne (1973 (a) & (b)) and Campbell (1966) have both discussed factors which influence the development of severe insect damage in eucalypt woodlands. Carne (1973 (a) & (b)) has warned of the dangers from insect pests in monocultures of *Eucalyptus* and has advocated urgent research on methods of vegetative reproduction so that forestry can take greater advantage of natural resistance to insects such as that demonstrated by Pryor (1952).

3.2.3 Nematodes—Though plant-parasitic nematodes have been associated with forest tree disease (Ruehle, 1967, 1973; Riffle and Kuntz, 1966) there is little information concerning their effects upon Eucalyptus. Two Australian records (Colbran, 1966; Meagher, 1968) are taxonomic accounts. A root lesion nematode is reported to have damaged eucalypt plantings in Brazil (Lordello 1967). This neglected area warrants investigation as nematodes can be vectors of viruses. They also are known to aid penetration of parasitic fungi by breaking host barriers including ectotrophic mycorrhizae which otherwise prevent entry of pathogens such as P. cinnamomi (Ruehle 1973). In some cases nematodes and fungal root pathogens appear to exhibit synergistic effects. A worrisome possibility is that parasitic nematodes may enhance the pathogenicity of weak root rot parasites.

3.2.4 Other animals—Apart from their roles as vectors of other pathogens the larger animals (excluding man) are probably minor agents causing eucalypt dieback. In a quaint historical note Bennett (1885) attributed a spectacular dieback of *E. rostrata* and *E. melliodora* in Victoria to possums, noting that the evidence of their foetid urine and numerous scratches on trees indicated their complicity. Around that time possums seemed to

have received popular blame as Macleay (1881), in attributing death of forest near Sydney to phasmatids, specifically rejected the theory that possums were responsible.

Doubtless possums contribute to some branch dieback by defoliation and by creating wounds for entry of other pathogens. Presumably koalas can be placed in the same category where their natural enemies are absent. Possums are a considerable cause of dieback in mature trees and a menace in protection forests in New Zealand. In Tasmania they appear to feed principally on regeneration on the ground and along with wallabies may cause severe defoliation and death of young regeneration up to 2-3 years of age over extensive areas (Cremer 1969). Other animals mentioned in the literature as agents contributing to dieback are cockatoos in search of cossid larvae (Carne, 1973(b)) and cattle girdling *E. macrorhyncha* by rubbing the bark (Jacobs, 1955; Carne 1973(a)).

3.2.5 Parasitic flowering plants—Parasitic phanerogams occur in fourteen dicotyledonous families (Kuijt, 1969), but in Australia only the Loranthaceae, Convolvulaceae, Santalaceae, Lauraceae and Rafflesiaceae are known to include parasites of native plants.

The numerous family Loranthaceae (Blakely, 1922-28; Barlow, 1966), which is widespread in all states except Tasmania, is by far the most important. It contains several genera of mistletoe which cause severe branch dieback of eucalypts over extensive areas of partly-cleared woodland (Turner, 1894; May, 1941; Greenham and Brown, 1957; Hartigan, 1971). Mistletoe infection produces a variety of adverse effects upon the host (Phillips, 1907; Wood, 1924) and multiple infections may cause serious loss of growth, dieback and death. Aspects of their biology including histology and host specificity have been treated by several authors (Brown, 1959 (a) & (b); Hamilton and Barlow, 1963; Wellman, 1964; Brown, 1968; Burbidge and Gray, 1970; Hartigan, 1971).

It has been said that levels of mistletoe attack seem to have increased in eucalypt woodlands since European settlement (Anderson, 1941; May, 1941; Coleman, 1949; Greenham and Brown, 1957; Hartigan, 1971). In the absence of widespread periodic survey, this generalisation is difficult to verify, but most early observers were definite in their opinion that a large increase had occurred following partial clearing and pasture improvement. The ways in which these changes might have removed previous constraints upon epidemic multiplication of mistletoes has been the subject of much speculation (Anderson, 1941; May, 1941; Coleman, 1949; Greenham and Brown, 1957; Hartigan, 1971). Control measures are discussed by several authors (Brown, 1959(b); Harding, 1959; Brown and Greenham, 1965; Hartigan, 1971).

Other genera of parasitic phanerogams are of much less importance. *Pilostyles* (Rafflesiaceae) is restricted to native legumes and *Nuytsia* and *Atkinsonia* (Herbert, 1919; Menzies and McKee, 1959) are not known to parasitise eucalypts. The true dodders of the genus *Cuscuta* (Convolvulaceae) are twining climbers

occasionally parasitic on eucalypts (Penfold and Willis, 1961).

The dodder laurels, genus Cassytha (Lauraceae), sometimes parasitise, entwine and strangle the leading shoots of eucalypts, particularly on rough-barked species (Hart, 1925; Pederick and Zimmer, 1961). The forest dodder laurel Cassytha melantha has been a serious nuisance on eucalypt regeneration on 3200 ha of drier sclerophyll forest in Victoria. It spread to eucalypts after multiplying rapidly on dense understorey vegetation which developed after the eucalypt overstorey was opened up by timber felling (Pederick and Zimmer, 1961). Though Cassytha occasionally causes deaths of leading shoots its principal effects are a smothering of foliage and breakage. Like many other parasitic phanerogams the dodders have potential as vectors of viral and bacterial pathogens (Wellman, 1964; Dijkstra and Lee, 1972), though there appear to be no records of such transfer in Eucalyptus.

Several genera of the Santalaceae notably Santalum (Herbert, 1925) and Exocarpos (Coleman, 1934) parasitise the roots of a range of native plants including Eucalyptus. Detail of their biology has been reported by Benson (1910) and by Herbert (1925). Usually, little damage is caused except where the host plants are young (Herbert, 1925), but Jehne (1972) reported the association of Exocarpos cupressiformis with deaths of Eucalyptus following drought. On stony sites patches of trees up to one hectare in extent were killed.

None of these parasites attains major economic significance in closed forests. It seems unlikely that any of them are capable of bringing about substantial changes in the structure or species composition on large areas of any of Australia's eucalypt forests.

3.2.6 Mycoplasmas, viruses, rickettias, flaggellates, bacteria and algae—There is little information on the importance of these organisms as pathogens of Eucalyptus, though each of these classes of organisms has been recorded in woody plants (Joubert and Rijkenberg, 1971; Schneider, 1973); and viruses (Seliskar, 1964) and bacteria (Kuntz, 1964) are agents of a number of destructive wilts and diebacks of forest trees. Three virus diseases have been reported on E. citriodora in India (Sastry et al., 1971) and virus symptoms have been observed on E. citriodora, E. maculata, E. propinqua and E. saligna (Fawcett, 1941). Similarly there are few records of pathogenic bacteria on Eucalyptus though some are important pathogens causing branch dieback, crown-gall and vascular wilt in other broadleaved genera. Crown-gall caused by Agrobacterium tumefaciens which has been reported on E. camaldulensis, E. citriodora and E. multiflora (Browne, 1968) progresses slowly but may eventually kill. The review of plant pathogenic algae by Joubert and Rijkenberg (1971) contains no reference to Eucalyptus.

3.3 Fungi

Fungi are recognised as the most important pathogens of forest trees (Hepting 1971) and this is probably true also for eucalypt diebacks. Among fungi which cause symptoms similar to those observed in the eucalypt die-

backs (i.e., crown dieback or sudden wilt), the rootrotting, vascular wilt, and branch canker fungi are most important. Foliage pathogens are only occasionally implicated.

3.3.1 Foliar pathogens—More than 57 genera of fungi have been recorded on eucalypt foliage but few cause serious damage (Newhook, 1964). A few cause seedling losses (Grasso, 1948; Glasscock and Rosser, 1958; Heather, 1961, 1967; Pandotra et al., 1971; Ashton and MacAuley, 1972). During unusually wet years some foliar pathogens have caused severe dieback of young trees in plantations. In Kenya, Botrytis cinerea infected foliage of E. globulus and spread to the stem causing dieback of the leading shoot for up to 65 cm (Nattras. 1949). In New Zealand, Gilmour (1966) reported that the same pathogen caused severe dieback of E. delegatensis up to 10 years of age and also affected E. maidenii, E. botryoides, E. saligna and E. ovata in the nursery. It has also damaged plantations of eucalypts in Latin America (Abrahao, 1948). In Costa Rica, Cylindrocladium scoparium causes a damaging leaf spot on eucalypts (Bazan de Segura, 1970).

3.3.2 Branch canker pathogens—A number of fungal pathogens are reputed to cause twig and branch dieback of eucalypts. Few cases have been rigidly proved so that some of the observed associations may be due to secondary infection. The pathogens reported include several species of Cytospora (Oxenham, 1960; Boden and Stahl, 1962; Krstic, 1964; Browne, 1968), Hypoxylon spp. (Scharif, 1964; Krstic, 1964), Ramularia sp. (Walker and Bertus, 1972), Irpex obliquus (Krstic, 1964), Endothia sp. (Boerboom and Maas, 1970), Botryosphaeria sp. (Hepting, 1971) Glomerella cingulata, Calonectria theae, Physalospora rhodina and Fomes robinae (Browne, 1968). Krstic (1964), citing a personal communication from Stahl, reported that Cytospora australiae and C. eucalyptina caused twig and branch dieback, stripe canker and killed young trees of almost all species of eucalypt. Generally very little is known of the host range and distribution of these fungi in native stands and there is practically no knowledge of the factors affecting their activity or the extent of damage they cause.

3.3.3 Vascular wilt pathogens—The vascular wilt fungi are few in number and are usually limited in the species which each pathogen attacks (Kuntz, 1964). They cause serious diseases which may be spectacular in their rapid and destructive effects. They enter the host through roots and wounds in leaves, twigs, branches and trunk and are often carried by insect vectors. They invade the vascular systems causing darkening of the tissues and form tyloses which block vessels especially in the outer sapwood. If the invasion is general, rapid wilt follows and if it is localised, branches dieback.

Among the most destructive vascular wilt pathogens is Endothia eugeniae which causes acute dieback of the clove, Eugenia caryophylla, (Booth and Gibson, 1973). Other species of Endothia, Ceratocystis, Fusarium and Verticillium cause wilts of various tree species but we know little of their role in eucalypt diebacks. Stahl (unpublished) has reported isolation of

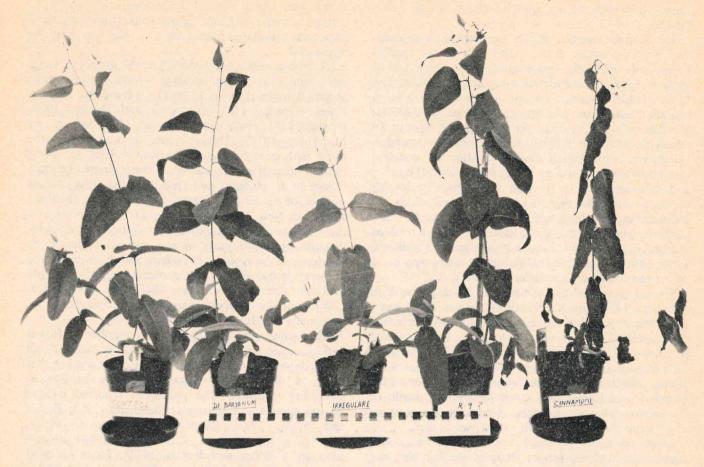


Fig. 17. Comparison of the pathogenicity of Pythium debaryanum (second from left), P. irregulare, an unknown forest Pythium spp. and Phytophthora cinnamomi, to E. sieberi. Note the severe wilting (followed by death) produced by the P. cinnamomi (Marks and Kassaby).

an Ambrosiella sp. from dying E. saligna. This seems to be transmitted by the borer Xyleborus truncatus. The only other Australian record encountered is Verticillium dahliae on E. citriodora (Newhook, 1964). In the Caribbean Endothia havanensis has killed eucalypts in plantations (Boerboom and Maas, 1970), in South Africa Pestalotia spp. has been associated with wilt and dieback of E. fastigata (Zeijlemaker, 1970), and in India Fusarium solani has been associated with wilt of E. camaldulensis (Mahmood, 1971).

3.3.4 Root-rotting pathogens—This group of pathogens includes fungi such as Armillaria (≡ Armillariella) which cause the decay of large woody roots, and others such as Pythium spp. which seems to be restricted to the decay of undifferentiated roots. Some fungi, notably Phytophthora, vary greatly in the size of roots which they invade depending upon the host species. Phytophthora spp. and Armillaria have received particular attention and their important roles in some eucalypt diebacks is widely recognised (Newhook and Podger, 1972; Pratt et al., 1972; Podger, 1972; Weste and Taylor, 1971; Weste et al., 1972; Marks et al., 1971; Kile, 1973).

Although Armillaria mellea is often a secondary pathogen of weakened trees (Wargo, 1972; Wargo and Houston, 1973; Kile, 1973) in some places it exhibits

clear evidence of primary pathogenecity (Podger et al., unpublished; Kile, unpublished). In the Strzelecki Ranges, Victoria, it has killed a small patch in a vigorous plantation of E. regnans and causes considerable damage at Mt. Cole and in the Wombat Forest in central Victoria. Gilmour (1966) reported that E. delegatensis is extremely susceptible.

Phytophthora cinnamomi is a widespread but not ubiquitous pathogen in eucalypt forest which has caused great destruction in vulnerable communities. In other places it seems to be under effective control by environmental factors (Broadbent et al., 1971; Newhook and Podger, 1972). Several other spp. of Phytophthora have caused severe root rot of certain species of Eucalyptus in pot tests, but no comprehensive account of their distribution, pathogenicity or role in eucalypt diebacks has been published.

Pythium spp. are now regarded by some workers as more serious pathogens of woody perennials than was believed earlier (Hendrix and Campbell, 1973; Robertson, 1973; Pratt and Heather (1972(a)). Pratt and Heather suggested that Pythium spp. may be important pathogens of Eucalyptus, but Marks and Kassaby (1973) reported pathogenicity tests with several Pythium spp. which indicated that they were very weak pathogens on the hosts tested (Figs. 17, 18).



Fig. 18. Comparative differences in pathogenicity between *Phytophthora drechsleri* (centre) and *P. cinnamomi* (right), to *E. sieberi* 30 days after inoculation. Note how the *E. sieberi* has started to wilt (Marks and Kassaby).

Many other root-rotting fungi have been recorded in Australian forests (Newhook, 1964; Stahl, unpublished) but little is known of their host relationships, distribution, virulence or of the factors affecting their activity. Most of the information available on root-rotting fungi and eucalypt diebacks is due to overseas sources. In South America Cylindrocladium scoparium has caused dieback of mature eucalypts (Batista, 1951). In young plantations deaths have been attributed to C. scoparium (Jauch, 1943) and C. clavatum (Hodges and May, 1972). The pink disease fungus Corticium salmonicolor has killed young eucalypts in South America (Bazan de Segura, 1970) and in India where up to 50 per cent mortality of 2-5 year-old E. globulus is reported (Bakshi et al., 1970). In South Africa Ganoderma collosum has caused extensive root-rot and patch death of pole-sized E. citriodora, E. maculata, E. paniculata and E. punctata (Luckhoff, 1955). In the Congo Phaeolus manihotis (Gibson, 1964) and in New Zealand Peniophora saccrata, Dematophora sp., and Rosellinia radiciperda (Gilmour, 1966) cause dieback. Sudden wilt of E. globulus and E. multiflora has been attributed to Macrophomina phaseoli (Browne, 1968).

4. THE EUCALYPT CROWN DIEBACKS

A degree of crown dieback symptoms is present in some trees in most of Australia's eucalypt forests. At community level this degree is generally well within the range regarded as typical of healthy stands in dynamic balance with their environments. However, there are increasingly large areas in which the frequency and degree of dieback has seriously affected stand structure and species composition or at least substantially reduced growth and expected yield.

There are at least five distinct types of these severe diebacks each with a number of separate occurrences of significant area. Unfortunately there is no satisfactory classification for these diseases. A classification based upon cause is not possible for the causes of most are unknown. A classification based upon the effects of the diseases upon community structure and composition is only partially successful because a single causal agency does not always produce the same effects in all communities.

Most diebacks have been given names useful only to the initiated and of little value in defining the disease. The scheme adopted in the following sections of this review is one arbitrarily selected for a recent review of the role of *Phytophthora cinnamomi* in eucalypt diebacks in Australian forests (Podger, 1974). In this treatment, the reactions of species of the eucalypt subgenera *Monocalyptus* (M) and *Symphyomyrtus* (S) are considered to be of diagnostic significance, the first being generally highly susceptible to *P. cinnamomi*, the second generally field resistant (Podger and Batini 1971; Marks *et al.*, 1973).

4.2. Jarrah dieback

This disease affects extensive areas of dry sclerophyll forests of *E. marginata* (M). It occurs as a mosaic of dead and dying patches which have gradually increased in size and number since at least 1921 when only a few small patches were known (Podger, 1972). It now affects an area estimated at up to 100 000 hectares. Interpretation of time sequences of aerial photographs has indicated an annual rate of increase of the area affected of 4 per cent per annum on several large sample areas (Batini and Hopkins, 1972).

The occurrence of the disease in relation to factors of the environment, its symptoms, and its effects upon the plant communities have been described in detail elsewhere (Podger, 1968; Podger, 1972; Podger et al., 1965). Although it is best known for its effects in the jarrah forest it also severely damages dry sclerophyll woodland and heath communities (Podger, 1972). In the overstorey only E. marginata (M) is affected severely; other overstorey species are either mildly affected, e.g. E. calophylla (subgenus Corymbia) or field resistant, e.g. E. wandoo (S), E. gomphocephala (S), E. diversicolor (S), E. rudis (S) and E. patens (M). In dry sclerophyll communities many species of trees and shrubs in the understorey and shrub layers are killed-particularly in the families Proteaceae, Epacridaceae, Xanthorrhoeaceae, Papilionaceae, Dilleniaceae and Myrtaceae. The disease does not cause damage to understorey species of the wet sclerophyll karri (E. diversicolor) forests where the families Rhamnaceae, Rutaceae, and Mimosaceae are prominent (Podger, 1968).

Because the incidence of jarrah dieback was seen to

be closely associated with timber cutting and roadmaking it was first thought that the disease was due to deterioration of the forest environment brought about by disturbance of sites already marginal for the susceptible species (Hamilton, 1951; Podger, 1959), but by 1963 there was strong circumstantial evidence that jarrah dieback was caused by a soil-borne pathogen. In 1964 P. cinnamomi was isolated from diseased forest (Podger et al., 1965) and later shown to be constantly associated with the disease (Podger, 1972). It has never been isolated from unaffected forest despite repeated attempts (Podger, 1968; Batini and Hopkins, 1972). By 1971 field inoculation trials made in 1966 provided proof that the introduction of P. cinnamomi to previously unaffected forest was sufficient to initiate the entire sequence of disease symptoms (Podger, 1972). This result, plus the spreading mosaic pattern of occurrence, the association of the disease with logging and roading, the apparent absence of the fungus in unaffected forest, and the extreme susceptibility of so much of the flora, has lead to the conclusion that P. cinnamomi is an introduced fungus in Western Australia (Podger, 1972).

The severity of the disease is attributed to the coincidence of the high susceptibility of the flora and its extreme vulnerability (Newhook and Podger, 1972; Podger, 1972). This vulnerability is due to a combination of circumstances including:

- (i) a large food base for inoculum build-up provided by the high proportion of susceptible species in the flora;
- (ii) low fertility of the soils and their low levels of microbial activity which results in low levels of antibiosis:
- (iii) the gravelly and sandy textures of soils which allows extensive rewetting of large volumes of soil by relatively light falls of rain so favouring zoospore formation and dispersal;
- (iv) the severity of the summer drought which places severe stress upon plants with root systems which were damaged during periods of spring rain (Newhook and Podger, 1972; Podger 1972; Podger et al., 1965). In North Auckland, New Zealand, where none of these environmental conditions are met, planted jarrah appears to be quite healthy in the presence of high population levels of *P. cinnamomi*.

4.3 Dieback on the Brisbane and Otway Ranges, Victoria

Perhaps the most dramatic of disease developments in Australian forests has been the explosive epidemic of *P. cinnamomi* infection in the Brisbane Ranges 60 km west of Melbourne, Victoria. In 1969 the fungus was isolated from four small patches of dying ground vegetation under low sclerophyll forest (Podger and Ashton, 1970). Although there were no signs of ill-health in the eucalypt overstorey the symptoms and the range of genera affected in the ground flora were strikingly similar to those of the initial stages of jarrah dieback. There was such remarkable similarity of soils, climate, and of composition and structure of the communities,

to those of the jarrah forest that these forests seemed likely to be vulnerable to *P. cinnamomi*. Weste and her colleagues have since reported:

- (i) rapid extension of the disease (up to 170 m per annum on slightly undulating terrain and 400 m per annum down drainage lines);
- (ii) close association of the disease with P. cinnamomi;
- (iii) severe dieback and mortality in E. obliqua (M), E. baxteri (M), and E. macrorhyncha (M);
- (iv) field tolerance in E. sideroxylon (S), E. viminalis (S) and E. aromaphloia (S), and apparent field immunity in E. ovata (S) and E. goniocalyx (S);
- (v) no success in isolating P. cinnamomi from unaffected stands in the same district;
- (vi) proof of the pathogenicity of pure cultures of local isolates within 12 months of inoculation into previously unaffected forest;
- (vii) strong circumstantial evidence of the introduction of the fungus on earth-moving equipment to both the Brisbane Ranges and the Wilson's Promontory National Park—180 km southeast of Melbourne (Veitch, 1973; Weste, 1973; Weste et al., 1972; Weste and Law, 1972; Weste and Taylor, 1971).

In the Otway Ranges (200 km southwest of Melbourne) G. C. Marks (personal communication) has associated *P. cinnamomi* with dieback virtually identical to that in the Brisbane Ranges.

The two diebacks treated above are the only eucalypt diebacks for which there is unequivocal evidence that P. cinnamomi is the primary cause. In the former case Koch's postulates have been satisfied under field conditions. Opinion on the role of P. cinnamomi in other diebacks is largely a matter of inference. This inference is based upon partially satisfactory information concerning the distribution of the fungus in relation to the diseases and upon the responses of the various components of the communities. The classic pattern of P. cinnamomi diebacks, that is the susceptibility of Monocalyptus and tolerance in Symphyomyrtus accompanied by susceptibility in many species of Proteaceae, Epacridaceae and Xanthorrhoeaceae and resistance of grasses and sedges, has been observed only in the presence of P. cinnamomi.

It might seem reasonable to suppose that *P. cinnamomi* is the cause of any dieback which presents this particular array of effects. In communities with susceptible species but no symptoms of the disease it would seem reasonable to assume that *P. cinnamomi* is either absent or that its activity is suppressed. However the situation in the diebacks of Tasmania, New South Wales and eastern Victoria is rather more complex and puzzling than the above model suggests.

4.4 Tasmanian east coast dieback

There is a dieback in lowland and foothill forests of Tasmania's east coast which meets the classic criteria for diagnosing P. cinnamomi infection. E. sieberi (M), E. obliqua (M), E. amygdalina (M), Banksia marginata, Epacris impressa, Xanthorrhoea australis, and

Hibbertia spp. are killed, but E. ovata (S), E. globulus (S) and the sedges are field tolerant (Palzer, 1973). P. cinnamomi has been isolated from the diseased areas, but was not detected in unaffected forest nearby (Palzer, 1973). Inoculation of pure culture of P. cinnamomi onto feeder roots of trees growing in the forest have indicated susceptibility to root-rot in E. obliqua (M), E. sieberi (M), E. amygdalina (M), E. viminalis (S) and Banksia marginata. The tests do not constitute proof of pathogenicity under field conditions as the excavated root systems, though attached to the parent trees, were cultured and inoculated in containers with moist vermiculite (Palzer, 1973). Field inoculation trials were established more recently (Tasmanian Forestry Commission 1973).

No estimates of the area affected, rates of spread or history of the problem have been reported.

4.5 Tasmanian gully dieback

This dieback which affects dry sclerophyll forest on the eastern slopes of Tasmania's north-eastern highlands was first described in 1972 by Felton. Comparison of aerial photographs taken in 1950 and 1969 showed that both the area affected and intensity of the disease increased markedly in the period. In an area of 32 000 ha sampled in 1969 at least 2400 ha were affected (Felton and Bird, 1972). The disease occurs principally on lower slopes and in gullies and occasionally on ridges. In the first areas examined there was strong evidence that P. cinnamomi caused this disease (Felton, 1972); E. obliqua (M), E. amygdalina (M), E. delegatensis (M) and E. viminalis (S) were killed but E. ovata (S) was unaffected. There was also mortality among species of the dry sclerophyll ground cover, but not among the understorey of wet scleropyhll gully species which are mainly from families Compositae and Mimosaceae. P. cinnamomi was isolated from three areas. Since then 21 diseased gullies have been tested but P. cinnamomi has been found in only two, both close to roads (Palzer, 1973). The negative samples were baited, rebaited, sown with susceptible plants which grew well and were then rebaited. It was concluded (Palzer, 1973) that gully dieback is not due to P. cinnamomi, though in some places the effects of this fungus are superimposed upon another disease the cause of which is unknown. It may involve a complex of pathogens including Pythium, Phytophthora and Armillaria as well as insect defoliators and drought (Palzer, 1973).

4.6 Tasmanian regrowth dieback.

This disease was first reported in 1968 (Bowling and McLeod, 1968) and has since been described in more detail (Bird, 1973; Felton, 1972; Felton and Bird, 1972). It affects regrowth eucalypts in tall wet sclerophyll forests ranging in age from 30 to 170 years. The tall understorey of species in the families Rhamnaceae, Pittosporaceae, Compositae and Mimosaceae is unaffected. E. obliqua (M) and E. regnans (M) are severely affected, but E. globulus (S), E. amygdalina (M), E. simmondsi (M) and E. johnstoni (S) are little affected. The extent of the problem is difficult to assess be-

cause dead and dying trees are diffusely distributed among apparently healthy trees and there are no marked effects on the understorey. The disease is common on some 16 000 ha in southern Tasmania and there are smaller occurances in northern parts of the island (Felton and Bird, (1972).

Evidence from growth plots established long before the disease was recognised suggests that this dieback is a very recent phenomenon which has not occurred previously in the life of the existing stands (Bird, 1973). Once decline has set in it seems to be irreversible though it may take up to ten years for a tree to die.

P. cinnamomi has been isolated from beneath regrowth dieback areas, but constant association has not been demonstrated. It has been suggested (Kile, 1973) that P. cinnamomi is unlikely to be an important factor as soil temperatures appear to limit activity of the fungus for the greater part of the year. Armillaria is intimately associated with the problem (Kile, 1973), but insect defoliation and drought may also be involved (Kile, 1974).

4.7 High altitude dieback.

This dieback kills E. delegatensis (M) over large tracts of country above 700 m in the northeast of Tasmania, but does not affect E. dalrympleana (S) or the understorey flora which includes Persoonia (Proteaceae) and Pultenaea (Papilionaceae) as well as wet sclerophyll and rainforest elements. In 1964 it was estimated (Ellis, 1964) that about 1800 ha of the 5000 ha sampled on the Mt. Maurice Plateau was severely affected. The cause of the disease is not known and efforts to isolate P. cinnamomi have produced negative results (Tasmanian Forests Commission 1973). Ellis (1964) is of the opinion that this dieback is a natural part of the succesional sequence toward climax rainforest of Nothofagus. It develops in fire-sere eucalypt communities when fire is excluded for long periods. Ellis (1964, 1971) has speculated on several possible causal mechanisms. The disease is not known in stands of E. delegatensis on mainland Australia even where understories of rainforest species occur.

4.8 Eucalypt diebacks in New South Wales.

Despite the widespread occurrence of P. cinnamomi in native forests in New South Wales (Pratt and Heather, 1972 (a) & (b)) there are no extensive areas of dieback which can be attributed solely to this fungus. Only one dieback has damaged significantly areas of eucalypt forest and its effects differ markedly from those of other eucalypt diebacks. The disease results in defoliation and death of E. saligna (S), E. propingua (S), E. paniculata (S), E. deanei (S), E. microcorys (S), E. acmenioides (M), E. umbra (M), E. pilularis (M) and Angophora intermedia (Moore, 1959, 1962). There are no detailed accounts of the effects of the disease upon the understorey though a few understorey plants were affected at Ourimbah in 1972 (Gerrettson-Cornell, 1973). Two areas of severely damaged forest near Nymboida on the Dorrigo Plateau and at Ourimbah examined in 1966 showed no marked effects in the understories though they contained Persoonia sp. and

Orites excelsa (both Proteaceae), and Trichocarpa laurina (Epacridaceae).

The disease occurs in scattered patches throughout coastal New South Wales, but is best known in the Ourimbah State Forest in the Gosford-Wyong district. Moore (1962) reported that in 1959 there were 150 separate occurrences which varied in size up to 1500 ha and that the disease had increased from minor importance in 1949 to local economic significance in 1958.

The cause of the dieback is unknown, but is almost certainly complex. Most trees had been continually defoliated for some years by leaf-sap-sucking psyllids and attacked by borers particularly Xyleborus truncatus (Moore, 1959) with which is associated an Ambrosiella sp. (Stahl, personal communication). Stahl found that this fungus in pure culture produced a water-soluble toxin which rapidly wilted cuttings of soft-leaved plants. Secondary borers of at least five other genera may also contribute to the decline (Moore, 1959). The disease occurs mainly on shallow soils over clay subsoils and its major development followed the unusually wet years between 1949 and 1956 (Moore, 1959). It has been suggested that these factors debilitated the trees so that they became more attractive to psyllids and more susceptible to Xyleborus. Armillaria mellea is associated with the disease in some places. More recently isolations of several pathogens in the Pythiaceae have been reported including P. cinnamomi and P. citricola (Pratt and Heather ,1972(a)). Although there are no published accounts of detailed surveys to indicate whether or not these fungi are constantly associated with the disease, there is some evidence that they may not be. In 1966 the author isolated P. cinnamomi from beneath dying E. saligna on farmland near Ourimbah but was unable to isolate it from beneath dying forest both at Ourimbah and at Nymboida where Pythium spp. were abundant.

The role of *P. cinnamomi* in this disease is far from clear. It may be that *P. cinnamomi* has an occasional distribution overlaying a disease due entirely to other causes. Alternatively the lack of damage to understorey and the susceptibility of both *Symphyomyrtus* and *Monocalyptus* may be an expression of an unusual array of pathogenic variants in the local populations of *P. cinnamomi*, but for this we have no direct evidence.

4.9 Eucalypt diebacks in eastern Victoria.

The first account of rapid decline and death of groups of eucalypts in eastern Victoria was given in 1959 (Lee, 1962). According to Marks et al. (1972), Lee's unpublished records showed a total of 20 ha affected in patches not exceeding 2 ha. On the basis of air-photo records and departmental reports it has been suggested that the disease originated in the late 1930s (Marks et al., 1972). It extended rapidly during unusually wet summer seasons in the 1950s and 1960s and is now estimated to affect about 15 000 ha of which 5000 ha are severely damaged (Marks et al., 1972).

The species now affected include E. obliqua (M), E. bridgesiana (M), E. consideniana (M), E. sieberi (M), E. muellerana (M), E. globoidea (syn. E. scabra)

(M), and E. radiata (M), but E. bosistoana (S), and E. sideroxylon (S) are field resistant (Lee, 1962; Marks et al., 1972). The understorey species Banksia marginata, Xanthorrhoea australis and Daviesia latifolia are also severely affected (Marks et al., 1972).

Although in many places the disease bears a striking resemblance to jarrah dieback, recent observation indicates that the disease situation and the role of P. cinnamomi in this region are more complex than had been suggested earlier (Newhook and Podger, 1972, p. 303). There seems to be little doubt that on poorly-drained sites on the coastal plain an introduced P. cinnamomi is the primary causal agent (Marks, personal communication). There are classic symptoms near Rosedale where E. consideniana (M), Banksia marginata, Epacris impressa and Xanthorrhoea australis are killed en masse and E. bridgesiana (M) is healthy. But recently the author has seen other areas where the symptoms are not consistent with the jarrah forest type of response to P. cinnamomi infection. Immediately west of the Mallacoota airfield there is an extensive area of advanced dieback in E. sieberi (M), E. muellerana (M), E. globoidea (M), and E. gummifera (Corymbia). Beneath this stand, a wide range of understorey species ordinarily considered to be susceptible to P. cinnamomi is apparently unaffected. The range includes Banksia marginata, B. spinulosa, Persoonia spp., Hibbertia sp., Xanthorrhoea* sp. and Callistemon citrinus. Yet nearby, on the Betka track, D. Cameron (personal communication) has observed typical early symptoms of P. cinnamomi infection where B. spinulosa and Hakea ulicina had died beneath apparently healthy E. sieberi. Further, dieback of susceptible species does not always occur in the presence of P. cinnamomi and the fungus occurs beneath extensive tracts of apparently healthy forest (Marks et al., 1971). Though it has been suggested that P. cinnamomi probably causes loss of growth in such places (Marks and Hartigan, 1972) it is not an invariable consequence (Incoll and Fagg, 1973) particularly where soil fertility and drainage are

The dieback situation in eastern Victoria is further complicated by the occurrence of Gosford-Wyong type dieback notably around Genoa where psyllids of the genera *Glycaspis* and *Eucalyptolyma* (Yen, personal communication) occur in plague proportions on eucalypts over an apparently healthy understorey.

5. CONCLUSION

A variety of factors cause eucalypt diebacks. In natural forests parasitic fungi, insects and drought seem to be more important causes. In partially cleared woodland insects and parasitic flowering plants assume greatest importance. In plantations insects, nutrient deficiency, frost and fungi seem to be most significant.

A few diebacks can be attributed to the introduction of a single new factor to vulnerable communities. The best examples are the diebacks due to the introduction

^{*} Ed. note: Xanthorrhoea minor the sp. found here is highly tolerant to root rot unlike X. australis.

of *Phytophthora cinnamomi* to south-western Australia and to the Brisbane Ranges and east Gippsland, Victoria. Even where such single factors are present their action and its consequences for the health of eucalypt forests are determined by interactions among a great variety of environmental factors and need not be damaging. There seems to be no pathogen of eucalypts which is capable of seriously damaging its hosts everywhere.

Some other diebacks are due to increase in the populations of native pests to epidemic proportions. The more notable examples include the plagues of phasmatids.

Most diebacks are of undetermined cause, but seem to involve a complex of pathogenic factors which may obscure the primary disease triggering factor. It seems that in certain cases this may be related in some way to disturbance of environmental balances by European man's activities. In other cases dieback occurs in forests long undisturbed, and there is no case for attributing all diebacks to the supposed sinister effects of European man's intervention. The kinds of disturbance which cause dieback in some communities seem to be necessary for the establishment of healthy regeneration in others.

For most diebacks we have only a superficial knowledge of the factors involved. In some we do not have so much as a bare understanding of the way in which the diseases have developed in time and space or a record of the circumstances in which the disease development occurred.

If we are to make progress in determining the causes of the various diebacks we will need to know much more about detailed symptoms, about the detailed effects of the diseases upon the plant communities, about pathogenic variation in some of our more important pathogens, and about how they are distributed in relation to the diseases. Only detailed information of this kind will allow us to make accurate diagnoses of the causes of an increasingly complex, varied and steadily overlapping set of diseases.

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