

PART 2

THE FACTORS CONTRIBUTING TO EUCALYPT DIEBACK

CHAPTER 5 THE ROLE OF INSECTS

The high levels of insect-induced defoliation of most trees which showed dieback on the Northern Tablelands led the Ministerial Working Group (1979) to consider insect grazing of prime importance in the dieback syndrome. However, prior to the early 1980s when apparent insect activity had already begun to wane there had been no systematic study to ascertain whether the observed defoliation levels result from abnormally high levels of insect grazing or relatively low levels of leaf replacement.

The favourable response of most declining trees to the application of systemic insecticides (Clark et al, 1981, and Section 4.5) provides indirect evidence for the importance of leaf feeding insects. However, depression of tree growth by insects appears to be a common feature of apparently vigorous eucalypt woodlands (e.g., Morrow and LaMarche, 1978) and some improvement in the condition of declining trees after restriction of insect grazing would be expected regardless of whether insect feeding initiated the original decline in vigour. Also, insecticides may affect tree growth in ways other than those intended (see Section 4.5). Thus the response of trees to insecticides is not unequivocal proof of the importance of insects.

Besides insects which feed on foliage, connective tissue feeding insects, primarily longicorn beetles, are involved in tree deaths (see Section 2.2). However, in general only trees which have been severely stressed by drought, or other factors, are affected by these insects. The following discussion is confined to insects which feed on foliage. Root feeding insects are mentioned in Section 6.2.

Attainment of a clear understanding of the role of foliage feeding insects in rural dieback requires consideration of:

- (i) the ecological significance of insects in eucalypt woodlands in general;
- (ii) the response of eucalypts to various levels of insect grazing;
- (iii) the differences between insect activity in healthy and declining woodlands; and
- (iv) the factors governing the fluctuations of insect populations in both situations.

The first three points are the subject of this chapter, while point (iv) is discussed in part 3.

5.1 The Ecological Significance of Insects

Insects are an integral part of terrestrial ecosystems. They have co-evolved in intimate association with plants for millions of years. The vast majority of phytophagous insect

species never reach population levels that severely affect plant productivity (Mattson and Addy, 1975; Lawton and McNeill, 1979). As a generalization, insect outbreaks severe enough to damage trees only occur sporadically. Recently attention has been given to the possible significance of positive aspects of insects' activities in forest ecosystems.

Regulation of productivity and nutrient cycling: Mattson and Addy (1975) suggested that usually the productivity of forest ecosystems is limited by the abiotic flux (i.e. the flow of nutrients, water and light required for plant production) and, in most cases, insect grazing has little long term effect on productivity. They suggested that insects could act as regulators of primary production, preventing over exploitation of resources and leading to greater long term stability of the ecosystem. Support for this case was provided from literature which revealed that there was a greater incidence of insect outbreaks in areas where nutrient deficiencies were evident. Much of Mattson and Addy's theory concerned the capacity of insects to respond to host condition in the fashion of a cybernetic regulator. They presented evidence suggesting an association between increased plant stress and increased insect activity. For the influence of phytophagous insects to be stabilizing at a community level, the benefits of insect grazing, in terms of increased nutrient recycling and reduction of standing biomass, must exceed the negative

effects of the grazing stress. Mattson and Addy's thesis has recently been challenged by Owen and Wiegert (1981), who consider that the interaction between herbivores and their hosts should be viewed in terms of fitness of individuals rather than regulation of productivity.

Following Mattson and Addy's (1975) argument, Springett (1978) stressed the possible connection between the harshness of the Australian environment, in particular the poor nutritional status of Australian soils, and reports of relatively high proportions of leaves being consumed by phytophagous insects in eucalypt forests. Springett considered it was likely that insect frass contained greater concentrations of nutrients than leaf litter and could be more readily decomposed, but offered little supportive evidence. He suggested that insects play an important role in nutrient cycling, providing a link between the slow rates of nutrient cycling through decomposition of leaf litter and the fast rate of nutrient cycling resulting from fire. However, this argument overlooks the existence of mechanisms facilitating internal redistribution of important mineral nutrient elements (e.g. phosphorus and nitrogen) within eucalypts (see Section 10.4).

Schowalter (1981) recently suggested that the synergistic interaction between insect consumption and plant stress speeds redirection of nutrients from stressed plants to vigorous plants. This suggests a feasible mechanism for insect grazing actually increasing total ecosystem

productivity.

Longevity of individual plants: Owen (1980) suggested that many plants could have evolved some dependence on their association with herbivores, in particular he noted that the life-span of individual grass tussocks is usually extended by periodic cropping. This maintains the grass in a vegetative state and prevents shoot growth from outstripping the supply from the resource base.

Such a relationship may also apply to eucalypts. Pryor (1976) suggested that the more gnarled appearance and slower growth rates of eucalypts grown in Australia, in comparison with exotic eucalypts, results from damage to the growing points and leaves of Australian eucalypts caused by defoliating insects. Since the onset of old age in trees is partly related to allometric imbalances arising as the size of the tree increases (see Section 11.2) it is probable that the life-span of eucalypts would be greater where growth is limited by moderate levels of insect grazing.

Jacobs (1955) also suggested that slower growth caused by insect grazing results in the formation of denser wood of higher quality. It is likely that such wood would be more resistant to decay, facilitating a longer life for trees that are grazed by insects.

Vegetation dynamics: The influence of herbivores on vegetation dynamics has recently become a topic of

discussion. The potential of insect herbivores to limit the survival of plants is illustrated by the success of a significant proportion of the recorded attempts to control weeds biologically (De Bach, 1974). Whittaker (1979) reviewed evidence which suggested there was a strong interaction between the effects of herbivory and other stresses such as interference by adjacent plants. This interaction is also critical to Schowalter's (1981) thesis concerning the effects of redirection of nutrients from stressed plants to vigorous plants by herbivores. He considered that this redirection of nutrients together with the stress directly imposed by the herbivores is often critical in determining the dynamics of succession.

Insects could play a role in determining which species of eucalypt grow in a particular place and their relative abundance. Morrow (1977a) stated that, for insect grazing to be involved in interspecific competition between eucalypts, then either the insects must feed differentially on the cohabiting species or the species must respond differentially to insect attack. The limited information available indicates that, at least under some circumstances, either of these conditions may be true.

Burdon and Chilvers (1974) systematically sampled insects and fungal leaf parasites from four distinct eucalypt associations. Each association contained one member of the subgenus *Symphomyrtus* and one member of the subgenus *Monocalyptus*. They concluded that only one out of

23 species of fungal leaf parasites recorded did not exhibit field specificity to one or other *Eucalyptus* subgenus. Of the seventeen most common insects, seven exhibited at least 90% field specificity to a particular subgenus. In a more intensive study of one particular sub-alpine association, Morrow (1977a) also noted a high level of host specificity amongst insects. Ninety-seven percent of individual insects belonged to species which were restricted to either one or two of the three eucalypt species present. She suggested that consumption of foliage by phytophagous insects probably contributed to the maintenance of the competitive balance between *Eucalyptus pauciflora* and the more heavily consumed *E. dalrympleana*.

Turning to the second way in which insects can affect interspecific competition between eucalypts, the capacity of different species of eucalypts to withstand defoliation varies considerably. Fast growing forest eucalypts such as *E. regnans* recover poorly after extensive defoliation (Cremer, 1973; Wilson and Bachelard, 1975) whereas woodland eucalypts such as *Angophora costata*, may survive repeated defoliations provided sapwood starch is not depleted (Bamber and Humphries, 1964).

Differences in the tolerances of different species of trees to defoliation means that the more heavily defoliated species are not necessarily the species placed at a disadvantage by insect grazing. As an example, consider the consequences of gypsy moth larvae defoliating mixed forests

in the New England Region of the United States of America.

The gypsy moth larvae usually preferred oaks to other species, but when infestations built up less preferred trees were also severely attacked (Campbell and Sloan, 1979). The less preferred trees were more sensitive to defoliation and a higher proportion died at a given level of defoliation. Even though a greater proportion of oaks died than non-oaks, it is conceivable that under some circumstances the reverse could occur. In such a case, species tolerant to insects would actually gain advantage over competing species by facilitating an insect outbreak and infestation of the entire community.

5.2 The Impact of Insects on Individual Trees

There are variations in the proportion of eucalypt leaves consumed by insects in Australia both between different plant communities and over time. In the mid 1970s several studies estimated that phytophagous insects consumed a much greater proportion of foliage in Australian forests and woodlands than was typical for forests and woodlands in other parts of the world. The estimated rates of consumption in Australia varied from 15 to 50% (Morrow, 1977b). Another study (Journet, 1981) estimated insect-induced defoliation of *E. blakelyi*, in woodland near Canberra, to be 70% annually when premature senescence of insect damaged leaves was taken into consideration.

•

However, the study did not extend for long enough to determine whether the trees could tolerate this level of defoliation indefinitely.

Ohmart (1983) challenged the validity of generalizations from these studies. In Australia workers* had concentrated on situations where insects were already known to be abundant whereas the European studies commonly cited were total ecosystem studies from sites that were not chosen on the basis of insect abundance. Ohmart (pers. comm.) determined insect consumption to be markedly less than 10% per annum in a project that was designed as part of a total ecosystem study.

Recently, Fox and Morrow (1983) reported assessments of leaf area removal for 44 eucalypt species growing under a wide range of conditions. The average rate of leaf area removal was reported to be about 15% still higher than the averages of less than 10% (Springett, 1978) reported for the Northern Hemisphere but significantly less than earlier estimates. More mesic, higher altitude communities (e.g. snowgum woodlands) showed the greatest defoliation.

Interpretation of the significance of these estimates of eucalypt defoliation is complicated by eucalypts' indeterminant growth pattern and efficient axillary and epicormic bud systems which enable rapid replacement of lost foliage. Extensive defoliation stimulates renewed shoot activity (compensatory growth). Thus, estimates of the

*e.g. Kile (1974)

proportion of foliage lost from the tree as a result of insect grazing, usually over-estimate the net effect of grazing on the tree's canopy. In addition, changes to the microclimate and internal physiology of leaves may also partly compensate for the leaf loss (McNaughton, 1983; Heichel and Turner, 1983). The lack of precise understanding of how much the life expectancy of leaves is affected by insect-induced damage as opposed to other factors such as moisture stress, which also reduces leaf life expectancy, further complicates assessment of the impact of defoliating insects.

Insects often feed on new leaves which are not yet fully expanded. In leaves which have been partially consumed before they have attained full size, the apparent leaf area removed by insects is much greater than the actual consumption. Thus estimates of leaf consumption, based on defoliation indices, may be greater than actual consumption (S.C. Cairns, pers. comm.).

Insect defoliation results in the direct loss of photosynthetic capacity and metabolic reserves within the tree (carbohydrates, mineral nutrients, etc.) are depleted to enable the replacement of lost foliage. Experiments involving the artificial defoliation of eucalypts have also demonstrated the importance of the survival of growing points and unexpanded leaves to tree growth (Cremer, 1972; Carne et al, 1974). The relative importance of growing points is also evident from studies involving insect-induced

defoliation. For example, Carne et al (1974) found that scarabs, feeding exclusively on fully expanded leaves, only caused mild reduction to the growth of *E. grandis* in plantations on the north coast of N.S.W. even when more than 60% of leaf tissue was removed. Severe growth reduction or mortality only occurred when growing tips and expanding leaves of the defoliated eucalypts were damaged by other insects.

Other possible detrimental effects of insect defoliation involve premature senescence of leaves that have been damaged by insects (Journet, 1981) and increased losses by leaching from damaged leaves. Further work is required to ascertain the importance of these two effects.

There is extensive circumstantial evidence directly or indirectly linking tree mortality with defoliation (Kulman, 1971). The ultimate death of trees often results from secondary agents, such as disease-causing fungi and connective tissue feeding insects, which appear to be capable of taking advantage of trees stressed as a result of insect defoliation (Kozlowski, 1969). In the northern hemisphere *Armillaria mellea* (Vahl ex Fries) Kummer is one of the most prominent examples of a root pathogen which ultimately causes the death of defoliated trees (Staley, 1965). *A. mellea* was found to grow faster in wood taken from the roots of defoliated sugar maples than in wood taken from roots of healthy sugar maples. Extracts from outer wood of the roots of sugar maples that were artificially defoliated

contained increased concentrations of sugars and some amino acids (Wargo, 1972). Similar increases in the concentrations of sugars and amino acids in the sap of *E. regnans* seedlings were also noted following defoliation (Wilson and Bachelard, 1975).

Bamber and Humphreys (1964) measured the depletion of sapwood starch reserves of a number of eucalypts in response to repeated defoliation. The death of the eucalypts appeared to coincide with the exhaustion of starch reserves. They suggested that the trees probably died because the starch reserves were not sufficient to maintain respiratory activity in the absence of photosynthetic tissue (Bamber and Humphreys, 1964). However, damage to roots and changes in root starch reserves were not monitored. Starch depletion is a common symptom of tree disorders, including disorders unrelated to insect damage (e.g. Hepting, 1945). Depletion of phosphates, nitrogen and other nutrients as a result of defoliation could also occur (see Section 10.4). The stress on trees could be exacerbated by shortages of nutrients or water retarding recovery.

The association of depletion of carbohydrate reserves with tree death provides a conceptual framework which explains the interaction between the impact of defoliation and season (Morrow, 1977a). Trees are most severely affected by defoliation during the spring flush, i.e. when carbohydrate reserves are rapidly being used up. Replacement of lost foliage places a severe demand on the

carbohydrate reserves. Hence, trees which have been repeatedly defoliated, or trees of low vigour are more likely to die from defoliation.

In some fast growing eucalypts, such as *E. regnans*, which are particularly sensitive to defoliation, death following defoliation is not closely correlated with depletion of carbohydrate reserves (Cremer, 1973). Wilson and Bachelard (1975) intensively investigated the response of *E. regnans* seedlings to artificial defoliation and found that an inhibitor appeared in sap from the roots of defoliated or detopped *E. regnans* seedlings. Lettuce seed germination was unaffected by *E. regnans* root sap taken 0-8 days after defoliation, but sap taken 13 days after defoliation completely inhibited lettuce germination. The *E. regnans* seedlings usually died between 12 and 30 days after defoliation. It was concluded that the inhibitor probably prevented recovery of the seedlings.

Other serious effects of insect defoliation include an immediate reduction in growth increment and an increase in rootlet mortality. Seventy per cent defoliation of spruce by the spruce budworm resulted in greater than 30% loss of fine rootlets; 100% defoliation resulted in death of over 75% of all fine roots (Redmond, 1959). The reason for rootlet death was unknown.

Wilson and Bachelard (1975) also found that root elongation of both *E. regnans* and *E. viminalis* seedlings stopped within four days of defoliation. Shortly afterwards, the root tips of both species died back. It is possible that root mortality in eucalypts exhibiting symptoms of rural dieback (see Section 2.3) could be directly related to defoliation.

5.3 Insects on the Northern Tablelands

The first attempt to systematically assess the proportion of leaves consumed by insects on an annual basis in the Northern Tablelands only commenced in 1982 (M. Lowman, pers. comm.) and is still in progress. Nevertheless, a number of estimates of the proportion of leaves lost due to insects are available.

During 1977, Clark et al (1981; unpublished) visually estimated the percentage defoliation of 640 trees in 30 semi-randomly chosen plots throughout the Northern Tablelands. The average estimate of defoliation was 43% over all species and sites, with *E. nova-anglica* and *E. blakelyi* more heavily defoliated than other species. Eight of the 30 plots were reassessed during 1979. There was a positive association between the percentage defoliation of trees in 1977 and the likelihood of death over the two-year period; 71% of trees with a 1977 whole crown defoliation score of greater than 81% were dead in

1979 compared with about 10% mortality for trees with a 1977 defoliation score of less than 50%.

Duggin (1981) reported the systematic assessment of defoliation of *E. blakelyi*, *E. melliodora* and the stringybark, *E. laevopinea* on four occasions between October 1979 and July 1980 near Armidale. Defoliation was estimated by approximating the leaf margins of partially eaten leaves. No account was made for missing leaves - thus estimates of defoliation were conservative. Defoliation reached 35% in *E. melliodora*-*E. blakelyi* forest and isolated trees during winter with less defoliation in open woodland or *E. laevopinea* associations. Defoliation also reached 35% in *E. melliodora*-*E. blakelyi* forest during late summer. At other times defoliation ranged between 15 and 25%. In contrast to the earlier estimates of defoliation made in the spring of 1977 by Clark et al (1981 and unpublished), the estimates made in 1979-80, reported by Duggin (1981), do not indicate unusually intensive grazing of eucalypts when they are compared to measured levels of defoliation in healthy eucalypt woodlands ranging from 20 to 50% (see Section 5.2). S.C. Cairns (pers. comm.), who conducted a survey of insects during the summer of 1979-80, also considered that insect damage to eucalypts was not severe in most places during that season, though intensity of insect feeding varied from site to site.

A summary of the observations concerning insect induced defoliation of tagged trees monitored as part of the current project was given in Section 4.3. Most trees were recovering during the period from 1980 to 1983; insects only caused minor damage to most of the trees during much of the period and severe infestations were usually localized. It is likely that insect activity since 1979 was much less intense than during the preceding period when tree decline had become extensive.

Prominent features in the pattern of occurrence of eucalypt dieback in rural areas of the Northern Tablelands accord with the behaviour of the syndrome expected if insect induced defoliation was of critical importance:

1. The vigour of all trees in severely affected areas was reduced to some extent (see Sections 3.6, 4.3).
2. Patches of more severely and less severely affected trees occur irregularly in much the same way that the impacts (intensity and duration) of individual insect outbreaks have varied (see Section 4.3).
3. The occurrence of dieback is not restricted by topographic or geological boundaries, though the intensity of dieback is affected by these factors. (This is expected because although insects are ubiquitous both insect abundance and trees' capacity to recover from defoliation vary with site factors.)
4. The condition of trees that are not severely moribund generally improves in years when insects are

scarce (see Section 4.3).

Other observations are also in accord with insects being an important determinant of dieback, e.g. the differences between the relative vigours of *E. melliodora* and *E. blakelyi* are associated with differences in their relative susceptibility to damage from *Anoplognathus* spp. (see Section 4.3).

5.4 Summary and Conclusion

Insects are an integral part of forest and woodland ecosystems and all the insects defoliating eucalypts on the Northern Tablelands are indigenous. Although there are contrasting accounts of the proportions of eucalypt foliage consumed by insects in Australia it is likely that the average proportions of eucalypt foliage consumed in Australia is greater than average proportions of foliage consumed by insects in Northern Hemisphere forests.

There has been recent speculation about possible beneficial influences of insect grazing on trees. Possible influences include: regulation of productivity; speeding of nutrient cycling; and increasing the longevity of trees. It is likely that insects speed redirection of nutrients from stressed plants to their successors. Different species of insects prefer to feed on particular species of eucalypts and eucalypts vary in their tolerance of defoliation. Thus

it is probable that insects affect interspecific competition among eucalypts.

Removal of leaf buds exacerbates the damage to trees resulting from defoliation. In various instances death of trees following defoliation has been found to be associated with secondary fungal attack, carbohydrate starvation, and hormonal factors (ash type eucalypts only).

Estimates of defoliation of eucalypts on the Northern Tablelands in the late 1970s were substantially higher than estimates of defoliation in the early 1980s.

Insects appear to be critical in the dieback syndrome. In addition to symptomatic evidence, i.e. regular association of insect induced defoliation with deterioration of crown condition (see Sections 2.2, 4.3), and evidence from field trials containing trees protected from insect grazing by insecticides (see Section 4.4), the pattern of incidence of dieback on the Northern Tablelands accords with the patterns expected if insects were of critical importance in the syndrome.

CHAPTER 6 THE ROLE OF PATHOGENS

This chapter is concerned with the role of pathogenic organisms, excluding foliage feeding insects (see Chapter 5), that are likely to affect the condition of eucalypts on the Northern Tablelands. Both the beneficial and harmful effects of microorganisms are discussed. Reports of a preliminary survey undertaken by the author on the *Phytophthora* spp. present in the region, and of pot trials studying the effects of *P. cryptogea* Peth. et. Laff. on eucalypt seedlings, are included.

Pathogens which cause disease in plants are not always obvious. The cause of jarrah dieback in Western Australia remained a matter of conjecture for more than 50 years before the organism primarily responsible for the disease, *Phytophthora cinnamomi* Rands, was first isolated (Newhook and Podger, 1972). Hence the possibility that a disease-causing organism is involved in rural decline of eucalypts in the Northern Tablelands required investigation. The involvement of pathogenic disease in many tree disorders initiated by excessive defoliation has already been mentioned (see Section 5.2). General reviews covering the major diseases known to occur in eucalypts are available (Gibson, 1975; Heather and Griffin, 1978; Marks et al, 1982).

6.1 Fungal Pathogens

Fungal shoot and leaf pathogens do not appear to have been important as agents affecting eucalypts on the Northern Tablelands (see Section 2.2). Any serious fungal disorders that

might have occurred are likely to have been root diseases. Pathogens which attack the fine roots leaving the major roots intact (Salt, 1979), could also have played a part in the syndrome. Woodrots are also prevalent in eucalypts that were affected by dieback (see Section 2.3). The dieback affected eucalypts that were examined (see Section 2.3) usually exhibited degeneration of the root system with extensive rootlet mortality. Rootlet mortality might have resulted from severe defoliation and it is probable that other forms of physiological stress would also have damaged root systems. However, the possibility that fungal root pathogens directly contributed to this mortality of rootlets required investigation.

Fungi which have been associated with dieback of eucalypts in Australia include: *Phytophthora* spp., *Pythium* spp. (Pratt and Heather, 1973), *Cylindrocladium scoparium* Morgan (Keirle, 1981), *Armillaria* spp. (Kile, 1981a), *Cylindrocarpon* sp. and *Fusarium* and *Verticillium* spp. (C.J. Shepherd, pers. comm.).

The biology of *P. cinnamomi* has been extensively studied (Old, 1979). Recent findings indicate that it is much more pathogenic to mature eucalypts than was formerly considered. It is able to grow into cambial tissue on the main roots and trunk, thus causing extensive damage (Marks et al., 1980; Shearer et al., 1981; Smith and Marks, 1982). In addition, Shea et al (1982) found that the jarrah trees which had suddenly died after *P. cinnamoni* established itself in the surrounding soil, almost invariably grew on soils containing a concreted lateritic layer at a depth of from 5-75cm. After intensive sampling of the

distribution of fungi within the root systems of 41 affected trees, *P. cinnamomi* was consistently recovered from major roots, in particular from the zone of the vertical roots where penetration of the lateric zone occurred. Invasion by *P. cinnamomi* had caused extensive lesions in these vertical roots. This damage apparently cut off the supply of water from the subsoil to the trees, so that they subsequently died of water stress. The authors postulated that the frequent ponding of storm water in the zone where vertical roots penetrated the lateric layer accounted for the zone appearing to be an ideal site for invasion by zoospores. The capacity of *P. cinnamomi* to invade major roots makes the fungus potentially more damaging to rural eucalypts than was previously considered. Root injuries resulting from cultivation and other agricultural activities might facilitate the entry of *P. cinnamomi* into the major roots (G.C. Marks, pers. comm.).

Eucalypts grouped in the subgenus *Monocalyptus* are much more susceptible to *P. cinnamomi* than eucalypts grouped in the subgenus *Symphyomyrtus* (Marks and Idczak, 1980). Eucalypts from both sub-genera show extensive dieback on the New England Tablelands, but the four most severely affected species are all from the subgenus *Symphyomyrtus* (see Section 3.5). Podger and Batini (1971) tested the pathogenicity of *P. cinnamomi* on 36 species of eucalypt seedlings including some species seriously affected by dieback on the Northern Tablelands. They found that there were no substantial differences in the vigour of *E. blakelyi* seedlings inoculated with *P. cinnamomi* compared to

uninoculated controls. However the rootsystems of the *E. melliodora* and *E. viminalis* seedlings were affected by the fungus, with *E. viminalis* showing a similar degree of root damage as *E. marginata* but no mortality. Podger and Batini (1971) rated *E. pauciflora*, a species which shows some apparent resistance to dieback on the Northern Tablelands, as one of the species most susceptible to *P. cinnamomi*. However the high mortality rates incurred by the control seedlings of that species in the experiment cast some doubt on the conclusion.

P. cinnamomi also causes severe damage to a large range of native understorey plants (Weste, 1974), but, with the exception of eucalypts, very few native plants that grow on the Northern Tablelands show evidence of decline (Section 3.5; also see discussion in Section 6.8).

At the commencement of the study reported in this thesis there were no published records of *P. cinnamomi* having been found on the Northern Tablelands. However, the fungus has been shown to be present on the nearby North Coast (R.N. Allen, pers. comm.) as well as the Central Tablelands of N.S.W. (Keirle, 1979). A survey of the *Phytophthora* spp. on the Northern Tablelands was initiated in an attempt to determine whether the fungus was present in this area.

Armillaria luteobubalina Watling & Kile is probably the most significant non-pythiaceous pathogen of forest eucalypts in Australia. It has been isolated from declining forest eucalypts in Victoria (Kile, 1981a) and Tasmania (Podger et al, 1978), but

there have been no reports of any association with eucalypts in areas subject to rural dieback. Investigations of the association of *A. luteobubalina* and eucalypt dieback (Podger, et al, 1978; Kile 1981a) have shown that the fungus appears to act as a primary pathogen (Table 1.2.1). The fungus often becomes established in old stumps and appears to spread vegetatively from tree to tree via root contacts. Thus a distinct patch of dieback-affected trees and shrubs is often evident, with the more recently dead or dying trees towards the outer margin.

A. luteobubalina has been found in the Australian Capital Territory* which has a similar climate to that of the Northern Tablelands: it is not known whether this fungus occurs as far north as the Northern Tablelands. However, the distinctive pattern of dieback associated with *A. luteobubalina* would have clearly indicated its presence on the Northern Tablelands had it been responsible for more than a small proportion of the dieback occurring in the region.

Other *Armillaria* species seem to have a secondary role in some eucalypt dieback syndromes (Kile, 1980, also see Table 1.2.1). There is a deficiency of work aimed at investigating the possible involvement of major root pathogens such as *Armillaria* spp. in rural decline of eucalypts.

Little work has been done to assess the significance of other fungi reported as being associated with declining eucalypts in Australia. *Cylindrocladium scoparium* Morgan (Keirle, 1981) is chiefly a pathogen of seedlings, but infected roots have been

* Kile and Watling (1981).

noted on older trees. It has a wide host range. *C. scoparium* was identified as an agent causing mortality of establishing eucalypts in a planting trial on the Dorrigo Plateau (on the eastern margin of the Northern Tablelands) and it has been isolated from Walcha Forestry Commission Nursery. However, its distribution on the Northern Tablelands is unknown.

Evans et al (1967) found that *Cylindrocarpon destructans* [syn. *C. radicola* Wr.] produced a toxin, nectrolide, which suppressed the growth of *E. pilularis* seedlings. Jehne (1976a, 1976b) found an unidentified species of *Cylindrocarpon* associated with *E. obliqua* showing symptoms of regrowth dieback in southern Tasmania. This fungus only invaded the cortical tissue of the fine roots, but the steles of the roots were damaged by a toxin, probably related to nectrolide. Jehne (1976b) considered that root infection by *Cylindrocarpon* sp. was accentuated in drought stressed trees.

The incidence of wood decay in eucalypts showing symptoms of dieback was discussed in Section 2.3. Most organisms involved in rotting of live wood are weak, opportunistic pathogens which require some port of entry such as a wound to enable infection (Shigo, 1979). In most cases a mixture of organisms is involved. The massive loss of branches which occurs in declining eucalypts would be expected to increase the possibility of fungal woodrots entering the tree. Also, entry of organisms through the root system is possible where degeneration of the root system is associated with crown dieback. Termites and other wood feeders probably act as vectors for wood rot causing organisms.

6.2 Nematodes and Other Soil-Borne Animals

Plant parasitic nematodes are usually associated with root disease, but some species feed on aerial parts of the plant (Ruehle, 1973). Lesions caused by nematodes facilitate the entry of fungal pathogens and nematode transmission of viral disease has been widely reported. No attempts have been made to associate rural dieback with nematode activity, though nematodes parasitic towards eucalypts have been noted (Colbran, 1966; Meagher, 1968; Khair, 1978). Root damage induced by other soil-borne animal parasites may also facilitate the entry of root pathogens (Beute and Benson, 1979). There is a need to investigate the feeding habits and possible impact of root-feeding scarab larvae which are commonly noted in soil surrounding Tableland eucalypts.

6.3 Viruses

The possibility of viral involvement in the decline of rural eucalypts has not been investigated. The tendency of trees to recover in the absence of observable stressing agents, such as insects, and the slow development of disease makes investigation of this possibility difficult. Virus particles have been isolated from diseased *E. macroryncha* saplings in Queensland (Brzostowski and Grace, 1974). However, the diseased saplings all showed symptoms involving chlorosis and a mosaic pattern in the new foliage. These symptoms are unusual amongst Tableland eucalypts.

Gibson (1975) described several virus diseases found on eucalypts grown outside Australia. Symptoms of the various diseases included: chlorosis and stunting, a mosaic condition with necrosis and witches' brooming, reduction in the quantity and quality of essential oils, leaf distortion and discolouration (a tobacco mosaic virus), reduced leaf size, and crinkling. All the diseases were graft transmissible.

Podger et al (1980) reviewed studies on regrowth dieback in Tasmania, and reported that mechanical transmission tests onto tobacco (*Nicotiana glutinosa*) and electron microscopy of leaf extracts gave no evidence of viral infection of eucalypts showing symptoms of regrowth dieback. However, they cautioned that such tests would not indicate the presence of less discernible viruses that were not pathogenic to tobacco or required vectors for transmission.

6.4 Parasitic flowering plants

Severe mistletoe infestations probably contribute substantially to the decline of eucalypts in some areas of the Tablelands. However, there has been little work done to quantify the impact of mistletoes on trees. Jacobs (1955) noted that mistletoes suppress shoot development beyond the point of their attachment. He considered that this suppression of the host was hormonally mediated. Growth rates of trees are suppressed by mistletoe. Radial increment of *E. polyanthemos* was reduced by more than 50% when mistletoe occupied slightly less than 40% of

the crown (Nicholson, 1955). It is probable that mistletoes depress growth of the host by acting as a sink for mineral nutrients and water without exporting carbohydrates to the root like normal photosynthetic organs (Knutson, 1979). Since haustoria from mistletoes which feed on eucalypts only contain xylem connections the mistletoes are unlikely to directly draw on the host's carbohydrate reserves. Calder (1981) considered that while mistletoes are not directly responsible for tree mortality the burden imposed on the tree by heavy mistletoe infestation lowers the capacity of the tree to withstand other stress.

Mistletoes appear to have increased in prominence in areas where vegetation has been partially cleared. May (1941) has shown that germination rates of drooping mistletoe, *Amyema miquelii* [syn. *Lorathus miquelii*], increase from 44% to 91% when exposed to light. However, *Amyema pressii*, which has no light requirements for germination (Lamont and Perry, 1977), is also more abundant in road verges than in uncleared forest (Lamont and Southhall, 1982) and it is unlikely that light intensity is the critical factor effecting an increase of mistletoe density. It is possible that increases in the abundance of mistletoes in partly cleared land can be related to changes in the vertebrate fauna. Mistletoe seeds are dispersed by small animals and birds, particularly the mistletoe bird, *Dicaeum hirundinaceum*. Destruction of mistletoe by possums and koalas, and destruction of mistletoe seeds by king parrots (*Alisterus scapularis*), has been reported (May, 1941).

The native cherry (*Exocarpus cupressiformis*) is another parasitic plant of possible significance to eucalypts. While investigating a patchy occurrence of dieback within stands of *E. dives*, Jehne (1972) found a positive correlation between dieback and the presence of *E. cupressiformis*. No other soil or root factors appeared to be associated with the dieback. An examination revealed root connections between the *Exocarpus* and the dieback affected eucalypts.

E. cupressiformis is not common enough to account for more than a small fraction of eucalypt dieback on the Northern Tablelands. Further work is required to ascertain the conditions under which parasitism of *Exocarpus* causes trees to decline.

6.5 Other Effects of Microorganisms

Eucalypts, as well as many other plants, often develop symbiotic mycorrhizal associations with fungi. Bowen (1981) emphasised the beneficial effects of mycorrhizae in tree nutrition. They vastly increase the effective surface area of the roots and, in times of stress, when conditions are unfavourable for root growth but favourable for the growth of mycorrhizae they may serve as an alternative root system. There is also some evidence suggesting that mycorrhizae can act as storage organs for phosphates (Ashford et al., 1975). Mycorrhizae and other non-pathogenic microorganisms associated with roots may also form a barrier against invasion of roots by pathogens (Marx, 1973). Some trees, such as some *Pinus* spp.,

cannot be established successfully without their symbiont mycorrhizae (Marx, 1974). Pryor (1956) suggested that deprivation of mycorrhizal symbionts was also a probable explanation for failures of eucalypts from the subgenus *Monocalyptus* to establish in plantations outside Australia. Eucalypts from the subgenus *Symphyomyrtus* are apparently less dependent on mycorrhizae and consequently their establishment was less problematic. Thus, though the importance of mycorrhizae in the biology of eucalypts has not been fully assessed, many species of eucalypts are known to be capable of growth on sites where mycorrhizae are absent.

It is possible that the abundance of eucalypt mycorrhizae has been affected by edaphic changes and altered species compositions associated with pasture improvement. Efforts to quantify changes in the populations of mycorrhizae and to determine their likely impact on eucalypts need to be undertaken. However, drawing conclusions from such studies is likely to be difficult. While investigating sugar maple decline in North America Spitko et al. (1978) found that the incidence of root infection by vesicular-arbuscular mycorrhizae was inversely proportional to the severity of decline. However, it was not possible to ascertain whether the condition of the tree was impaired because the incidence of mycorrhizal infection was reduced or whether the incidence of mycorrhizal infection was determined by the condition of the tree or by some other factor correlated with tree vigour.

6.6 Allelopathy

The importance of chemical leachates from higher plants interfering with neighbouring plants has been widely discussed in recent years [e.g. Rice (1979), Newman (1978)]. This phenomenon is known as allelopathy. Eucalypts have been shown to chemically suppress growth of competing herbaceous plants (del Moral and Mueller, 1970), as well as suppressing growth of their own seedlings (Ashton, 1956). This suppression of seedling growth by mature trees is considered to be highly significant ecologically and removal of chemical inhibitors by fire or massive disturbance appears to be a crucial prerequisite for the establishment of seedlings in some ecosystems.

Recent work indicates that insect frass from *E. globulus* ssp. *bicostata* severely suppressed the growth of a number of pasture species whereas the influence of leaf leachates was insignificant (Trenbath and Fox, 1976; Trenbath and Silander, 1978). The authors suggested that transport in frass may allow growth inhibitors in leaves to reach the ground. Thus the capacity of trees to interfere with competing pasture plants may be linked with the level of insect grazing.

Allelopathic effects of herbaceous plants on trees have also been demonstrated, e.g. Walters and Gilmour (1976) found that water draining through pots containing fescue (*Festuca arundinacea* Shreb. var Ky 13) reduced the growth of sweetgum (*Liquidambar styraciflua* L.) by up to 60%. The allelopathic chemicals released by different species of plants vary and it is

possible that some exotic plants introduced into pastures or some native plants that have increased in abundance following pasture improvement have toxic effects on eucalypts.

6.7 A survey of *Phytophthora* spp. in the Northern Tablelands

Phytophthora spp. were isolated from soil samples using *E. sieberi* cotyledon baits using the method of Marks and Kassaby (1974) (Appendix B). In the initial phase of this project exploratory sampling was undertaken in scattered localities. However since the isolation techniques had not been perfected during these preliminary studies only a brief report of these results is included. Soil samples were systematically collected from all 14 sites where tagged eucalypts were monitored (samples were collected during May 1980, see Tables 4.1.1 to 4.1.3 for locations) and at "Kiparra". Hymexazol agar was used in to facilitate separation of *Phytophthora* spp. from *Pythium* spp. in sites 1 to 14. The isolations from "Kiparra" have already been discussed (Section 4.4).

The fungal isolates were classified as being either *Phytophthora* or *Pythium*. The *Phytophthora* spp. were sent to C.J. Shepherd for identification but identification of the *Pythium* spp. was not intensively pursued.

Results.

The presence of only one species of *Phytophthora*, *P. cryptogea* Peth. et. Laff. (Syn. *P. dechsleri* Tucker), was confirmed (identified by C.J. Shepherd). The sporangia of at least one other *Phytophthora* spp. were observed on a cotyledon (recovered from soil from the base of a *E. blakelyi* located 2 km south-east of Armidale, grid ref: 726 213, 6/9/79) but separation of the fungus from *P. cryptogea* which had colonized the same cotyledon was not successful. At least 5 species of *Pythium* were isolated. The identity of the most common *Pythium* was confirmed as *P. ultimum* Trow (by C.J. Shepherd) but the other species were not identified. *Phytophthora cryptogea* was only recovered from sites 3 and 11 out of the 14 sites. *P. cryptogea* was also recovered from some other localities including: just north of Glencoe (777 923), near Armidale (695 257, 726 213) and at "Kiparra". Since pythiaceous fungi are waterborne *P. cryptogea* is capable of being dispersed over significant areas of the Northern Tablelands from these sites via watercourses. The watercourses involved include Beardy Waters, Commissioners Waters and Cooney Creek where dieback, especially of *E. nova-anglica*, has been intense.

6.8 The role of *Phytophthora cryptogea*.

The role of *Pythium* and *Phytophthora* spp. other than *P. cinnamomi* in eucalypt diebacks has not been firmly established. Pratt and Heather (1973) maintained that pythiaceous fungi other than *P. cinnamomi* were often associated

with declining eucalypts, but offered no supportive evidence in the form of pathogenicity tests. Pathogenicity tests are usually carried out on potted seedlings so that growth conditions can be controlled and contamination of the surrounding can be prevented. Marks and Kassaby (1974a) showed that a number of species of *Pythium* and *Phytophthora cryptogea* caused some mortality of *E. sieberi* seedlings at the two leaf stage of plant growth, but did not cause mortality of older seedlings. In comparison, *P. cinnamomi* caused extensive root rotting and death of older seedlings. Further tests indicated that *P. cinnamomi* was substantially more pathogenic to *E. sieberi* seedlings than a range of other *Phytophthora* spp. including a number of isolates of *P. cryptogea* (Marks and Kassaby, 1976). In these tests, inoculation with *P. cryptogea* and *P. megasperma* Drechsler resulted in some mortality of three to four month-old seedlings, while other species of *Phytophthora* caused no mortality. On the other hand, Sedgely (1974) found that inoculation with some strains of *P. cryptogea* resulted in similar rates of mortality to inoculation with *P. cinnamomi*. Sedgely's tests involved a range of eucalypt species, but only very young seedlings of about 6 weeks old, were used.

The combination of waterlogging and the presence of *P. cryptogea* has frequently been associated with disorders of *Pinus radiata* in South Australia. In an attempt to discern the nature of this association, Bumberis (1976) found that *P. cryptogea* could cause feeder-root damage in *Pinus radiata* seedlings up to one year old and that this damage was intensified

by waterlogging.

P. cryptogea has also been associated with the decline of *E. viminalis* in the Dandenongs near Melbourne (Weste, 1975) and in Tallaganda State Forest on the Southern Tablelands of New South Wales (Shepherd, 1979). In both cases no other major pathogens were found. Weste (1975) inoculated six month old seedlings of *E. viminalis* with *P. cryptogea*. The soil was saturated each week, allowed to dry and then watered as required. No mortalities had resulted after four months. The average height of treated seedlings was less than that of the controls but this difference was not statistically significant. Weste concluded that *P. cryptogea* was unlikely to severely damage mature *E. viminalis* in the absence of other stressing agents.

While investigating the dieback of *E. viminalis* reported by Shepherd (1979) at Tallaganda, Halsal (1978) found that the Tallaganda soils were suppressive to *P. cinnamomi*, but able to support *P. cryptogea*. When *E. sieberi* seedlings were potted in the Tallaganda soil, inoculation with *P. cryptogea* resulted in a higher mortality of seedlings than inoculation with *P. cinnamomi* (64% mortality compared with 42%; 50 seedlings in each sample). The soil was described as a grey brown solodic soil with low total Nitrogen, organic Carbon and exchangeable Calcium, and slow drainage.

P. cryptogea can survive saprophytically in some soils for extended periods (Bumberis, 1978) and produces toxic metabolites. These toxins have been found to adversely affect tobacco

seedlings even when they are physically separated from the fungus (Csinos and Hendrix, 1977).

The studies cited indicate that *P. cryptogea* is a weak pathogen of eucalypts and likely to be a much more serious problem in younger seedlings than in mature trees. However, it is possible that this fungus, and perhaps related pythiaceus fungi, could be important as agents intensifying damage to trees associated with waterlogging or other stressing factors.

Experimental

Two pot trials were conducted to ascertain the pathogenicity of *P. cryptogea* to local eucalypt seedlings. In addition, the fungus was inoculated onto wounds on the stem of a *E. viminalis* sapling.

Methods

Experiment 1. Seedlings of three common eucalypt species, *E. caliginosa*, *E. nova-anglica* and *E. blakelyi*, were grown from locally collected seed. The potting mix consisted of sand, loam soil and peat in a ratio of 3:2:1. Cylindrical plastic pots (14.5 cm high and 8 cm in diameter) were used. Twelve vigorous 6 month old seedlings of each species were selected for the trial; allowing for 6 treatment plants and 6 controls of each species.

Prior to inoculation the height and number of leaves on each seedling were recorded and the seedlings were removed from the glasshouse to a controlled environment unit. Temperature in the unit fluctuated between 20 C and 27 C and a diurnal light regime with 12 hours light/ 12 hours dark was followed. The unit was illuminated by a mixture of incandescent and fluorescent lights; the flux density ranged from 0.35 to 0.5 x 1000 μEm^{-2} throughout the unit. The seedlings were placed in plastic trays approximately 10 cm deep and watered to excess with distilled water so that about 5 cm of water remained at the bottom of each tray.

After 2 days the trays were topped up and inoculated with a 5 day old culture of *P. cryptogea* grown on V8 agar. The success of the inoculation and freedom from contamination in the controls were tested by floating *E. sieberi* cotyledons in the trays.

The seedlings were watered to excess every 4-7 days and then allowed to dry out between waterings (Weste, 1975). The position of the trays was rotated to reduce variation related to position. After 3 weeks the trays were retested for the presence of *P. cryptogea*. Six weeks after inoculation the seedlings were removed from the controlled environment unit and examined. The height, number of live leaves and dry weight of each seedling were recorded. One seedling of each species was tested for the presence of *P. cryptogea*.

Experiment 2 This was basically a repeat of Experiment 1 but seedlings were grown in pots containing coarse river sand rather

than the potting mix and the plants were subjected to prolonged waterlogging in an attempt to induce mortality. Prior to planting the sand was steamed at 65 C for 4 hours. The seedlings were all 4 months old at the time of inoculation. No controlled environment unit was available during the period of investigation. As an alternative the seedlings were placed in a laboratory in a position sheltered from direct sunlight. Temperature extremes were recorded using a maximum-minimum thermometer; the temperature during the experiment was within the range of 16-25 C.

The seedlings were placed in 20 cm deep plastic trays and flooded with deionized rainwater to a depth of 15 cm. Inoculation was carried out following the same procedure as experiment 1. The trays were retested for *P. cryptogea* after 8 weeks. Heights of the seedlings were measured 14 weeks after inoculation. The trays were drained and the seedlings allowed to dry out. The time of death of each seedling was recorded.

Experiment 3. A potted sapling of *E. viminalis* approximately 1.5 m tall was purchased for the experiment about one month before the expected date of inoculation. Small portions of bark on the main stem were removed with a razor blade resulting in 6 wounds each about 2 sq.cm. A piece of a 4 day old culture of *P. cryptogea* grown on V8 agar, was placed on 3 of the wounds and sterile V8 agar placed on the other 3 wounds. The wounds were then bound with plastic tape and sealed with wax. The sapling was left in the glasshouse for 4 months before examination.

Results

Experiment 1. There was no mortality of any seedling. After 3 weeks *P. cryptogea* was present in all the inoculated trays and absent from all the control trays. However, after 6 weeks the attempts to isolate *P. cryptogea* directly from the roots of the seedlings failed.

The tips of some seedlings had died back while other seedlings continued to grow. There was some mortality of rootlets among the inoculated *E. caliginosa* seedlings, but no rootlet mortality amongst either treatments or controls for the other species. However, despite the rootlet mortality, the density of live rootlets in the *E. caliginosa* inoculants was still high. Table 6.8.1 shows changes in the height and leaf number of the seedlings. The height loss of the inoculated *E. nova-anglica* seedlings was significantly greater ($p < 0.05$) than the controls. Differences of height increment between treatments and controls of the other two species were not significant. The dry weights of treated and control plants were not significantly different.

Experiment 2. All seedlings survived the protracted waterlogging, however, height extension was minimal. *P. cryptogea* could not be recovered from any trays after 8 weeks. There was no significant difference in the rate at which inoculated plants died compared to controls (Table 6.8.2). In addition there was no significant linear relationship between

TABLE 6.8.1: Effects of inoculation with *Phytophthora cryptogea* on mean height increment and mean changes in leaf number in eucalypt seedlings

		<i>Eucalyptus caliginosa</i> [†]	<i>E. nova-anglica</i>	<i>E. blakelyi</i>
Mean change in height#	Treatment	10.0	-3.7*	3.5
	Control	6.3	-36.7	4.3
	LSD [‡]	7.7	31.5	22.4
Mean change of leaf number	Treatment	3.5	-1.9	1.7
	Control	0.8	5.8	0.3
	LSD	9.9	4.29	2.8

† Six replications of each treatment for each species.

Negative changes are due to shoot dieback.

‡ LSD = least significant difference (P < 0.05).

* Difference between treatment and control significant (P < 0.05).

TABLE 6.8.2: Effect of inoculation with *Phytophthora cryptogea* on survival of eucalypt seedlings without addition of water (see text for details)

		<i>Eucalyptus caliginosa</i>	<i>E. nova-anglica</i>	<i>E. blakelyi</i>
Mean period of survival (days) standard deviation	Treatment	18.3±7.1	21.5±3.5	13.6±2.2
	Control	16.8±5.0	20.3±4.3	16.2±3.1

138a

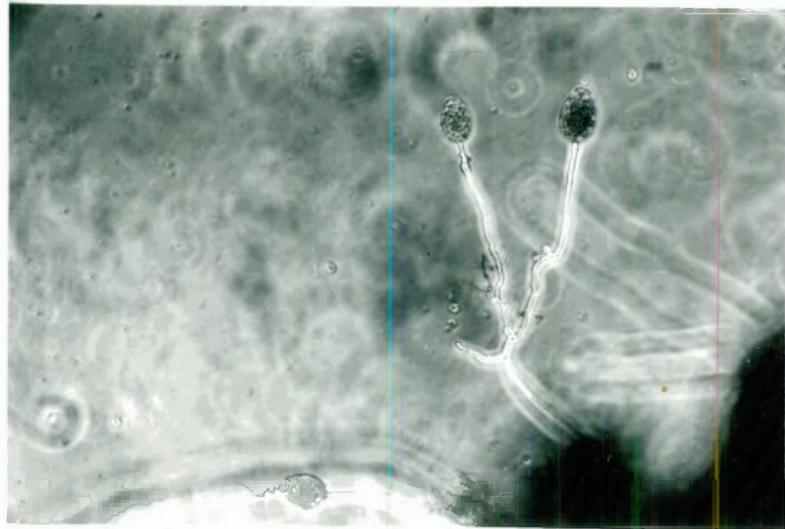


Fig 6.7.1 Sporangia from *Phytophthora cryptogea* on the surface of a eucalypt cotyledon.



Fig 6.8.1 Tip dieback of *Eucalyptus nova-anglica* after inoculation with *Phytophthora cryptogea* (Experiment 1).

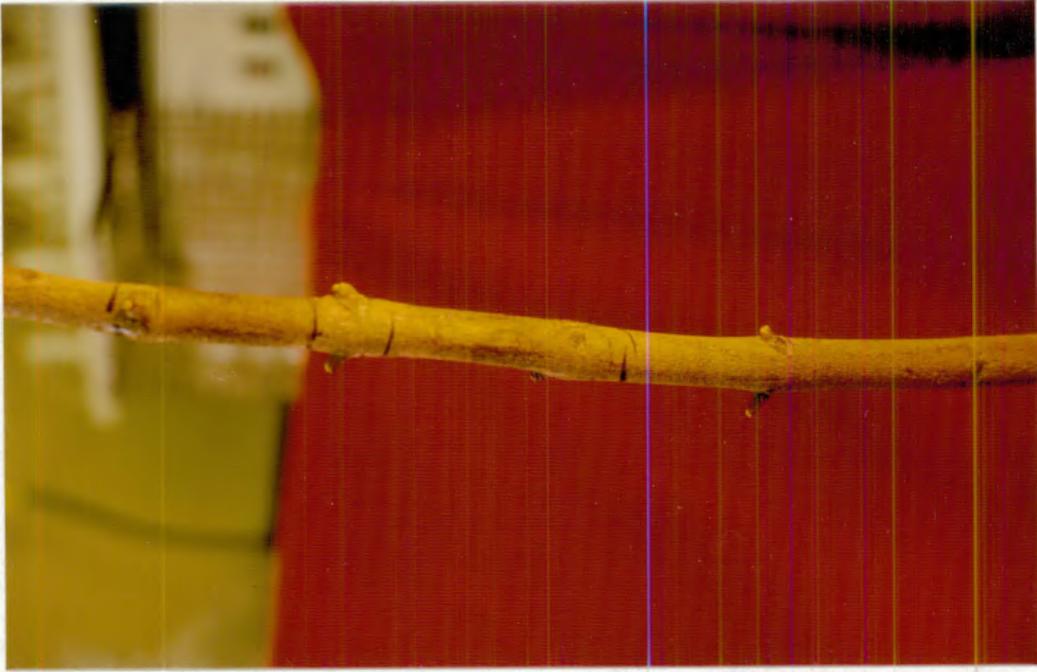
survival and seedling size, as defined by height ($R = 0.042$ at 35 degrees of freedom, i.e. all data pooled). The raw data is shown in see Appendix E.

Experiment 3 The sapling remained in a fair condition throughout the experiment. Some extending shoots wilted, but most of the crown stayed intact. *P. cryptogea* could not be isolated from the stem tissue after the 4 month period. However, all inoculated wounds formed cankerous swellings (Fig. 6.8.2) and were associated with discoloured wood, whereas two of the control wounds healed completely without the formation of an abnormal swelling while the third control wound developed a slight swelling. The largest swelling on an inoculated scar was about 4 mm deep covering an area as large as the original wound. The normal stem diameter at the point of wounding was 16.3 mm.

Discussion

In summary, inoculation with *Phytophthora cryptogea* did not result in any mortality of eucalypts in any of the experiments. However, the shoots of the inoculated *E. nova-anglica* seedlings died back to a greater extent than the shoots of the *E. nova-anglica* controls. *P. cryptogea* could no longer be recovered from any of the test pots or plants at the conclusion of any of the 3 experiments.

1399



B



A

Fig 6.8.2 The result of wound inoculations of a Eucalyptus viminialis stem with Phytophthora cryptogea: (a) treatment, (b) control inoculated with sterile agar.

The results of these experiments corroborate evidence from Weste (1975) and Marks and Kassaby (1976) that *P. cryptogea* is only a weak pathogen of older eucalypt seedlings. Nevertheless, *P. cryptogea* was able to induce mortality in very young seedlings (Sedgely, 1974). [Halsal (1978) did not specify the age of the *E. sieberi* seedlings used in her experiment, but presumably the seedlings were also very young.] The absence of any association between the presence of *P. cryptogea* and tree vigour at "Kiparra" and the general failure of the mature eucalypts to respond to fungicides in the absence of insecticides (Section 4.4) both accord with the hypothesis that, under most circumstances, *P. cryptogea* is not a strong pathogen of older eucalypts.

The damage caused by *Phytophthora* species is influenced by the composition of the soil (e.g. Halsal et al. 1983); stimulation and antagonism by other soil organisms also occur. The presence of peat in the potting mix in Experiment 1 probably increased the likelihood of fungal damage (Sivasithamparam, 1981). However, chemical or microbial inhibitors which reduce the activity of *P. cryptogea* may have been present in both potting mixes used in the experiments. Hence, the results of both experiments should be treated with some caution, especially since the fungus could not be recovered at the conclusion of either pot trial. Nevertheless, poor recovery rates of *Phytophthora* spp. have been reported by other workers carrying out similar pot trials even though test seedlings were severely damaged by the fungi (e.g. Podger and Batini, 1974).

The reaction of the *E. viminalis* to wound inoculation with *P. cryptogea* was typical of the hyposensitive response of a resistant host: colonization by the fungus was prevented and the formation of callus scar tissue was induced.

Other circumstantial evidence suggesting *P. cryptogea* is not important in the dieback syndrome includes: (1) the absence of symptoms of fungal damage in understorey shrubs that are susceptible to *Phytophthora* root rots (see Section 3.5; Old, 1979); and (2) lack of a consistent association between dieback and soil parent materials and drainage conditions, etc. [see Sections 3.4, 3.6 cf. *Phytophthora* root rot (Old, 1979)].

However, during the first phase of dieback (see Section 3.4) the reports indicated that the areas most severely affected by dieback were on broad valleys and plains subject to impeded drainage. These are the areas where waterborne fungi are likely to cause the most damage and are often devoid of non-eucalypt native shrubs (Section 3.2) that would indicate the presence of fungal root rots. In addition *Pinus radiata*, which is susceptible to *P. cryptogea* (Section 6.8), also showed some signs of premature decline in some of these areas (Section 3.5). So the possibility of involvement of *P. cryptogea*, or a similar fungus, in eucalypt decline cannot be totally dismissed.

6.9 Conclusion

In conclusion, there is no evidence that a single primary pathogen is responsible for rural tree decline on the Northern Tablelands. However the literature survey has uncovered many deficiencies in the present state of knowledge concerning eucalypt pathology, particularly with respect to woodland eucalypts. Thus there is still a remote possibility that a serious eucalypt pathogen remains undiscovered.

P. cryptogea was the only species of *Phytophthora* found during the survey. Pathogenicity tests have supported the published evidence that indicates that *P. cryptogea* is a weak pathogen of eucalypts, but capable of causing some damage to eucalypt seedlings.

Declining eucalypts are affected by a number of pathogenic problems including: mistletoes, wood rotting fungi, and possibly allelopathic interference and *P. cryptogea*. Such disorders reduce the capacity of trees to recover from defoliation or other injuries. Hence measures designed to minimize the effects of these disorders would assist the recovery of trees.

CHAPTER 7 WEATHER INDUCED DAMAGE

This chapter discusses the importance of physical damage of eucalypts on the Northern Tablelands induced by extremes of weather, other than drought or deluge (see Chapter 8). Damage from agencies such as frost, wind and hail is usually localized but can influence the proportions of moribund trees in areas affected. The effects of frost and wind have undoubtedly been accentuated by changes to the microclimate resulting from clearing.

7.1 Frost

Most eucalypt species are only moderately resistant to frosts. Levitt (1980) has discussed the physiology of frost damage in plants.

Severe frosts are common on the Tablelands especially in higher areas such as Guyra, where 14% of July minimum temperatures are below -4.4°C (Bureau of Meteorology, 1975). The severity of frosts is usually much greater on valley floors due to cold air drainage. Thompson (1970, 1973) studied the mesoclimatology of the Armidale district including topographic variations in minimum temperatures. He observed that over a period of one year (1967-68) the daily minimum screen air temperature on the floodplain averaged 1.7 degrees C less than that of a nearby hillcrest 93 m higher. These temperature inversions reached their greatest values in the late autumn, winter and early spring when the long nights

aided maximum long wave radiation loss and cold air drainage. In these months the extreme inversions ranged from 6.1 to 9.4 degrees C; they coincided with the most severe frost development and were associated with periods of anticyclonic stability.

Minimum temperatures close to the ground also tend to be several degrees colder than screen air temperatures; thus stress on seedlings is much greater than stress on trees. It is not known whether eucalypt roots, close to the soil surface are directly damaged by frost, but low soil temperatures definitely depress the rates of water absorption by plant roots, though the influence varies between species (Kramer, 1969).

Harwood (1976), in a study of the inverted treelines in snowgum communities in the Snowy Mountains, found that the shelter afforded by mature trees was critical in the protection of seedlings from severe frosts. Expansion of woodland could only occur as a distinct front from existing woodland. Seedlings sometimes became established in the open but seldom grew higher than the surrounding tussock grasses. It seems likely that frost would also be an important mortality factor in seedling regrowth dynamics in cleared areas on the colder sites of the Northern Tablelands. In timberline areas of the Snowy Mountains severe shoot dieback of mature trees has also been attributed to the direct effects of frosts on shoots (Slatyer, 1976).

Frost hardening is the critical process which affords protection against frosts. Unseasonal frosts tend to be more damaging than frosts in winter. Frost affects new growth more than old growth; the Ministerial Working Group (1979) reported that severe frost damage occurred where late season growth flushes had been stimulated by insect attack. Some moribund trees monitored in the present study (see Section 4.3) were also severely damaged by frosts in 1982, while frost damage of seedlings on the same sites was much more extensive. There is also an interaction between the hardening process and the nutritional status of the tree. Grose (1960) found that use of phosphate or nitrogen fertilizer significantly reduced the frost hardiness of *Eucalyptus delegatensis*.

The frost records for Armidale between September 1965 and August 1983 are summarized in Table 7.1.1. Minimum winter temperatures recorded during the late 1970s are noticeably warmer than minimum winter temperatures in the late 1960s and early 1970s. Between 1966 and 1972 there are 9 months with minimum temperatures of less than -7.0 C, but no records of temperatures as low since. Below zero temperatures were recorded in April in only 6 out of the 18 years. Notably 1978 and 1982 were the only years in which a below -2.0 C temperature was recorded during the first April frost; the lowest minimum temperature for May recorded during the period was also in 1982. The data suggest that 1982 was an exceptional year in terms of early frosts and that the 1980 and 1981 seasons, when only minor frost damage to the tagged

TABLE 7.1.1: Minimum screen temperatures ($^{\circ}\text{C}$) for each month between September 1965 and August 1983 at the Armidale Radio Station (2AD) meteorological station

Year	M o n t h											
	J	F	M	A	M	J	J	A	S	O	N	D
1965									-0.4 (?)	0.0 (?)	0.2	2.2
1966	7.8	6.1	2.2	3.4	-4.1 (15)	-6.4 (17)	-8.2 (20)	-5.9 (16)	-1.4 (5)	-0.3 (5)	1.1	7.2
1967	10.0	9.4	0.5	0.8	-5.6 (8)	-3.4 (4)	-5.0 (24)	-6.1 (11)	-9.7 (15)	3.9	-0.1 (1)	5.0
1968	9.1	5.8	5.0	0.0 (1)	-2.8 (5)	-7.0 (15)	-8.1 (23)	-4.7 (15)	-3.6 (8)	-1.4 (4)	2.5	4.4
1969	8.9	8.8	7.2	1.5	-1.1 (1)	-4.5 (9)	-4.7 (17)	-3.4 (8)	-4.4 (19)	1.4	3.8	4.7
1970	7.8	10.0	2.2	-2.2 (3)	-9.5 (14)	-7.5 (14)	-9.3 (25)	-6.4 (17)	-5.6 (9)	0.5	2.7	8.2
1971	7.5	11.4	5.6	-0.3 (1)	-3.1 (11)	-7.5 (14)	-9.2 (20)	-7.2 (17)	-2.7 (4)	-0.6 (2)	0.3	5.5
1972	4.4	4.9	5.3	-3.0 (4)	-3.5 (5)	-4.7 (13)	-7.3 (23)	-5.3 (12)	-6.0 (12)	-2.0 (2)	2.9	6.0
1973	9.6	9.9	4.0	3.5	-3.0 (7)	04.5 (8)	-3.0 (3)	-3.0 (9)	-1.0 (1)	4.0	5.8	8.3
1974	10.3	8.0	7.1	5.0	0.0 (1)	-6.0 (13)	-5.3 (14)	-5.7 (11)	-2.0 (10)	1.0	0.8	3.8
1975	6.5	9.5	4.5	0.0 (1)	-4.3 (12)	-3.5 (11)	-4.8 (17)	-3.1 (8)	-1.0 (3)	0.0 (1)	4.4	8.8
1976	7.1	10.4	7.0	-0.8 (2)	-2.7 (6)	-4.4 (12)	-4.5 (11)	-3.4 (13)	-2.2 (12)	0.0 (1)	2.6	6.2
1977	7.8	11.0	7.3	3.0	-2.0 (3)	-4.2 (6)	-6.0 (17)	-5.0 (17)	-1.7 (4)	1.1	4.6	5.6
1978	12.1	9.4	6.7	-2.1 (4)	-2.3 (3)	-3.0 (4)	-6.4 (13)	-5.1 (15)	-2.2 (4)	0.7	3.4	6.0
1979	11.0	10.5	4.9	4.7	-0.9 (3)	-3.0 (8)	-5.0 (17)	-5.5 (14)	-3.1 (4)	-1.7 (1)	5.1	8.0
1980	9.1	8.1	4.8	2.9	-2.0 (3)	-3.0 (8)	-5.2 (16)	-4.9 (14)	-1.4 (5)	3.9	4.0	6.1
1981	9.8	9.4	4.3	2.5	-2.8 (3)	-1.6 (8)	-3.9 (11)	-3.7 (9)	-1.9 (5)	0.5	1.3	9.0
1982	11.3	10.5	5.4	-2.2 (1)	-5.7 (16)	-6.6 (15)	-6.0 (26)	-5.9 (17)	-3.6 (4)	-2.1 (3)	3.1	6.3
1983	7.8	8.1	6.1	1.6	0.2	-4.6 (8)	-3.9 (8)	-3.6				

The numbers in brackets show the number of days in each month with temperature recordings of 0°C or less.

trees was noted, were more typical. Thus it is likely that the Ministerial Working Group (1979) overstated the role of frost in the syndrome.

Some late frosts were also recorded, with one below zero temperature in November 1967 and some relatively severe October frosts in 1968, 1972, 1979 and 1982. These frosts could have damaged some of the new shoot growth beginning to develop on trees.

7.2 Wind

The severity of windstorms depends on the local relief, and thus wind is only a problem of localized importance. However, the places most exposed to wind include the broad plains where dieback is most severe. Several authors have associated various tree declines with chronic wind stress exacerbating other problems (White, 1974; Papp, et al, 1979) and there is clearly a need to quantify the effects of wind on trees.

The strongest winds near Armidale are westerlies blowing during winter and spring; easterly winds prevalent during summer are gentler (King, 1980). Thus a relationship between tree mortality and aspect could be expected where wind was an important determinant of mortality.

Damage as a result of wind may involve: uprooting of the tree; snapping of the trunk; branch loss; or shoot pruning (Daubenmire, 1974). Destruction of naked buds due to branches knocking against each other also occurs in eucalypts and chronic wind damage often results in tip dieback of the upper branches (Jacobs, 1955). There is often a higher proportion of dead twigs on the windward side of eucalypts growing in exposed positions. Shaking also reduces the growth of plants (Ashby et al, 1979). Allocation of reserves into secondary thickening is increased as a result of wind (Wilson, 1975) and less reserves are available for other purposes. Depression of temperature by wind will often result in substantially reduced productivity during winter (Grace, 1977). The degree to which wind increases transpiration depends on the effectiveness of stomatal control, which appears to vary markedly between closely related species (Grace, 1977). At present there is no detailed information available concerning the effect of wind on the stomatal physiology of woodland eucalypts.

7.3 Hail

Trees near Armidale were severely damaged by a hailstorm in 1975. Leaves and twigs were stripped and trees showed little sign of recovery in the following years. A large proportion of the affected trees are now dead (R.L. Davidson, pers. comm.). Though this type of damage is localized it can greatly influence the pattern of dieback within the affected area and there is little available information concerning the

incidence and severity of such events.

7.4 Snow

Costin (1954) reported that unusually heavy snowfalls occasionally occurred on the tablelands in the Monaro region. These snowfalls cause widespread mechanical damage to forest and woodland communities. Snowfalls heavy enough to damage significant numbers of trees are rare on the Northern Tablelands but Norton (1886) reported one instance of this type of tree damage.

8.0 Direct Influences of Grazing Management on Trees

This chapter is concerned with the direct deleterious influences of pasture management on rural trees. More subtle influences affecting the soil water balance and nutritional status of trees are discussed in chapters 9 and 10.

8.1 Damage by stock

Livestock directly damage seedling eucalypts by browsing and sometimes also girdle mature trees. The paucity of eucalypt seedling regrowth in grazed paddocks in comparison with adjacent roadside reserves appears to be a direct consequence of damage to seedlings by stock. The intensity of such damage has increased following pasture improvement. Preference for eucalypts appears to be partly dependent on the availability of alternative sources of roughage (R.L. Clark, pers. comm.); available roughage is often significantly reduced in improved pastures. Sheep appear to graze on seedling eucalypts more intensively than cattle, however, where feed is in limited supply, cattle will also browse on eucalypt seedlings.

Cattle will browse on some native shrubs such as *Jacksonia scoparia* and *Acacia filicifolia* even at low stocking intensities (personal observation). Browsing

damage is often sufficiently severe to completely exclude these plants from grazed areas. Eades (1980) found that the diversity of native plant species was markedly richer in travelling stock routes than in adjacent paddocks, even when pastures were unimproved. Grazing pressure was probably the major factor involved in the selective removal of plant species within paddocks.

The intensity of damage to regeneration caused by livestock makes it necessary for stock to be excluded, or at least kept at a low stocking rate, while regrowth is becoming established. Bryant (1969, 1971) found that the density of snowgum (*E. pauciflora*) seedlings in alpine woodland increased when stock were excluded. When sheep were re-introduced, growth of seedlings of less than one metre in height was suppressed and their survival rate was reduced. Seedlings more than one metre tall were unaffected. Knowles and Tahau (1979) successfully used a repellent containing egg and red dye to protect radiata pine seedlings from sheep-damage. Control was only temporary, but could enable sites to be intensively grazed for a short period. However, it is doubtful whether such measures would be economical (G.W. Anderson, pers. comm.). Further research into the level of protection against browsing necessary to enable seedlings to regenerate in rural woodlands is clearly required.

Both cattle and horses often strip bark off mature trees. This behaviour is probably accentuated by a deficiency of available roughage. Both animals also damage trees by rubbing their bodies against the trunks. Stringybarks are the trees most easily girdled by livestock (see Fig. 8.1.1) though girdling of other eucalypts with fibrous bark, such as *E. nova-anglica*, was also noted in the survey. Girdling of trees has been especially severe during the recent drought, apparently because of the reduced availability of feed. In some areas girdling of stringybarks by stock appeared to be the most important determinant of stringybark mortality.

Prevention of tree girdling can only be effected by careful management. However, feeding on bark appears to be a learned response (Clark et al., 1979). This suggests that remedial action may have to involve direct protection of trees. Table 8.1.1 shows the proportion of stringybarks severely girdled by cattle in a woodlot east of Wollomombi after several months of severe drought. The site was not revisited, but all the trees classed as completely girdled and at least some of the trees that were girdled more than 50% are expected to have died.

8.2 Clearing Practices

1519



Fig 8.1.1 Girdling of stringybarks (Eucalyptus caliginosa) caused by cattle. Note that the boxes (E. conica) are scarcely damaged.

Four methods of destroying trees to create space for agriculture have been commonly used on the Northern Tablelands: removal of the entire tree, felling, ringbarking, or poison-axing. Only removal of the entire tree assures complete destruction. In most areas where clearing by felling, ringbarking or poison-axing has been carried out a small proportion of standing trees have survived the attempted destruction: consequently their condition has suffered. Eucalypts that have been felled without removal of the stump often coppice profusely. In some areas, a large proportion of trees appear to be of coppice origin. Trees of coppice origin frequently have multiple trunks. Where a single trunk has assumed dominance, the new wood eventually encircles the original stump completely, however, trees formed by coppicing can usually still be distinguished by deformities of the lower trunk. In European trees, shoots of coppice origin have a

Table 8.1.1 Severity of girdling of *Eucalyptus caliginosa* by cattle in a woodlot on Wallamumbi Station (15/10/83; Grid ref: 9337-140 270).

	No. of trees	% of total
Little damage	6	9
Noticable damage	24	36
Severe damage	10	15
More than 50% girdled	16	24
Completely girdled	10	15
Total	66	99

152a



Fig 8.2.1 Poison axed trees on the Parlour Mountains, west of Guyra (13.6.82). The tree in the foreground is *Eucalyptus bancroftii*.

greatly reduced life expectancy compared with trees of seedling origin (Jacobs, 1955). Premature ageing of coppice has been attributed to reduction of the ratio of active roots per leaf (Kazaryan et al., 1974). Little data concerning the relative life expectancy of eucalypt coppice is available but a similar trend is possible.

Coppice growth utilizes the main roots of the original tree. Thus trees with old senescing roots produce poor coppice. Also, compartmentalization of wood decay spreading from the cut surface of the stump is less of a problem when the cross-sectional area of the stem is small.

Eucalypt roots growing in close proximity sometimes form natural grafts. Kozlowski (1971) noted a case where a stump was sustained by a neighbouring tree for several years following felling was noted. When the neighbouring tree blew over in a storm the stump sprouted. Root pathogens can spread from stumps to adjacent trees, or between trees, through graft unions (see Section 6.1). Eucalypts which have recovered from incomplete ringbarking are relatively common in many parts of the Tablelands. The massive injury, impeded phloem transport and subsequent entry of woodrot organisms probably has severely reduced the life-expectancy and vitality of these trees.

In recent years, most trees which have been cleared have been poison-axed. This technique (Truman, 196) usually involves cutting a fringe around the tree and

applying a herbicide, usually 2,4-D or 2,4,5-T. Death usually results within one year, but sometimes treatment is ineffective and only severe loss of vigour is achieved. In some trees, such as elms, translocation of herbicides from trees which have been poison-axed to adjacent trees through root unions has caused extensive mortality. Such translocation also occurs in dense eucalypt regrowth treated with 2,4,5,-T (Henry, 1958).

8.3 Damage From Tillage and Earthmoving

Often the major roots of eucalypts spread horizontally just below the surface of the soil. This is especially true on skeletal soils or where vertical drainage is impeded by a hardpan below the surface. The degree to which root depth is influenced by the soil environment varies between species and particular species are predisposed to the formation of either deep or shallow root systems (Ashton, 1956). On the Northern Tablelands *E. nova-anglica* appears to be predisposed to the formation of shallow roots (see Fig 2.3.1). Cultivation can severely injure roots and resultant wounds facilitate the entry of woodrotting fungi and root pathogens (see Section 6.1). However, there was no strong association between cultivation and dieback at "Kiparra" (see Section 3.6), and there was no other direct evidence available to confirm the importance of cultivation as a cause of injury to eucalypts on the Tablelands.

Changed drainage conditions resulting from embankments, ditches, roadworks, etc. often lead to localized mortality of trees through excess or deficiency of water. Extra soil heaped about trees can lead to anaerobis which severely damages roots; if heaped soil reached the bole of the tree, collar rot often results (Hadlington and Johnston, 1977). Trees apparently damaged by earthmoving were commonly noted adjacent to roadways during the survey. This type of damage was not confined to eucalypts, e.g. European elms were also affected (Armidale, grid reference: 9236 698 255). In addition the death of at least two tagged trees monitored during the project was associated with roots being exposed by gully erosion (see Section 4.3).

8.4 Direct damage to trees from biocides

Herbicides are frequently used for control of blackberries and other weeds, especially on crown land. A diluted solution of 2,4,5-T is commonly used. Severe damage to eucalypt seedlings and other native shrubs growing nearby often occurs due to spray drift. Damage has also been noted in mature trees (see Section 4.3).

Damage to trees often also results from application of systemic insecticides at greater than recommended rates (see Section 4.5). Application of biocides to elms via holes bored into the trunk was found to be associated with the entry of wood decay organisms (Shigo and Campana, 1977).



Fig 8.4.1a Herbicide damage to a *Eucalyptus nova-anglica* sapling (Chandler River, 27.3.81).



Fig 8.4.1b The same sapling one year later (24.3.82).

The drilling of holes in trunks when the availability of water is critical often leads to the development of severe cracks in the trunk. Anti-helminthic drugs, from the faeces of drenched livestock, are often deposited under trees. The accumulation of toxins from these drenches is associated with a build-up of soil organic matter about trees probably as the result of the death of soil decomposers (Southcott, 1980).

8.4 Fire

Little is known about the fire history of the Northern Tablelands in pre-European times. However, the available evidence suggests that Aborigines frequently set fire to extensive areas (see Section 3.3). Suppression of regrowth was probably a reason behind graziers adopting the practice of burning-off paddocks each year in early spring. Burning-off is still practised in some of the unimproved grazing areas, especially in the acid swamps and snowgrass woodlands in eastern parts of the Tablelands. Also, fuel reduction burns are used on roadside reserves, in areas managed for forestry and in other areas where fire could become a problem. Localized bushfires may also occur. Apart from these instances, fire has been almost completely absent from the Tablelands during the last 30 years.

Fire will seriously damage young saplings, though the degree of damage depends on the intensity of the fire as well as the size and species of the sapling (Gill, 1975). Several studies (Cremer, 1969; Bryant, 1971; Leigh and Holgate, 1979) indicate that fire, followed by grazing, is a highly destructive combination causing a high rate of mortality to regenerating eucalypts. Even though burning off has been largely discontinued in recent times, where it is carried out there is usually little consideration given to minimizing the impact of fire on regeneration.

Overmature trees are also severely affected by fire. Fire results in scarring of the trunk which enables penetration of wood rotting organisms. Decaying wood increases the flamability of the trunk leading to further scarring during subsequent fires. Eventually, hollowing of the tree allows the creation of a chimney effect which further increases the proneness of the tree to fire damage (Gill, 1974, 1975). Damage resulting from past fires is considered a major determinant of the mortality of ageing trees in rural areas of Victoria (Kile et al., 1980).

Though frequent fires exert severe stress on establishing and overmature trees, fire is also an agent which allows rejuvenation of ageing communities. Fire instigates complex changes which include: i) removal of existing vegetation and litter to provide space for regeneration; ii) destruction of seed destroying ants (Ashton, 1979); iii) changes to the soil micro-flora

(Renbuss et al, 1972); iv) destruction of allelopathic inhibitors which affect seedling growth; and v) rapid replenishment of nutrients to the soil (Raison, 1979). The removal of ground cover following fire may also result in greater temperature fluctuations in the soil - thus killing scarab larvae (Davidson et al., 1979) and affecting other components of the soil biota. Growth of eucalypts is stimulated markedly following fires and fire is commonly used in the establishment of a number of species (Cremer et al., 1978).

CHAPTER 9 THE ROLE OF WATER

The supply of water is a critical factor affecting both the condition and productivity of eucalypts and the abundance and condition of the other organisms that interact with the eucalypts. The direct affects of water deficits on trees have been well documented (e.g. Kozlowski, 1981). Excess water that restricts the movement of gases, such as oxygen and carbon dioxide, between the atmosphere and the soil may also damage trees where drainage is impeded.

Prolonged wet spells are especially damaging to trees in the warmer seasons when root metabolism and the activity of soil micro-organisms - and the oxygen demand of both - are greatly increased (Drew and Lynch, 1980). Some foliage feeding insects are also favoured by wet conditions (see Chapter 13).

The last leaves on dying eucalypts severely affected by rural dieback usually wilt while they are still intact on the tree (see Section 2.2). This suggests that water stress is likely to be a critical factor in the etiology of the syndrome.

There are three plausible ways in which the water balance of rural eucalypts subject to dieback could have been deleteriously altered: 1) changed patterns of precipitation (i.e. abnormal seasonal conditions or climatic change); 2) changed precipitation disposal patterns (associated with agricultural development); and 3) disfunctions of water uptake and transport in trees. This chapter is a discussion of how these changes might have affected the hydrology of eucalypt woodlands and the

water relations of the trees.

9.1 The water balance of woodland eucalypts

Trees have certain advantages over herbaceous strata in the maintenance of their water balance. Trees have a greater capacity to store water. The few available estimates of tissue capacitance in hardwoods suggest that hardwoods are generally able to store more than 24 hours supply of water within their systems, while the storage capacity of conifers is much greater (Hinckley et al, 1978; Chaney, 1981). Also trees usually develop two discrete root systems, a system of surface roots, which enables the tree to rapidly take advantage of surface water after rain, and deep roots which supply the tree during dry spells (Jacobs, 1955). In contrast the root systems of herbaceous plants usually do not have roots that penetrate as deeply (Rutter, 1968). However, grass roots tend to dominate the surface layers of the soil and the depth of tree surface roots appears to be greater where grass swards are dense, especially towards the edge of the drip zone of the tree (del Moral and Muller, 1970). Thus, in simplistic terms, conditions involving frequent periods of rainfall would be more likely to favour herbs, while periods without precipitation when much of the soil profile reaches wilting point will usually put greater stress on herbs than on woody plants (e.g. see Walker, 1981).

There is a paucity of information specifically concerned with the water balance of woodland eucalypts. In a study involving *E. blakelyi* from a number of sites near Canberra in 1975, when climatic conditions were fairly average for the region, Journet (1979) found that stem water potential never went below -1.8 MPa. Even during the driest parts of the year dawn stem water potentials ranged between -0.2 and -0.3 MPa, indicating complete replenishment of water. The usual maximum stem water potential was about -0.9 to -1.1 MPa. *E. blakelyi* appeared to have an effective regulation system which prevented stem water potentials from going below -1.8 MPa. Pock et al. (1966) showed that some eucalypts could tolerate a relative moisture content $[(\text{fresh wt} - \text{dry wt}) / (\text{turgid wt} - \text{dry wt})]$ as low as 40%. Ladiges (1974) found population differences in the amount of desiccation that seedlings of *E. viminalis* originating from different provenances could tolerate: the tolerance of leaves to desiccation appeared to be related to the amount of water bound in the cell walls; this water could act as a buffer preventing rapid desiccation of the protoplasm. Interspecific differences in desiccation tolerance have also been found (Clayton-Greene, 1983).

9.2 Examination of rainfall patterns

In recent years, the concept of climatic instability is becoming widely accepted; a marked climatic drift over extended periods is the rule rather than the exception (Kelly, 1979).

Cornish (1977) noted a significant increase in annual and summer rainfall in central New South Wales since 1946. Records from the north of the state also showed a similar trend though differences were not so marked. Fig. 9.1.1 shows changes in mean summer rainfall recorded in Armidale.

Meteorological records have been kept for only a little over one hundred years in the Northern Tablelands; we have limited information on the climatic conditions during the first 55 years of European settlement (i.e. 1830 to 1880) and even less on long-term climatic changes. As changes in the composition of vegetation commonly lag behind climatic changes it is possible that the naturally occurring trees are not the most suitable species for all of the sites on which they occur.

Seasonal rainfall trends for the region are masked by local variations because a large proportion of the total rainfall results from local storms. However, the occurrence of both prolonged wet periods and prolonged dry spells is a notable feature of the rainfall patterns in the Armidale region over recent decades. Fig. 9.1.2 illustrates the changes in rainfall in the period from the beginning of 1941. Monthly rainfall readings were computed as three-monthly running means to smooth short-term fluctuations in rainfall: monthly rainfall totals are shown as the mean of the rainfall that fell in a particular month and in each of the two preceding months. A running mean of the average potential evapotranspiration for the equivalent periods (Smith and Stephens, 1976) is provided for comparison. Actual evapotranspiration becomes markedly less than potential

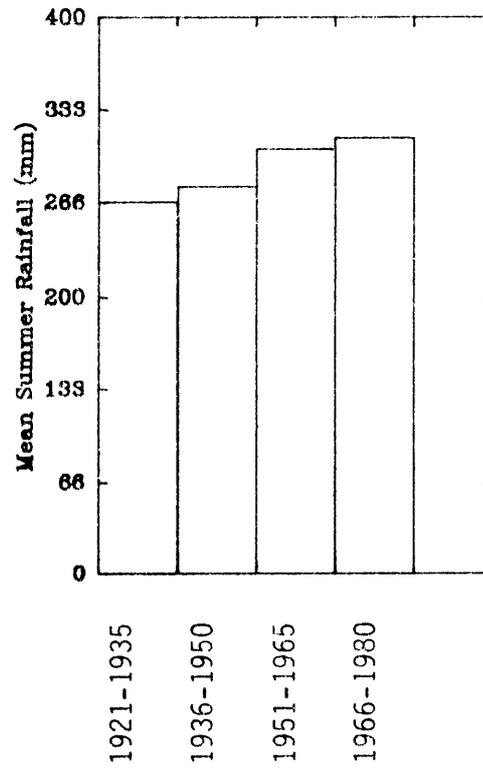
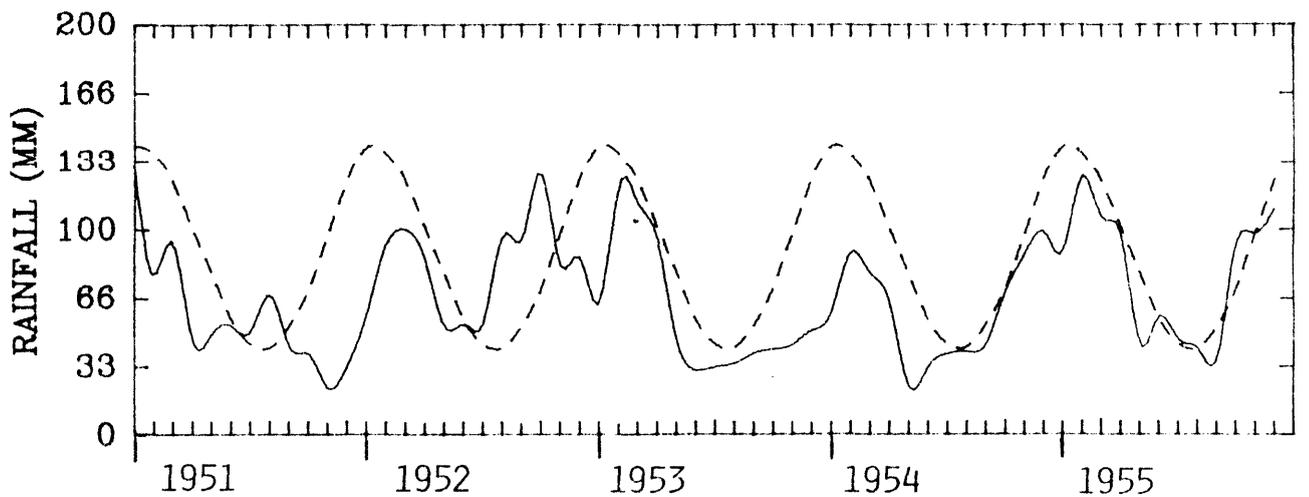
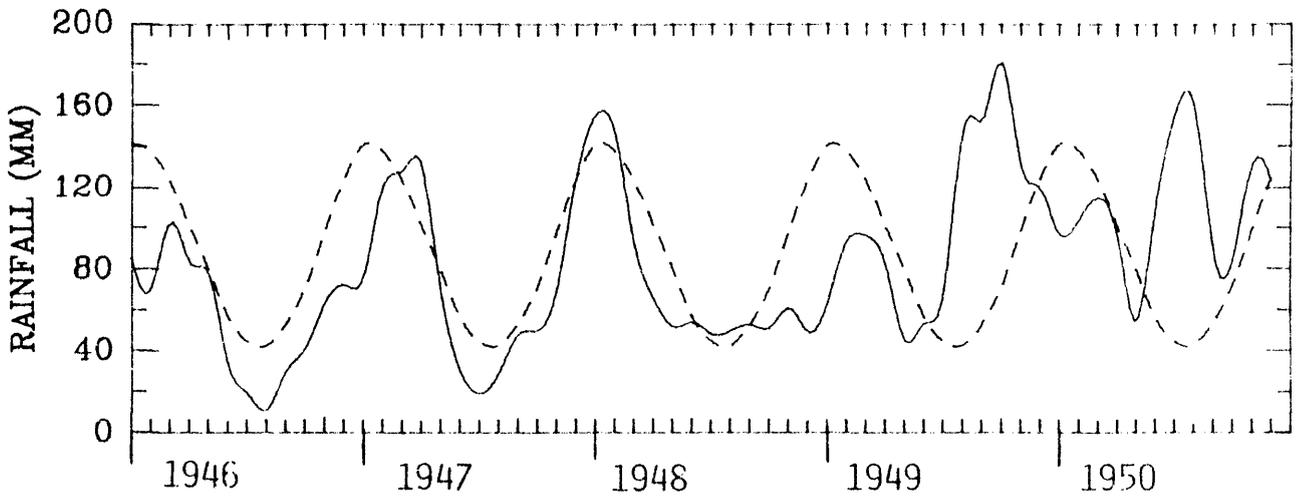
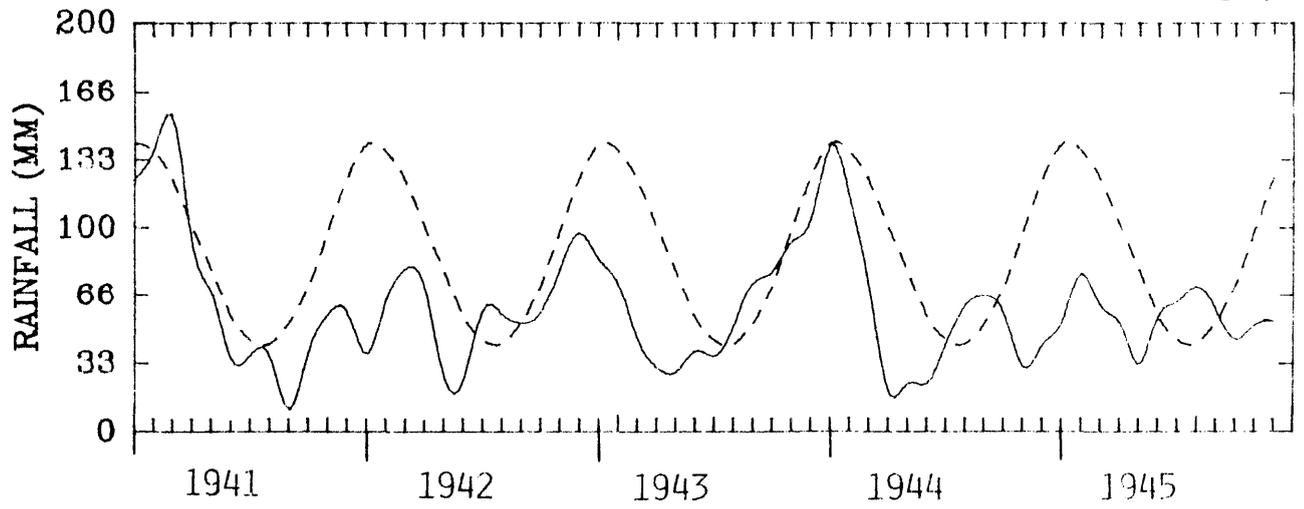


Figure 9.2.1 Changes in mean summer (December-February) rainfall at Armidale in 15 year periods from 1921 to 1980.



9.2.2 Armidale rainfall from 1941 to 1983, taken as a 3 month running-mean and compared with a 3 month-running mean of the average potential evapotranspiration. (see text for details). The solid line indicates rainfall; the dashed line indicates potential evapotranspiration.

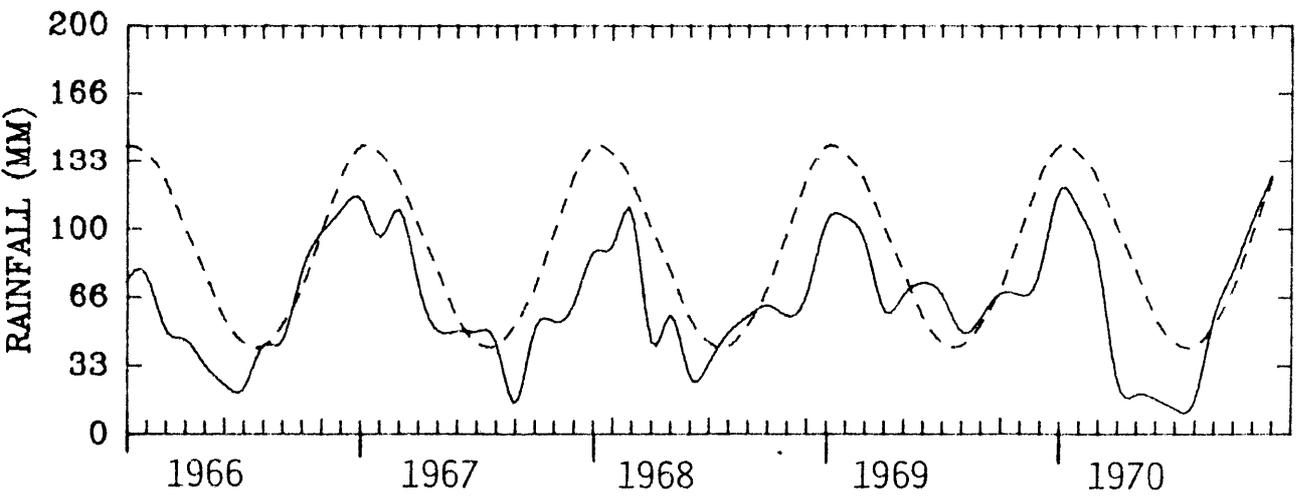
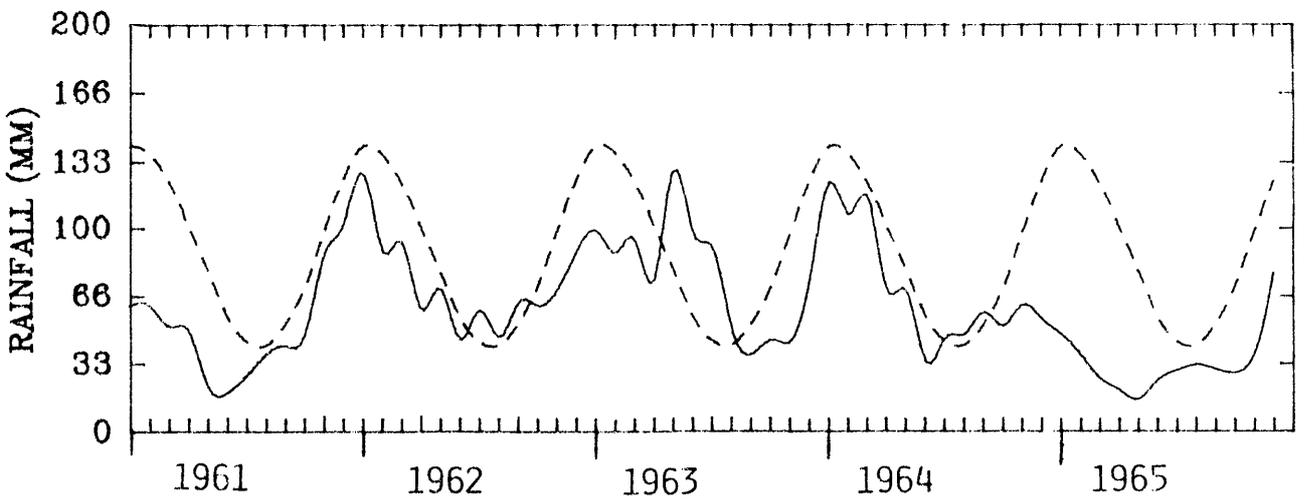
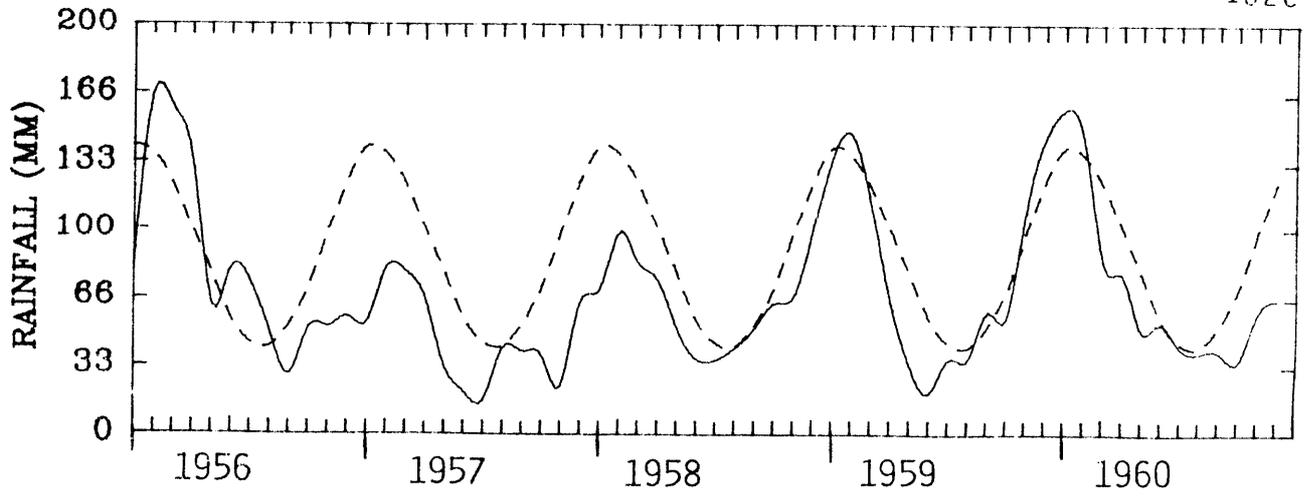
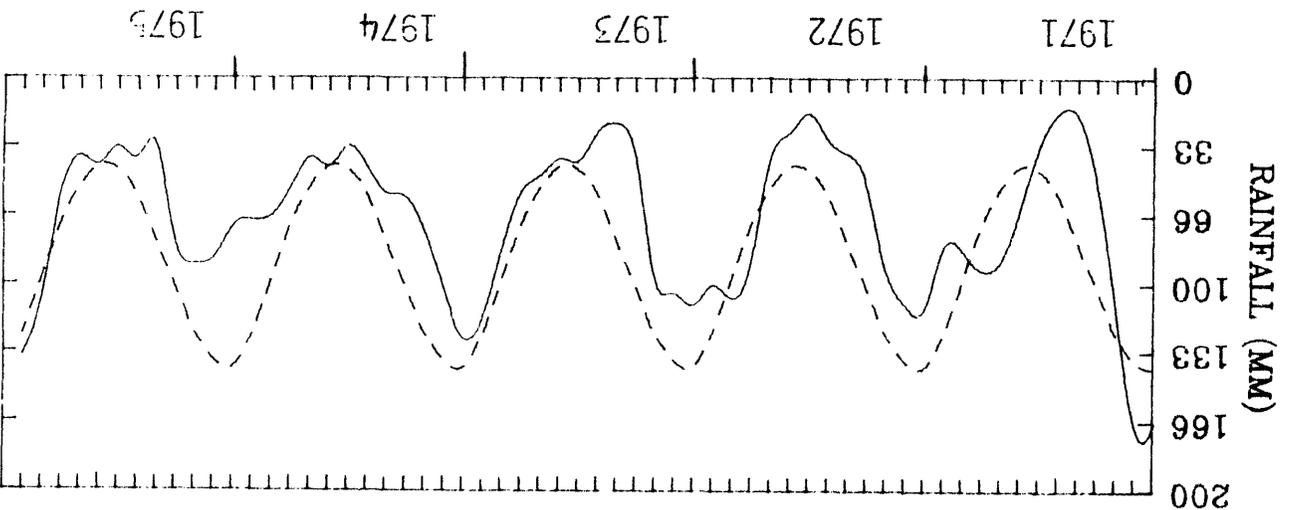
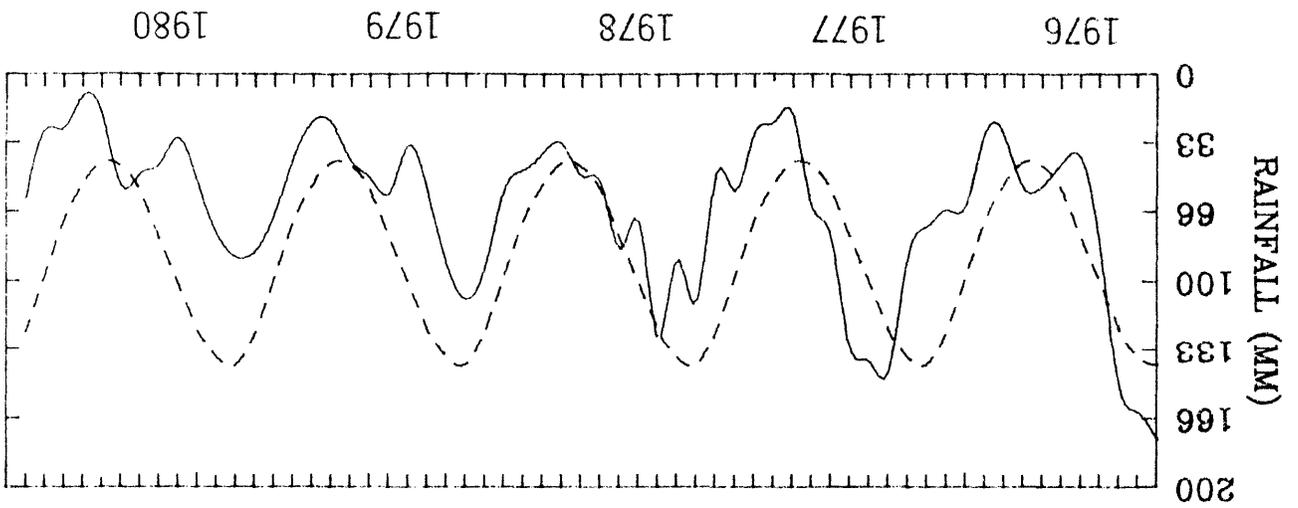
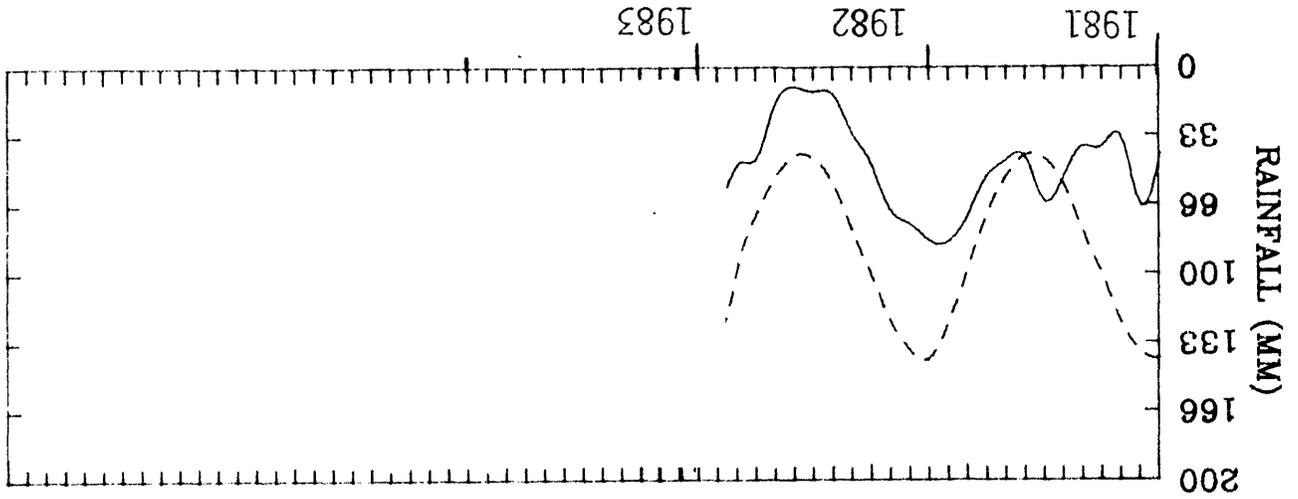


Figure 9.2.2 (continued)

Figure 9.2.2 (continued)



evapotranspiration when the water content of the soil is reduced (Smith and Johns, 1975). There are also some variations in potential evapotranspiration between years. For example, examination of the data collected at the CSIRO Pastoral Research Laboratory at "Chiswick", 16 km south of Armidale, (George et al, 1977) shows that potential evapotranspiration is usually greater than average in drought periods, when cloud cover and humidity are low.

The prolonged wet spells in late winter and spring of both 1949 and 1950 (Fig 9.1.2 [Armidale data]; Table 12 in George et al, 1977 ["Chiswick" data]) coincided with the first reports of extensive mortality of *E. nova-anglica* on river flats surrounding Saumarez Creek near Armidale (T. Edmonds, pers. comm.; see Section 3.4). Other extended periods when rainfall exceeded potential evapotranspiration occurred in the winter and spring of 1952, the summers of 1955-56 and 1959-60, and the autumn of 1963.

The severe drought of 1964-1966 caused extensive damage to trees (see Section 2.2). Drought damage was most severe in dry sclerophyll forest on ridges while nearby woodlands were much less affected. Pook et al. (1966) considered that the relative resistance of woodland eucalypts to drought was related to the greater water storage capacity of woodland soils. Woodland soils were able to store 4 to 10 times as much water as soils in nearby dry sclerophyll forests: 442 mm and 300 mm of water were available from the top 133 cm of two woodland soils at field capacity. The depression of xylem water potential found by

Journet during the summer of 1975, which was an average year, was roughly equivalent to deficits recorded by Pook et al. (1966) during the 1964-1966 drought (Journet, 1979). It is worth noting that the Wollomombi district was not as severely affected by the drought as the Armidale district: Wollomombi rainfalls for 1965 and 1966 were 675 and 742 mm, respectively, compared to 479 and 684 mm for Armidale.

Relatively light rainfall in the years immediately following the initial breaking of the 1964-66 drought may have prevented the complete recharging of subsoil moisture in woodlands in many parts of the Northern Tablelands. This rainfall pattern could have accentuated any competitive advantage which enabled pasture plants to take up surface water more readily than trees.

During the 1970s both the severity of dieback and its geographical extent increased markedly (see Section 3.3). After an initial dry spell in the winter of 1970 the 1970s were comparatively wet. Periods when precipitation exceeded average potential evapotranspiration included: the summer of 1970-71, the springs of 1971 and 1972, and the summers of 1975-76 and 1977-78. Waterlogging could have adversely affected some trees that grew on sites with impeded drainage, e.g. a substantial proportion of *E. nova-anglica*, but many trees that were affected by dieback grew on sites that were relatively well drained (see Section 3.5). The dry season of 1974-5, falling in the midst of this wet period, could be expected to put stress on some trees. The effects of unusually dry weather in the early 1980s has already been mentioned (Sections 2.2 and 4.3).

9.3 Changed precipitation disposal

Factors likely to affect precipitation disposal, and thereby soil water status, include: clearing, establishment of improved pastures, increased stocking rates and, on a local scale, changed drainage patterns (see Section 8.3) due to earth-moving, road construction and erosion.

Clearing The effects of clearing on the soil water balance of eucalypt woodlands remain uncertain. Reports from a large number of catchment studies in forested areas have consistently concluded that where most precipitation is in the form of rain, stream-flow increases following the removal of trees, though the level of increase varies (Hibbert, 1967; Langford and O'Shaughnessy, 1977). It is probable that reduced evapotranspiration would be the major cause of this increase, though decreased infiltration rates and increased deep drainage could also occur. Extrapolation of these results to woodlands is questionable since trees make up a much smaller proportion of woodland's productive biomass. Costin et al (1964) reported that evapotranspiration did not vary significantly between subalpine woodland and tussock grassland communities in the Snowy Mountains. Hibbert (1969) studied a catchment that originally contained poor quality deciduous hardwood forest. He found that when grass growth was stimulated by the application of fertilizer no discernible change in stream-flow was noted following removal of the tree cover. Stream-flow only started to increase after several years when the original response of the pasture to the

application of fertilizer had worn off. The age of a forest stand is also an important determinant of water-use: generally a dense stand of eucalypt regrowth would use more water than a mature stand which has thinned out (Langford and O'Shaughnessy, 1977; MMBW, 1980). Connor et al (1977) found evidence suggesting that the differences in water use between eucalypt stands of different ages could partly result from the reduced resistance to water flow in juvenile foliage.

The effect of clearing on the distribution of soil water within the profile is also uncertain. Johns and Lazenby (1973), while monitoring changes in soil moisture in a Wiesenboden soil near Armidale, found that there were no changes in soil moisture below a depth of 120 cm beneath introduced pasture, even though severe deficits occurred near the surface. Roots of the pasture plants were not observed below 120 cm. Eucalypt roots would be expected to penetrate to much deeper levels (Ashton, 1975), and thus utilization of soil moisture at lower levels in the soil would probably be greater near trees. As a consequence, subsoil moisture beneath trees would probably be depleted during dry spells and more precipitation would be required to recharge the entire soil profile to saturation point than in herb dominated sites. Hence, removal of trees could increase the incidence of waterlogging.

Other hydrological changes resulting from clearing include the removal of fog drip as component of precipitation; removal of interception as a component of precipitation disposal; and microclimatic changes involving increased exposure to sun and

wind, with consequent effects on evapotranspiration.

Pasture improvement Begg (1959), while investigating variations in soil moisture under four types of pasture at "Chiswick", the CSIRO Pastoral Research Laboratory near Armidale, found that greater water deficits occurred under a sown pasture of phalaris-white clover than under with the three types of native pasture examined. The greater moisture deficits were probably due to increased evapotranspiration of the phalaris-white clover. Findings by Dunin (1970), working near Bacchus Marsh, Victoria, also indicate greater water usage by sown pastures. Dunin also measured infiltration and concluded that infiltration was greater in sown pastures probably because a build up in fertility of the upper soil layer had increased the water holding capacity of this layer. However, in Dunin's work domestic livestock were excluded from the experimental plots.

Stocking rates Livestock may influence infiltration rates by compacting the soil or by reducing the grass cover. Soil compaction reduces the volume of pore space within soil thus affecting both percolation rates and water-holding capacity. The reduced water-holding capacity of compacted soils also renders them more prone to water-logging. Reduction of grass cover allows raindrop action to alter the structure of the exposed surface, thereby creating an impermeable barrier. Reductions of infiltration rates associated with high stocking rates of cattle have been consistently reported in investigations carried out overseas, but this trend was less consistent where paddocks were

stocked with sheep (Adams, 1975). However, Langlands and Bennet (1973), working in phalaris - white clover pastures at Chiswick near Armidale on a grey-brown podzolic soil, found that ponded infiltration rates were significantly reduced as stocking rates of sheep were increased. Their data suggest that under normal conditions, the minimum infiltration rate expected at 17 sheep/ha would be about 35 mm/hr and reduced infiltration would only become a problem at higher stocking rates.

Costin (1980), after an intensive study of runoff on a phalaris-subterranean clover pasture at Ginninderra on the Southern Tablelands of New South Wales, found that even at moderate to high stocking rates (12-30 sheep/ha) runoff was minimal provided ground cover was above 70%. In this study, infiltration capacities on the improved pasture averaged between 50 and 75 mm/hr. Lang (1979) also found evidence for a similar threshold of ground cover below which runoff (and consequently water erosion) became important. Incidentally, Costin suggested that the tunnelling of scarab beetle larvae, which were abundant in the soil beneath the improved pasture, partly compensated for the soil compaction that resulted from the high stocking rates.

The preceding studies of infiltration involved treeless paddocks and no work has been done to show changes in infiltration rates associated with the presence of trees. Grass cover is usually reduced around trees (Story, 1967) and soil is further compacted by expansion of roots (Greacen and Sands, 1980). In pristine conditions, reduced grass cover was compensated by accumulated leaf litter which formed a mulch.

However, in many areas an increased proportion of leaves appear to have been consumed by defoliating insects and when only isolated trees remain a greater proportion of litter is removed by wind. The use of sawdust mulch greatly increased the capacity of a range of planted seedlings to survive the drought of 1980-1 (Hitchcock, 1981) and mulching could be equally beneficial to larger trees.

Banens (1981) carried out a pilot study of the hydrological changes in the Severn Valley, north-east of Glen Innes. After examining the rainfall and runoff data from the last 40 years he found that when periods with similar rainfall were compared there was a gradual reduction in the ratio of runoff to rainfall over the period. The ratio of runoff to rainfall had decreased from 24% between 1947 and 1956 and to 16% between 1970 and 1973, even though the latter period was actually slightly wetter. The main change in landuse in the properties surveyed involved conversion of native pasture to improved pasture; the relative change in tree cover was small (but positive). The survey indicated that all significant changes in the flow of ground water from bores and wells in the region were negative, so increased deep drainage was unlikely to have been responsible for the decreased runoff. Increased wateruse by improved pasture plants is the most likely explanation of the change. Changes in the hydrology of other Tableland areas are likely to have been similar to those reported for the Severn Valley.

9.4 Disfunction of water transport within trees

Landsberg and Wylie (1983) found that though pre-dawn water potentials of matched dieback and healthy eucalypts were similar, the diurnal depression of water potential in the dieback trees was greater. In trees showing dieback the disfunctions that may affect water balance include: reduction of the length of rootlets and associated mycorrhizae (see Section 6.5) capable of absorbing water (surface rootlets and/or deep roots); increased resistance within the vascular system; reduced storage capacity within plant tissue; disfunctions in stomatal control; physical damage to leaves reducing cuticular resistance; and changed leaf surface areas.

Richards (1981) suggested that root disfunction is probably the final cause of the death of most declining eucalypts on the Northern Tablelands. The greatest density of tree rootlets is near the surface and maintenance of the surface root system involves a considerable allocation of food reserves. Severe rootlet mortality of surface roots is a common feature of trees showing dieback (see Section 2.3). Such loss of rootlets would be expected to reduce the rate at which trees could exploit available soil water (and nutrients); thus giving herbs a competitive advantage over the declining trees.

After chronic defoliation total exhaustion of metabolic reserves (see Section 5.2) might result in the death of roots and living cells within the conductive tissues (disrupting semi-permeable membranes). However, declining trees that still

had sufficient energy to maintain existing cells would be susceptible to attack by weak, opportunistic root pathogens and would also lack the capacity to respond to diminishing soil moisture with increased root growth. This partly explains the occurrence of a number of mortalities among severely moribund eucalypts in 1980-81 while the vigour of most eucalypts was improving (see Section 2.2).

It is almost certain that the woody growth of trees showing symptoms of dieback is markedly less than the growth of more vigorous eucalypts (see Section 5.2). Generally vascular tissues are only able to conduct water for a finite period ranging from one year in some ring porous hardwoods to several years in diffuse porous species [e.g. eucalypts (Penfold and Willis, 1961)] and longer in some conifers. The functional life of vascular elements is related to the occurrence of severe water deficits within the tree and to the size of the elements, with larger vessels tending to cavitate sooner than smaller tracheids (Hinckley et al, 1981). Non-replacement of senescent conductive tissue would be expected to reduce the tree's capacity to store usable water and to increase the resistance of the flow of water between the roots and leaves.

Landsberg and Wylie (1983) also found that the daytime stomatal diffusion resistances of dieback trees were lower than those of healthy trees and appeared to be less sensitive to environmental fluctuations. They associated this finding with a study by Blake (1980). Blake compared the water use of coppice that sprouted from decapitated 12 month old *E. camaldulensis*

seedlings and intact seedlings from the same batch. The coppice transpired 5-8 times as much water per unit leaf area as the intact seedlings. This greater transpiration rate was associated with increased stomatal length and higher stomatal density on the lower surface of the coppice leaves.

Little is known about how damage to leaf cuticles and partial defoliation affects transpiration of eucalypts. The increased exposure of the remaining leaves to the sun and wind may reduce the effects of any savings due to the reduction of leaf area.

9.5 Conclusions

The major long-term change in precipitation patterns in the region appears to have been a gradual increase in the summer rainfall. Since the 1940s there have been two droughts of sufficient intensity to cause visible drought damage in trees over extensive areas, but only on well drained sites with shallow soils. There is little evidence to suggest that the vigour of most woodland trees in areas later affected by rural dieback were severely affected by the first (1964-66) of the two most recent severe droughts, and the vigour of many woodland trees affected by dieback actually improved during the second drought (1979-82).

The 1970s, when dieback became severe, were characterized by a number of seasons in which precipitation exceeded potential evapotranspiration. However, it is unlikely that water logging per se could account for many of the trees lost during this

period and, if the wet spells were causally connected with dieback, it is likely that the connection was indirect, e.g. via insects (see Section 13.4).

Though the ratio of runoff to precipitation has probably been significantly reduced in the region at a macro scale, it is unclear how the waterbalance of eucalypts has been affected by the changed disposal of precipitation. A likely major effect would have been reduced depletion of soil water at lower levels in the soil profile in areas from which most eucalypts have been cleared. Infiltration rates may have been reduced by high stocking rates and reduction of vegetation cover but increased by pasture improvement. Improved pastures have been shown to use more water than native pastures. Little is known about how infiltration rates vary beneath woodland eucalypts, but the absence of accumulated litter may have reduced infiltration rates beneath trees.

The capacity of eucalypts affected by dieback to avoid water stress is reduced by:

1. diminished ability to maintain roots and water conductive tissues in functional order;
2. the greater proportion of juvenile foliage; and
3. the damaged state of leaves.

The degree to which these factors are mitigated by the reduced surface area of leaves is not known, but the last leaves remaining on eucalypts fatally affected by dieback usually wilt. Thus disfunction of the water transport system within trees appears to be an important direct cause of mortality. This breakdown could result from starvation of the living tissues associated with the uptake and transport of water, from invasion of the weakened roots by pathogens, or from inability of the degenerating system to cope with water stress.